VERTICAL DISTRIBUTION AND COMPETITIVE INTERACTIONS OF ANT-FOLLOWING BIRDS

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Abstract: Ant-following bird species display different foraging behaviors while following swarms of the army ant *Eciton burchelli*, which may influence where birds distribute themselves in the vertical strata above the swarm front. We hypothesized the existence of two main guilds within the ant-following birds: those that hunt in the air (aerial sallies) and those that hunt on the ground (ground sallies). We looked at height and competitive interactions within and between these strata as a way to evaluate the existence of these foraging guilds. We hypothesized that (1) ant-following bird species would be stratified according to the foraging guilds to which these bird species belong, and (2) that agonistic interactions would occur within the same height strata predicted by foraging guild. The results supported both hypotheses, suggesting that ant-following birds are vertically stratified based on partitioning of feeding zones between foraging guilds, and that the majority of agonistic interactions are within foraging guilds using shared resources.

Key Words: resource partitioning, foraging guilds, ant-following birds, competitive interactions, vertical stratification

INTRODUCTION

Ant-following birds are a group of unrelated insectivores that forage in areas disturbed by swarms of the diurnal army ants, *Eciton burchelli* (Janzen 1983). These birds generally track the front of the army ant swarm, where ground arthropods and other animals are flushed by the advancing ants. Antbirds, woodcreepers and other species compose mixed-species flocks, which draw from the same resource base of terrestrial invertebrates found at the swarm front (Stiles and Skutch 1989). This prompts speculation on how resources are divided between bird species. We propose, based on foraging behavior and life history traits, the existence of two major foraging guilds, ground and aerial foragers, which spatially partition insect resources (Table 1).

We developed two linked hypotheses of how bird behavior may indicate foraging guild. First, we predicted that vertical distribution over the ant

Table 1: Feeding habits and theoretical feeding guild assignments for ant-following species at La Selva Biological Station, Costa Rica.

Species	Feeding Habits[1]	Guild
Tawny-Winged Woodcreeper	Aerial sallies for spiders, insects, lizards	A
Ruddy Woodcreeper	Aerial sallies for spiders, insects; sometimes on ground	A
Chestnut-backed Antbird	Ground sallies for insects, spiders, lizards	B
Spotted Antbird	Ground sallies for smaller insects, spiders	B
Ocellated Antbird	Ground sallies for large insects, spiders, small vertebrates	B
Slaty Antshrike	Ground sallies for large insects, spiders, lizards	B
Plain Antvireo	Gleans insects and spiders from vegetation	B

[1] from Stiles and Skutch (1989)

swarm front of each species would be non-random, with each species found at the same level as other members of its foraging guild. Second, we hypothesized that agonistic interactions occur mainly between species in the same guild and therefore occur within the same vertical strata, indicating that competition exists mainly within foraging guild. Alternatively, vertical distribution may be random without these foraging guilds and all species compete equally for the same foraging position.

METHODS

We observed three different ant-following multi-species flocks at La Selva Biological Station, Costa Rica; one between 08:30 and 12:00 on February 14, 2006 and two between 8:30 and 11:00 on February 15, 2006. Following the army ant swarm front, we recorded the number of individuals of each bird species, their (visually estimated) height above ground, their foraging behaviors, and their agonistic interactions with other individuals. We considered an interaction agonistic when it involved one bird apparently forcing another bird to leave its perch or deviate from its foraging pattern.

RESULTS

We recorded 212 observations of ant-following birds, representing seven species (Chestnut-backed Antbird, *Myrmeciza exsul*; Ocellated Antbird *Phaenostictus Mcleannani*; Spotted Antbird, *Hylophylax naevioides*; Plain Antvireo *Dysithamnus Mentalis*; Ruddy Woodcreeper *Dendrocincla homochroa*; Tawny-winged Woodcreeper, *Dendrocincla anabatina*). We made 99 observations of members from guild A (ground sallying) and 113 observations of members from guild B (aerial sallying). We observed one Great Tinamou, which appeared disoriented. Height differed significantly by species ($F_{6,212} = 31.8$, $P < 0.001$) and guild (Fig. 1).

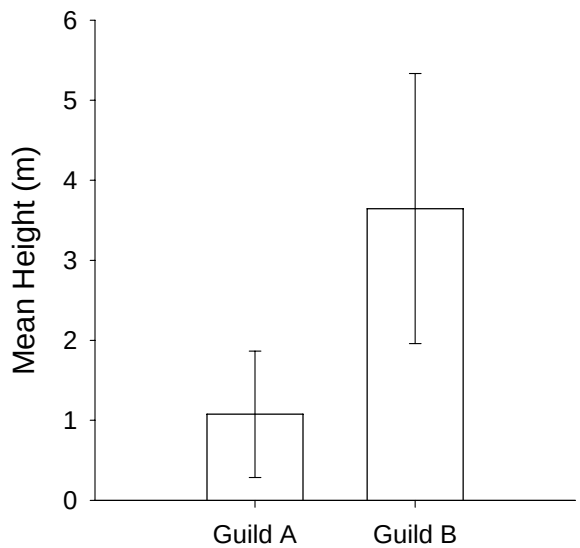

Figure 1: Relationship between foraging guild and the height (mean ± SD) above the ground at which it is typically found ($t = 5.96$, $df = 210$, $P < 0.0001$). Guild A represents five species (Chestnut Antbird, Ocellated Antbird, Plain Antvireo, Spotted Antbird and Slaty Antshrike), while Guild B represents two species (Ruddy Woodcreeper and Tawny-winged Woodcreeper).

We did not observe any agonistic interaction between individuals of guild A and guild B. We observed 18 agonistic interactions among individuals of guild A and 26 agonistic interactions among individuals of guild B (Table 2). We did not observe a substantial difference in agonistic interactions per observation between guild A (0.19 interactions/ observation) and guild B (0.23 interactions/ observation).

Table 2: Number of observed agonistic interactions between ant-following birds by species near La Selva Biological.Station, Costa Rica, with species generally found lower to the ground further to the upper left.

Species	Ocellated Antbird	Spotted Antbird	Chestnut Antbird	Plain Antvireo	Slaty Antshrike	Tawny -winged Woodcreeper	Ruddy Woodcreeper
Ocellated Antbird	1	0	1	0	0	0	0
Spotted Antbird		8	6	0	0	0	0
Chestnut Antbird			1	0	1	0	0
Plain Antvireo				0	0	0	0
Slaty Antshrike					0	0	0
Tawny –winged Woodcreeper						8	6
Ruddy Woodcreeper							12

DISCUSSION

Ant-following bird species at the front of an army ant swarm were distributed non-randomly with respect to height, as predicted by the guild assignments in Table 1. This suggests that vertical position of bird species is based on their foraging location and is not based on a dominance hierarchy of species that monopolize the best foraging space.

Agonistic interactions were also well correlated with foraging guild: interactions occurred exclusively within the strata but without regard to species. These agonistic interactions also support our foraging guilds because it is expected that birds in the same foraging guild are competing for access to the same resources. Since interactions are limited to vertical strata, we reject the alternative hypothesis that a more dominant species is excluding all other species from a certain strata. All species share a common resource: the terrestrial insects that are flushed from the forest floor by army ant swarms. However, the differentiation in height through resource partitioning by foraging guild appears to create niches and allows more species to co-forage than would be expected with one resource.

LITERATURE CITED

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