COMPETITION IN TROPICAL BIRD FLOCKS: ARMY ANT FOLLOWERS VERSUS MIXED SPECIES FORAGING GROUPS

MATTHEW T. KEMP AND J. KHAI TRAN

Abstract: Multi-species flocks are a prominent feature of many Neotropical bird communities. Theoretical benefits and costs of flock membership for individual birds differ between two flock types: army ant followers and mixed species foraging flocks. We hypothesized that aggressive interactions and sensitivity to perceived predation risk would be greater in the ant following flocks. While our test of predation sensitivity yielded no change in response behavior in either flock type, we did record significantly more aggressive interactions among the ant followers than in the mixed flocks. The high number of aggressive interactions in the ant followers was largely a product of intraspecific interactions among gray-headed tanagers. Elucidating the mechanisms underlying these behaviors helps us to understand why birds choose to participate in multi-species flocks, which are a major theme in the structure of tropical bird communities.

Key words: aggressive interactions, Corcovado, Eciton burchelli*, intraspecific, interspecific, predation*

INTRODUCTION

Multi-species flocks are a prominent feature of many Neotropical bird communities. In lowland wet forest on Costa Rica's Osa Peninsula, two distinct types of flocks occur: aggregations of birds that follow army ant swarms and mixed species groups of insectivorous birds that forage together daily.

Theoretical benefits and costs of flock membership for individual birds differ between the two flock types. Ant followers profit from abundant arthropod prey flushed by the raiding ants, but they may be subject to competition with other birds attempting to exploit this same resource. In this view, the existence of the flock is an incidental byproduct of a localized resource, and benefits often associated with group foraging, such as increased vigilance against predators, might not apply. In fact, the active, noisy nature of these ant-following flocks could easily attract bird-eating predators, and ant-followers are indeed noted to be shy and wary of disturbance (Stiles and Skutch 1989).

In contrast, members of mixed species foraging flocks should enjoy benefits derived from the flock itself, including increased foraging efficiency and reduced predation risk. For foraging benefits of flock membership to be realized, resource competition among flock members should be minimized. Also, because some members of these flocks (e.g. shrike-tanagers, *Lanio* sp.) are known to act as sentinels (Munn 1986), birds enjoy greater perceived security and therefore should be relatively insensitive to predation risk. That is, they should resume normal foraging behavior more quickly than ant followers after perceived predation pressure.

To test these ideas, we observed the behavior of individual birds within both ant following flocks and mixed species foraging flocks. We hypothesized that there would be more aggressive interactions among ant following birds than among mixed species flock birds, and that ant followers would respond more strongly to a simulated predation risk than mixed species flock members.

METHODS

On 4 February 2004, from 0800 to 1100, we observed an army ant (*Eciton burchelli*) following flock approximately 3.5 km north of Sirena Biological Station along the Los Patos trail

in Corcovado National Park, Costa Rica. To maximize observation time, we selected focal individuals that were readily visible and followed them until they were out of sight. We recorded amount of time observed as well as the number of intraspecific and interspecific aggressive interactions. We defined aggressive interactions to include displacement of or by the focal bird as well as any other obvious confrontations between the focal bird and another bird.

On 4 February from 1430 to 1730 and 5 February from 0800 to 1100, we located and followed two mixed species flocks (one flock was observed on both days). We observed focal birds, recording aggressive interactions as with the ant-following flock. We compared the difference in total aggressive interactions between ant-following and mixed species flocks using a chi-square analysis. Expected values were calculated based on the observation time in each flock type (i.e., the total number of aggressive interactions multiplied by the proportion of total observation time for each flock type).

To test sensitivity to perceived predation risk, we played an audio recording of a collared forest-falcon (*Micrastur semitorquatus),* a bird eating raptor, and observed any changes in bird behavior, as well as the amount of time before the birds resumed normal foraging behavior. We only observed birds that were less than 10 m from the audio source. The recording was obtained from a commercial compilation of Costa Rican bird songs (Ross 1998).

Results

We obtained 80.5 min of focal individual data for one ant following flock and a total of 46.25 min for two mixed species flocks (Table 1). We recorded significantly more aggressive interactions among the ant followers than in the mixed flocks (observed vs. expected = 22 vs. 17 and 5 vs. 10, respectively; $\chi^2 = 3.76$, df = 1, P = 0.05; Table 2). We observed no change in behavior in response to the forest falcon call in either flock type; birds appeared not to notice the vocalizations at all.

Discussion

Our test of predator response was inconclusive because the birds were clearly not threatened by the recorded forest-falcon call. This lack of response may be due to poor quality or insufficient volume of the recording, or perhaps auditory cues do not trigger an alarm response in general. Because forest falcons and other raptors are probably silent when hunting, birds may only respond to visually perceived predation risks. However, our findings did support the hypothesis that there are more aggressive interactions among individuals in ant-following flocks than among those in mixed species foraging flocks.

Aggressive interactions in the ant-following flocks were dominated by gray-headed tanagers, which were the most numerous and active species present. Though chestnut-backed and bicolored antbird interactions both involved tanagers, all other gray-headed tanager interactions were intraspecific. Other ant-following species may show similarly elevated levels of competition, but more observation time is needed to test this.

Ideally, investigation of flock type on intensity of competition should be done at the species level; however, since no species occurs regularly in both ant-following and mixed species flocks, comparisons within phylogenetic groups or foraging guilds would be the most informative approach. For example, testing effects of flock type on woodcreepers would be more valuable than combining all species within each flock type, as was necessary with our study.

Obtaining a larger number of observa-

Table 1. Estimated numbers of each species in observed flocks. Mixed flock 2 was observed on two separate occasions.

Species	Scientific name	Number of individuals in flock.
Ant-following flock		
Barred Woodcreeper	*Dendrocolaptes certhia*	2
Tawny-winged Woodcreeper	*Dendrocincla anabatina*	2
Chestnut-backed Antbird	*Myrmeciza exsul*	2
Bicolored Antbird	*Gymnopithys leucaspis*	4
Russet Antshrike	*Thamnistes anabatinus*	1
Gray-headed Tanager	*Eucometis penicillata*	6
Total		17
Mixed flock 1		
Buff-throated Woodcreeper	*Xiphorhynchus guttatus*	2
Streaked-headed Woodcreeper	*Lepidocolaptes souleyetii*	1
White-shouldered Tanager	*Tachyphonus luctuosus*	3
Tawny-crowned Greenlet	*Hylophilus ochraceiceps*	1
Total		6
Mixed flock 2		
Buff-throated Woodcreeper	*Xiphorhynchus guttatus*	2
Streaked-headed Woodcreeper	*Lepidocolaptes souleyetii*	1
Black-striped Woodcreeper	*Xiphorhynchus lachrymosus*	1
Plain Xenops	*Xenops minutus*	2
Buff-throated Foliage-gleaner	*Automolus ochrolaemus*	2
Black-hooded Antshrike	*Thamnophilus bridgesi*	2
Dotted-winged Antwren	*Microrhopias quixensis*	2
White-throated Shrike-Tanager	*Lanio leucothorax*	1
Scarlet-rumped Cacique	*Cacicus uropygialis*	1
Total		13

tions for all flocking species would also allow an explicit test of the relative importance of intraspecific versus interspecific competition. Intraspecific competition should be minimized in mixed species flocks, where each species is represented by only one or two individuals. In ant-following flocks, however, many individuals of the same species can occur together, increasing

Table 2. Minutes of observation time and number of aggressive interactions for each species in each flock type. Woodcreepers in mixed flocks were grouped because not all individuals were positively identified during each observation period.

Species	Time observed (min.)	Intraspecific interactions	Interspecific interactions	Total interactions
Ant followers				
Barred Woodcreeper	25.5	2	0	2
Tawny-winged Woodcreeper	4	1	0	1
Chestnut-backed Antbird	9	0	1	1
Bicolored Antbird	7.5	0	1	1
Russet Antshrike	2.5	0	0	0
Grey-headed Tanager	32	17	0	17
Totals	80.5	20	2	22
Mixed flock				
Woodcreeper sp.	11.5	2	0	2
Plain Xenops	1	0	0	0
Buff-throated Foliage-gleaner	11	0	2	2
Black-hooded Antshrike	4	0	1	1
White-throated Shrike-Tanager	14.5	0	0	0
White-shouldered Tanager	3	0	0	0
Scarlet-rumped Cacique	1.25	0	0	0
Totals	46.25	2	3	5

the probability of intraspecific interactions (as evidenced by the gray-headed tanager in this study). The prevalence of interspecific interactions, then, would indicate the degree of niche partitioning among flocking species. Resource partitioning in mixed species flocks is expected, given the variety of foraging behaviors exhibited by its members (i.e., aerial insectivores, dead leaf searchers, leaf gleaners, bark probers; Powell 1979 and Munn and Terborgh 1979). Among ant-following species, spatial partitioning is well-documented (Swartz 1997 and Willis and Oniki 1978), though whether this is congruent with resource partitioning or simply the result of a dominance hierarchy is unclear.

Clearly, the nature of tropical bird flocks influences the behavioral ecology of individuals and species within those flocks. Elucidating the mechanisms underlying these behaviors helps us to understand why birds choose to participate in multi-species flocks, which are a major theme in the structure of tropical bird communities.

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