cluded statistical tests for most species. By sampling more logs or by sampling during the wet season when fruiting bodies are more abundant, we could determine whether species tended to be more strongly associated with decay level or with other species on the same successional trajectory.

It could be that neither the deterministic nor the alternative trajectory model is adequate for understanding community assemblage and succession on decaying logs. An alternative hypothesis is that fungi and other decomposers are dispersal limited, and community composition is simply a function of which species make it to the log. From this hypothesis, we would predict clumped dispersions of species in the landscape. Another alternative is that fungal communities depend upon the tree species of the decaying log. A third possibility is that communities are not structured with respect to space, time or other species (random assemblages). These alternatives warrant further consideration. However, our results suggest non-random species associations and temporal patterns in species distributions. We recommend sampling during the wet season, when fruiting bodies are more abundant. In addition, spores and mycelial fungal cells could be cultured to more completely describe the fungal community composition.

There could be important ecosystem implications depending on which model of succession applies to decomposer communities inhabiting coarse woody debris. If communities follow the alternative trajectory model of succession, we would expect increased variance among these communities over time. This could affect nutrient recycling rates, potentially creating a more heterogeneous soil environment, which could contribute to increased plant and animal diversity (Bembenek et al. 1996). This model also predicts that strong associations among species are more common than in the deterministic model of succession. This implies that keystone species would be more frequent in communities that match the alternative trajectory model, and that ecosystem processes such as nutrient cycling will be more sensitive to the addition or deletion of particular species.

Literature Cited

Bembenek, S. A., D. S. Canny, J. W. Hourdequin and J. Z. Ruben. 1996. Effects of environmental heterogeneity and gap dynamics on b-diversity in a tropical wet forest. Pp. 86 - 88 *in* A. L. Mannan and D. S. Canny, eds. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.

Are bicolored antbirds parasitized by other species of ant-following birds?

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Abstract: Mixed species foraging flocks are a striking feature of tropical bird communities. The mixed species flocks that forage with army ant swarms may be communities of mutualists that all benefit from the association or core species that are parasitized by other species who are less able to find ant swarms on their own. We tested this by observing aggressive interactions between birds associated with army ant swarms and by observing the response of two species of antbirds to recorded calls of each species. One chestnut-backed antbird, a facultative species, responded strongly to the obligate bicolored antbird playback by approaching the recording device and scanning the ground, but we were unable to conduct replicate tests. As predicted, bicolored antbirds seemed more likely to receive than to initiate an attack and were sometimes displaced from prime foraging areas, but sample sizes were too small for a statistical test. Unfortunately, we were unable to quantify differences between foraging success of bicolored antbirds in single species and multi-species groups; this would be valuable in determining whether bicolored antbirds are gaining or losing from their association with other species of ant followers.

Key Words: army ants, barred woodcreeper, bicolored antbird, chestnut-backed antbird, Eciton burchelli, *gray-headed tanager, mixed-species flocks, mutualism, parasitism, tawny-winged woodcreeper*

Introduction

One striking feature of avian ecology in the tropics is the presence of mixed species foraging flocks. The prevailing explanation for mixed species flocks is that benefits of decreased predation for individuals in mixed flocks outweigh the increased costs of interspecific competition (Stuchbury and Morton 2001). This may be permitted by efficient resource partitioning among bird species. The multi-species foraging aggregations around army ant swarms are a poorly studied example of such mixed-species flocks. As in other such flocks, there are core species and species that are associated with groups less predictably. However, resource partitioning in ant-following flocks is less clear than in better studied systems because birds associated with ant swarms all appear to compete for the same pool of escaping arthropods.

We evaluated the consequences of this apparently incomplete resource partitioning in antbird flocks on the Osa Peninsula of Costa Rica. Specifically, we tested whether participation in the multi-species aggregation represents an overall cost for the bicolored antbird (*Gymnopithys leucaspis*), which is the only ant-associate in this area that is regarded as an obligate associate of army ants. Several other species in the area, including the chestnut-backed antbird (*Myrmeciza exsul*), tawny-winged woodcreeper (*Dendrocincla anabatina*) and gray-headed tanager (*Eucometis penicillata*), forage opportunistically around ant swarms (Stiles and Skutch 1989, Swartz 1997). Our preliminary observations suggested that the facultative species were using the bicolored antbirds' call to locate ant swarms, which implies the possibility that facultative antbirds are functioning as parasites of the bicolored antbird. We tested this hypothesis by evaluating responses of facultative ant followers to foraging calls of the bicolored antbird and assessing whether bicolored antbird foraging success declines in the presence of facultative species.

Methods

From 2 - 4 January 2002, we observed birds associated with swarms of the common diurnal army ant, *Eciton burchelli*, in the vicinity of Estación Sirena, Corcovado National

Park, Costa Rica. For each swarm, we recorded the abundance of each bird species and the number of aggressive interactions between foraging antbirds within 15 min observational periods. We also recorded the bird species that initiated each interaction, the species that was the recipient of this aggression and any changes in foraging position (relative to the ant swarm) resulting from aggressive interactions.

Using a digital recording device (Sony ICD-MS1), we recorded the calls of the bicolored antbird, chestnut-backed antbird and riverside wren (*Thryothorus semibadius*). The call of the riverside wren, a sympatric species not associated with ant swarms, was used as a control. For each ant swarm without antbirds, we played the control and then both the bicolored and chestnut-backed calls in a random order. Each call was played for 3 min with 2 min between calls. Calls were also played if antbirds were encountered away from ant swarms. We noted behavioral responses of birds to the calls.

Results

We monitored 5 bivouacs of *Eciton burchelli*, 2 of which, at some point during 3 days of frequent monitoring had antbirds associated with their foraging swarms. The bicolored antbird was present at 3 of the 4 foraging swarms attended by at least one species of ant-following bird. The bicolored antbird often called while foraging at a swarm regardless of the presence of other birds. The call was a quiet, low-pitched chirp that lasted approximately 1 sec and was repeated at a frequency of about 20 calls per min (reference call deposited on course computer as "bicolored.antbird.wav"). Chestnut-backed antbirds made a two-tone call both in the presence and absence of ant swarms (reference call deposited on course computer as "chestnut-backed.antbird.wav"). The gray-headed tanagers also made a high pitched *chip* while foraging around ant swarms.

Playback experiments conducted at swarms without antbirds never recruited a species known to forage at ant swarms (n = 5 bouts of 15 min of playbacks spread across 3 swarms on 2 days). However, on one occasion the bicolored antbird call elicited a strong response from a chestnut-backed antbird not associated with a swarm. The chestnut-backed antbird reacted immediately to the bicolored antbird playback by becoming increasingly alert and more frequently scanning. The focal individual dropped to the ground and approached the bicolored antbird playback (moving from ~5 m to ~0.5 m from the researcher). The bird then circled the recording device for 2 min before flying away. On no other occasion did we have the opportunity to repeat this experiment with a chestnut-backed antbird that was apparently within hearing distance and was not already with an ant swarm.

TABLE 1. Frequencies of aggressive interactions between birds foraging at ant swarms. Columns represent the species that initiated the aggression; rows represent the recipients of aggression. Sample sizes indicate bird observation periods, where each is one individual present during one of the four 15 minute sampling periods.

	Bicolored Antbird (n = 8)	Chestnut-backed Antbird (n = 8)	Tawny-winged Woodcreeper (n = 7)	Barred Woodcreeper (n = 3)	Gray-headed Tanager (n = 15)	Total (n = 41)
Bicolored antbird	0	0	2	0	2	4
Chestnut-backed antbird	0	0	0	0	0	0
Tawny-winged woodcreeper	1	0	0	0	0	1
Barred woodcreeper	0	0	0	0	0	0
Gray-headed tanager	0	1	3	0	10	14
Total	1	1	5	0	12	19

Aggressive behavior varied among bird species, with tanagers and woodcreepers initiating most of the aggressive intra- or interspecific interactions and the bicolored antbird being more likely to receive than to initiate such an attack (Table 1). We observed the displacement of bicolored antbirds from central foraging positions by tanagers (n = 2) and by woodcreepers (n = 1). We never observed intraspecific aggression between bicolored antbirds or interspecific aggression between bicolored and chestnut-backed antbirds.

Discussion

As predicted by the parasitism hypothesis, bicolored antbirds received more aggressive attacks than they initiated and these attacks sometimes resulted in displacement from their foraging positions at the front-center of the swarm. This would be meaningful because bicolored antbirds apparently occupy the best position most of the time. Calvi et al. (2000) found that bicolored antbirds, of the four species that were present, tended to preferentially occupy the front-center of ant swarms and have the highest foraging success. Unfortunately, our study was unsuccessful in obtaining enough observations of interspecific interactions to test whether patterns of interspecies interactions were different than would be expected by chance given the frequency of each bird species in the flock.

Because they are present in most flocks and often roost at ant bivouac sites (Swartz 1997), bicolored antbirds probably receive little help from other bird species in locating ant swarms. Conversely, the strong response of a chestnut-backed antbird to a bicolored antbird playback suggests that they may be using bicolored antbird calls to aid in the location of swarms and thereby increase their foraging success. However, our study was unable to provide replicated tests for the predicted asymmetries in responses of obligate vs. facultative ant followers to the calls of heterospecifics. A simple and valuable test of this prediction could be made by comparing foraging success of bicolored antbirds while associated with facultative species and while foraging alone. A higher rate of successful foraging when associated with facultative species would reject the hypothesis that the bicolored antbird is parasitized by these species. This result would support the alternative hypothesis that bicolored antbirds, like other participants in mixed species flocks, are able to forage more efficiently when associated with other species due to decreased predation risk (Stutchbury and Morton 2001).

Even if bicolored antbirds suffer from the presence of other species at their ant swarm, their only options upon the arrival of facultative species are to remain or attempt to locate an unoccupied swarm elsewhere. It is possible, given our results, that bicolored antbirds are members of interspecies flocks only because they have no better option than tolerating the presence of parasitic facultative species. Further research is required to clarify the costs and benefits for each species of participation in ant following flocks and to evaluate whether relationships are best characterized as mutualistic, commensalist or parasitic.

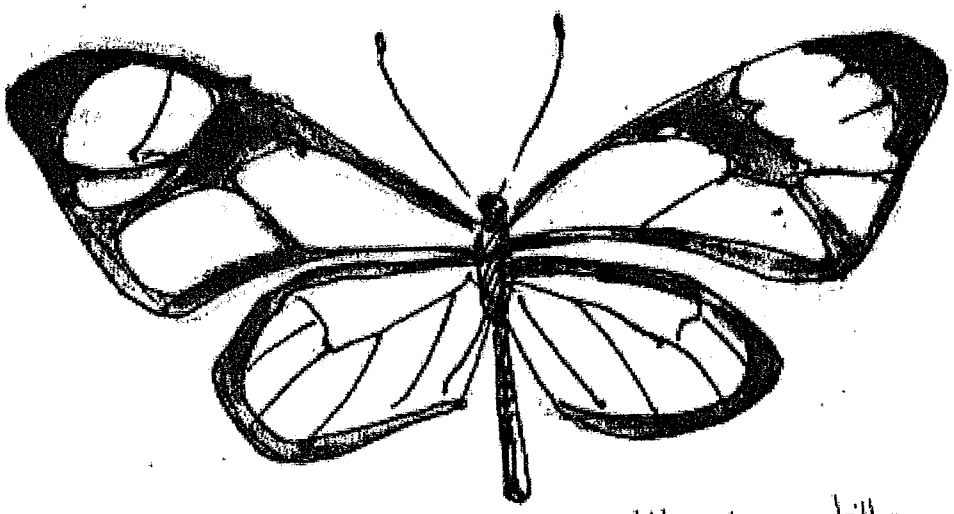
Literature Cited

Calvi, M. S., M. K. Jennings, M. D. Foote and L. R. Nagy. 2000. Resource partitioning in army ant bird communities. Pp. 89 - 94 *in* L. E. Aucoin, M. N. Conte and J. A. Macintosh, eds. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.

Stiles, F. G. and A. F. Skutch. 1989. *A Guide to the Birds of Costa Rica*. Ithaca, New York: Cornell University Press.

Stutchbury, B. J. and E. S. Morton. 2001. *Behavioral Ecology of Tropical Birds*. New York, NY: Academic Press.

Swartz, M. B. 1997. Behavioral and population ecology of the army ant *Eciton burchelli* and ant-following birds. Ph.D. dissertation, University of Texas at Austin.



Ithomia patilla
Ithomiinae