DELAYED COMPENSATORY RESPONSES IN A GUILD OF ANT-FOLLOWERS

by

JANEENE M. TOUCHTON

B.Sc. The University of Oregon, 1998

A THESIS SUBMITTED IN PARTIAL FULFIILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

DEPARTMENT OF ZOOLOGY

THE UNIVERSITY OF BRITISH COLUMBIA

July 2005

© Janeene M. Touchton 2005

ABSTRACT

I studied the influence of competition on the maintenance of a dominance structured multi-species guild of ant-following birds. I explored the numerical and behavioral responses of bicolored (*Gymnopithys leucaspis*) and spotted (*Hylophylax naevioides*) antbirds several generations after the extirpation of the dominant ocellated (*Phaenostictus mcleannani*) antbird on Barro Colorado Island, Panama. I compared the abundances and behavior of these species to data collected by E.O. Willis and others prior to the decline of ocellated antbirds on Barro Colorado, and to a nearby mainland control in Parque Nacional Soberania, where the complete guild of these ant-followers still exists.

Populations of bicolored and spotted antbirds increased in density on Barro Colorado, completely compensating in combined biomass for the loss in overall biomass by ocellated antbirds. Historical records suggest that complete population turnover of these species occurred before density compensation was detectable. At ant swarms on Barro Colorado, the numbers of spotted antbirds doubled from historical records and in comparison to Soberania. The increased proportion of biomass of spotted antbirds at swarms on Barro Colorado compensated for the reduced proportion of biomass of ocellated antbirds. No shifts in microhabitat use by bicolored antbirds was observed after the loss of the dominant ocellated antbird. Bicolored antbirds foraged at similar rates, showed similar aggression towards conspecifics, and equal activity at ant swarms on Barro Colorado and in Soberania. Rates of aggression between bicolored and spotted antbirds on Barro Colorado, however, increased. Ocellated antbirds rarely interacted directly with spotted antbirds in Soberania, consistent with historical observations. Thus,

ii

the limited swarm use by spotted antbirds historically on Barro Colorado and in Soberania likely results from indirect competitive pressure promoted by ocellated antbirds and mediated through direct interactions with bicolored antbirds.

My results suggest that interspecific competition actively maintains guild structure in this complex tropical foraging association through direct and indirect interactions. Behavioral adaptations in guilds may occur over several generations, delaying the onset of compensatory responses. Detailed long-term experiments and/or comparative analyses are needed to fully understand the role of competition in the structuring of multi-species guilds in tropical forests.

iii

Abstract		ii
Table of Conte	nts	iv
List of Tables.		vi
List of Figures	· · · · · · · · · · · · · · · · · · ·	vii
Acknowledgen	nents	viii
CHAPTER 1	General Introduction: Compensatory Responses in Depauperate Communities	1
	Introduction Literature Cited	1 6
CHAPTER 2	Delayed Numerical and Behavioral Responses in a Guild of Ant- Following Birds	9
	Introduction Methods Study areas and species Foraging resources Ant-following birds Statistical analyses and data presentation Results Foraging resources	9 13 13 16 18 20 22 22
	Population responses of focal ant-followers Use of ant swarms Behavioral interactions at swarms Discussion Effects of competition on the abundance of	23 24 25 28
	The abundance of guild members at ant swarms Behavioral responses in relationship to the	28 31
	abundance of guild members Seasonal impacts on microhabitat use Conclusion Literature Cited Appendix 2.1 Species observed at ant swarms Appendix 2.2 ANOVA Table: Individuals per swarm Appendix 2.3 ANCOVA Table: Foraging rates Appendix 2.4 ANCOVA Table: Activity rates	32 34 35 51 57 59 60 61

TABLE OF CONTENTS

iv

CHAPTER 3 General Conclusion.....

Summary of thesis	62
Avenues for future research	63
Literature cited	66

. 62

ν

LISTS OF TABLES

Table 2.1:	Estimated mean E. burchelli colonies and width	36
Table 2.2:	Mean dry biomass of flushed arthropods	37
Table 2.3:	Estimated population densities of ocellated, bicolored, and spotted antbirds	38
Table 2.4:	Maximum numbers of ocellated, bicolored, and spotted antbirds per ant swarm	39
Table 2.5:	Mean total number of birds and bird biomass per ant swarm	40
Table 2.6:	Prey preference of flushed arthropods by bicolored antbirds	41
Table 2.7:	Mean rates of aggression between bicolored antbirds and conspecifics, and other species	42

LISTS OF FIGURES

Figure 2.1:	Niche partitioning at ant swarms	43
Figure 2.2:	Map of Barro Colorado and Soberania, Panama	44
Figure 2.3:	Detailed maps of Barro Colorado and Soberania study areas and census plots	45
Figure 2.4:	Mean individuals of spotted, bicolored, ocellated, and other antbirds per swarms	46
Figure 2.5:	Relative portion of total biomass at swarms of spotted, bicolored, ocellated, and other antbirds	47
Figure 2.6:	Percentage of aggressive interactions directed from of to bicolored antbirds at swarms	48
Figure 2.7:	Rates of foraging small and large prey per minute at swarms by bicolored antbirds	49
Figure 2.8:	Rates of hops and flights per minute by bicolored antbirds at swarms	50

vii

ACKNOWLEDGEMENTS

I would first like to extend my gratitude towards my supervisor, James N. M. Smith, for supporting my wish to work with the antbirds and encouraging me and mentoring me throughout this project in many ways. James N. M. Smith provided valuable insight to my research ideas and questions, detailed editing, and was an inspiration by sharing wonderful tales of his field adventures, along with a Scottish jig or two. He also provided the beautiful sketch of niche partitioning at an ant swarm. I am also indebted to my committee members, Peter Arcese and Diane Srivastava for invaluable advice, support, and editing. I have greatly benefited from and enjoyed many wonderful conversations about tropical ecology and antbirds with Egbert Leigh Jr., who encouraged me to continue with tropical studies. Martin Wikelski also provided insightful discussions about antbirds, motivation, assistance, and support throughout this project for which I am very appreciative. I am additionally grateful for the advice provided by Douglas Robinson and his willingness to share numbers of the population abundances of antbirds on Barro Colorado Island.

This project would not have been possible without the tireless assistance from David Bradley, Paula Capece, Kyle Elliott, Jessica Knowlton, and Jonathan Reum, who willingly braved chiggers, ticks, thousands of ant stings, and spared no hesitation to brag profusely after sighting an ocelot. My time spent at the Smithsonian Tropical Research Institute was made enjoyable by the well-functioning and supportive staff, particularly Oris Acevedo. I am also grateful for the residents on Barro Colorado Island and in Gamboa for delightful conversations about tropical ecology, singing, and dancing.

viii

Susan Shirley provided much needed statistical advice, general support and wisdom for which I am thankful. Several other hut dwellers also provided support, advice, and made my experience at UBC enjoyable.

This project was financially supported by a NSERC operating grant to James N. M. Smith. I am grateful for fellowship support from the University of British Columbia and the Smithsonian Institution.

I would like to acknowledge my parents, Jim and Jo Touchton, for amazing amounts of encouragement and for supporting my love of birds and bugs. Finally, I would like to share my appreciation for my partner, Christian Ziegler. Christian helped me in all aspects of this thesis; from emergency ant-tracking, running errands, making coffee and dinner, fixing figures in Photoshop, spending hours upon hours talking about competition or differences between the tropics and temperate zones, and in sharing a love of wildlife and all of its many intricacies.

ix

CHAPTER 1

GENERAL INTRODUCTION: COMPENSATORY RESPONSES IN DEPAUPERATE COMMUNITIES

The absence of species in communities may lead to compensatory responses in remaining community members, such as density compensation and niche breadth shifts (defined below) (MacArthur et al. 1972). The absence of putative competitors in species depauperate communities has commonly been suggested as the primary cause for observed density compensation or niche shifts (e.g., Diamond 1978). Evidence of density compensation or niche shifts has thus been utilized to suggest the importance of competition in structuring communities, particularly when there is simultaneous indication of both patterns (Diamond 1978).

Density Compensation

Some island faunal communities have been observed to contain equal or higher summed population densities of all species than those of mainland communities (e.g., Crowell 1962, MacArthur et al.1972, Case 1975, Diamond 1975, Morse 1977). MacArthur and others (1972) defined this pattern, 'density compensation', as the degree to which the summed species density on islands approaches mainland levels. Density compensation can result with or without niche shifts (a change in niche position towards space that is occupied by other species elsewhere) (MacArthur et al. 1972). Bottom-up or top-down processes can cause density compensation to occur (Faeth 1984). Greater focus has been granted to consumer-driven resource theory (e.g., Colwell and Futuyma

1971, Tilman 1982), and thus, bottom-up processes have generally been considered more important for observed density compensation (Faeth 1984).

Community-wide density compensation

Community wide density compensation contradicts conventional niche theory, which predicts that depauperate communities should have lower summed densities than mainland densities in similar habitats (MacArthur et al. 1972). This argument is based on the rationale that the species absent from depauperate communities should be more efficient at utilizing the niche space into which the remaining species expanded (Case and Gilpin 1974). Higher density per species, but lower overall community density would be expected under this scenario.

Niche shifts are thought to occur in conjunction with community-wide density compensation, although it is difficult to measure niche dimensions for an entire community. Cox and Ricklefs (1977) observed broader niches in some Caribbean avifaunas compared to their mainland equivalents. These colonists, however, had broadniches and a widespread distribution to begin with. More convincing examples were provided in the Pearl Islands off Panama, where vertical shifts were observed in foraging heights of birds (MacArthur et al. 1972), and off New Guinea, where spatial expansions in elevational ranges were observed (Diamond 1970).

Niche shifts, however, are not necessary for density compensation. Species populations may increase in density because resource availability increases. It is often assumed that the absence of interspecific competitors can liberate extra resources (Case et al. 1979). Conversely, top-down processes, such as a reduction of predation or

parasitism, could also increase densities of species in a community (Price et al. 1986, Faeth 1984).

Density compensation in species populations

When community-wide density compensation does not occur, some species populations still recognize higher densities on islands. Song sparrows (*Melospiza melodia*) occupy smaller territories on islands than mainlands, for example (Yeaton and Cody 1974) although some of these populations fluctuate strongly (Arcese et al. 1992). As with community-wide density compensation, increases in density in species populations need not necessarily follow a niche shift. An increase in common snipe (*Gallinago gallinago*) and wren (*Troglodytes troglodytes*) density on the Faroe Islands was attributed to an increase in suitable habitat (Bengtson and Bloch 1983). Blackthroated sparrow densities, however, were higher on islands in the Sea of Cortez not only from habitat differences, but other unknown factors (George 1987).

Problems underlying island-mainland comparisons

Early studies of island-mainland comparisons illustrating density compensation and niche shifts had several shortcomings. A lack of competitors was assumed to be the mechanism behind observed density compensation or niche shifts. This assumption reflected the close intertwining of competition theory and niche theory in the 1970's (Chase and Leibold 2003). Actual substantive evidence of an absence of competitors, however, was rarely presented and alternative mechanisms were only considered infrequently. For example, changes in predator communities can affect the diversity and

abundance of prey through direct and indirect interactions (Holt 1977, Schmitz et al. 2000). Climatic factors can also play a role in abundances of populations and niche characteristics (Bejer and Rudemo 1985), as can habitat characteristics or hidden patchiness that is not detectable by the observer (Abbott 1980, Simberloff and Abele 1982). Additionally, differences in parasitism (Price et al. 1986), colonization and dispersal (MacArthur and Wilson 1967), and disturbance regime (Sousa 1984) may also influence population densities and niche breadth. Many island-mainland comparisons failed to adjust for sampling error discrepancies, such as different census methods or temporal variation in sampling duration (Wiens 1992). There was also a lack of statistical rigor and insufficient use of null models (e.g., Simberloff 1978, Strong et al. 1979).

A strong body of theoretical literature relating the overlap of species niches, coexistence, and abundance to competitive interactions thus developed (Chase and Leibold 2003). Empirical studies to test this theory have so far been limited to testing basic hypotheses about the very presence or absence of competition. Controlled competitor removal experiments have primarily documented niche shifts (review in Schoener 1983). Some studies have revealed density compensation; e.g., in coral reef fish guilds (Robertson 1996), surfperches (Schmitt and Holbrook 1990), and herpetofaunal assemblages (Rodda and Dean-Bradley 2002). In addition, communitywide density compensation has been documented in controlled experimental microcosms (McGrady-Steed and Morin 2000).

Although the original theory of density compensation was largely based on patterns in avian communities (MacArthur et al. 1972), the mechanisms underlying

density compensation in avian guilds remain unclear. My objective in this study was to explore numerical and behavioral responses in a tropical avian guild of ant-following birds after the removal of a dominant guild member.

LITERATURE CITED

- Abbott, I. 1980. Theories dealing with the ecology of landbirds on islands. Advances in Ecological Research 11:329-371.
- Arcese, P. J., J. N. M. Smith, W. M. Hochachka, C. M. Rogers, and D. Ludwig. 1992. Stability, regulation, and the determination of abundance in an insular song sparrow population. Ecology 73:805-822.
- Bejer, B., and M. Rudemo. 1985. Fluctuations of Tits (Paridae) in Denmark and their relations to winter food and climate. Ornis Scandinavica 16:29-37.
- Bengtson, S. A., and D. Bloch. 1983. Island land bird population-densities in relation to island size and habitat quality on the Faroe Islands. Oikos 41:507-522.
- Case, T. J. 1975. Species numbers, density compensation, and colonizing ability of lizards on islands in Gulf of California. Ecology **56**:3-18.
- Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences of the United States of America 71:3073-3077.
- Case, T. J., M. E. Gilpin, and J. M. Diamond. 1979. Overexploitation, interference competition, and excess density compensation in insular faunas. American Naturalist 113:843-854.
- Chase, J. M. and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago.
- Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology **52**:567-576.
- Cox, G. W., and R. E. Ricklefs. 1977. Species-diversity and ecological release in Caribbean land bird faunas. Oikos 28:113-122.
- Crowell, K. L. 1962. Reduced interspecific competition among the birds of Bermuda. Ecology **43**:75-88.
- Diamond, J. M. 1970. Ecological consequences of island colonization by Southwest Pacific Birds, .1. Types of niche shifts. Proceedings of the National Academy of Sciences of the United States of America **67**:529-536.
- Diamond, J. M. 1975. Assembly of species communities. Pages 342-444 in M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts.
- Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. American Scientist **66**:322-331.

- Faeth, S. H. 1984. Density compensation in vertebrates and invertebrates: a review and an experiment. Pages 491-509 in D. R. J. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle, editors. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey.
- George, T. L. 1987. Greater land bird densities on island vs. mainland relation to nest predation level. Ecology **68**:1393-1400.
- Holt, R. D. 1977. Predation, apparent competition, and structure of prey communities. Theoretical Population Biology **12**:197-229.
- Martin, P. R., and T. E. Martin. 2001. Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. Ecology **82**:189-206.
- Macarthur, R., J. M. Diamond, and J. R. Karr. 1972. Density compensation in island faunas. Ecology **53**:330-342.
- Macarthur, R., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.
- Mcgrady-Steed, J., and P. J. Morin. 2000. Biodiversity, density compensation, and the dynamics of populations and functional groups. Ecology **81**:361-373.
- Morse, D. H. 1977. The occupation of small islands by passerine birds. The Condor **79**:399-412.
- Munday, P. L., G. P. Jones, and M. Julian Caley. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology 82:2177-2189.
- Price, P. W., M. Westoby, B. Rice, P. R. Atsatt, R. S. Fritz, J. N. Thompson, and K. Mobley. 1986. Parasite mediation in ecological interactions. Annual Review of Ecology and Systematics 17:487-505.
- Robertson, D. R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology 77:885-899.
- Rodda, G. H., and K. Dean-Bradley. 2002. Excess density compensation of island herpetofaunal assemblages. Journal of Biogeography **29**:623-632.
- Schmitt, R. J., and S. J. Holbrook. 1990. Population responses of surfperch released from competition. Ecology **71**:1653-1665.
- Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. American Naturalist 155:141-153.
- Schoener, T. W. 1983. Field Experiments on interspecific competition. American Naturalist 122:240-285.

- Simberloff, D. 1978. Using island biogeographic distributions to determine if colonization is stochastic. American Naturalist **112**:713-726.
- Simberloff, D., and L. G. Abele. 1982. Refuge design and island biogeographic theory effects of fragmentation. American Naturalist **120**:41-50.
- Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics **15**:353-391.
- Strong, D. R., L. A. Szyska, and D. S. Simberloff. 1979. Tests of community-wide character displacement against null hypotheses. Evolution **33**:897-913.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey.
- Wiens, J. A. 1992. The ecology of bird communities volume 2: Processes and variations. Harvard University Press, Cambridge.
- Yeaton, R. I., and M. L. Cody. 1974. Competitive release in island song sparrow populations. Theoretical Population Biology **5**:42-58.

CHAPTER 2

DELAYED NUMERICAL AND BEHAVIORAL RESPONSES TO COMPETITIVE RELEASE IN A GUILD OF ANT-FOLLOWING BIRDS

INTRODUCTION

The coexistence of ecologically similar species has been of interest to ecologists because theory predicts that strong competitors will exclude others when resources are limiting (e.g., MacArthur and Levins 1967, May and MacArthur 1972, Roughgarden 1974). According to competition theory, intraspecific competition must be greater than interspecific competition for species coexistence (Lotka 1932). Resource partitioning by specialization on distinct resources (MacArthur and Levins 1967, Cody and Diamond 1975, Tilman 1982), temporal partitioning of the same resources (Armstrong and McGehee 1976), and spatial partitioning through spatial heterogeneity and variability enabling different dispersal and colonization or storage effects (Tilman 1982, Chesson 2000) all may promote species coexistence. Alternatively, frequency-dependent predation (Oaten and Murdoch 1975) or disturbance (Sousa 1983) may prevent populations from reaching levels where resources become limiting. Neutral models, on the other hand, that assume ecological similarity of species, predict short-term coexistence by chance alone (Hubbell 2001). The extent and circumstances under which competition structures communities is not entirely clear.

Removal and addition experiments have sometimes been used to investigate the significance of interspecific competition in structuring guilds of potential competitors (reviews in Schoener 1983, Gurevitch et al. 1992). In such experiments, the magnitude

of behavioral or density compensation following competitive release is generally considered to indicate the interaction strength between competing species (Paine 1992). Microhabitat shifts are a common form of behavioral compensation (e.g., Chappell 1978, Griffis and Jaeger 1998) but may be unrelated to demography and may have limited influence on the structure of communities (Schmitt and Holbrook 1990). Density compensation has been demonstrated less often (e.g., Robertson 1996, Martin and Martin 2001, Munday et al. 2001), possibly because experiments ended too soon for effects to be detected (MacNally 1983). Furthermore, indirect interactions between species may obscure density compensation following species loss (Menge 1995, Werner and Peacor 2003), particularly in dominance-structured multi-species guilds (MacNally 1983, Palmer et al. 2003).

In the tropics, tighter guild packing has historically been thought to result from competitive forces that are or were more intense than in temperate communities (Dobzhansky 1950, Connell 1978). This view largely stemmed from the notion that tropical climates are more stable than their temperate counterparts (MacArthur 1972). Resource stability is theoretically produced by climatic stability (Leigh 1982), in turn leading to levels of equilibrium in populations of consumers (Connell and Orias 1964). Nevertheless, tropical climates are not as stable as once thought. They recognize distinct seasonal fluctuations in rainfall (Leigh 1999) and additionally are subject to periodic climatic disturbances such as cyclic El Niño Southern Oscillations (Wright et al. 1999). The impact that tropical seasonality has on competitive interactions between species remains equivocal.

Here, I examine the role of interspecific competition in maintaining a dominancestructured Neotropical avian guild. Competition in multi-species avian guilds has rarely been demonstrated (Williams and Batzli 1979, Wiens 1992a,b), despite the historical importance of avian competition in community ecology (e.g., MacArthur 1958, Cody 1974, Wiens 1992a,b). In particular, I explore the role of interspecific competition several generations after the loss of a dominant competitor from a specialized guild of ant-following birds.

Ant-following birds are unique to the Neotropics. They follow army ant swarms to forage on leaf-litter arthropods that flee from the ants. Nearly fifty species of birds (primarily of the families Thamnophilidae and Dendrocolaptidae) regularly follow army ant swarms (Willis and Oniki 1978). The spatial arrangement of an ant swarm permits different mechanisms of niche partitioning by ant-followers. For example, species use different perch types and can be segregated at ant swarms by their dominance rank (Figure 2.1; Willis and Oniki 1978). Dominant birds at ant swarms include large species of the "clinger" guild that occupy the two-dimensional foraging space at the advancing swarm front near the forest floor (Willis 1967, 1972, 1973). Other species use tree trunks or walk along the ground, and generally interact less with the clinger species than the latter do with each other (Figure 2.1, Willis and Oniki 1978).

In Central America, the clinger guild consists of three species of regular antfollowers (listed in decreasing dominance): the ocellated (*Phaenostictus mcleannani*), bicolored (*Gymnopithys leucaspis*), and spotted (*Hylophylax naevioides*) antbirds. The ocellated antbird was extirpated on Barro Colorado Island, Panama, by 1978 (Willis and Eisenmann 1979), but still persists on the adjacent mainland in Soberania National Park

(Robinson et al. 2000). The clinger guild was studied extensively on Barro Colorado prior to the disappearance of ocellated antbirds (Willis 1967, 1972, 1973). This guild of ant-following birds was thus suitable for exploring numerical and behavioral responses several generations after the loss of a dominant competitor.

In this study, I examined the population density, biomass, and behavioral use of ant swarms of professional ant-followers in the clinger guild on Barro Colorado to test for compensatory responses since the 1960s. I then compared the clinger guild on Barro Colorado to the clinger guild in Soberania as a reference to test the hypothesis that competition maintains avian guild structure (i.e., the relative abundances of guild members) through interactions in dominance hierarchies, affecting only immediate subordinates. Alternatively, I hypothesized that competition maintains avian guild structure affecting all guild members, both through direct interactions and indirect interactions mediated through guild members. To test these hypotheses, I addressed the following questions: 1) Do dominant guild members limit the population abundance and biomass of subordinates through competitive interactions? 2) Do dominant species limit resource use (the use of ant swarms), affecting behavioral interactions, and is this coupled to the overall abundance of guild members? 3) Are there strong seasonal influences on resource use that might influence interaction strengths between guild members?

Under my general hypothesis that competition actively maintains guild structure through interactions with immediate subordinates, I predicted only bicolored antbirds would experience compensatory responses on Barro Colorado. I expected current population densities and biomass of bicolored antbirds to be higher on Barro Colorado than both in the 1960s and in Soberania, resulting from an increase in microhabitat use at

ant swarms. Specifically, I expected bicolored antbirds on Barro Colorado to exploit larger prey items, experience lower rates of interspecific aggression, and suffer higher rates of intraspecific aggression than in Soberania. I expected bicolored antbirds to experience higher rates of activity (movement) at swarms on Barro Colorado than in Soberania either by avoiding or pursuing intraspecific attacks. If all guild members interact directly and indirectly, as under my alternative hypothesis, I predicted that other guild members, in addition to bicolored antbirds, would exhibit compensatory responses on Barro Colorado since the 1960s and as compared to Soberania. Under both hypotheses, I expected stronger interactions in the dry season between guild members because fewer arthropods should occur on Barro Colorado at that time (Levings and Windsor 1982).

METHODS

Study Areas and Species

Study Areas

This study was conducted on Barro Colorado Island (9°09'N, 79°51'W) and in Parque Nacional Soberania (9°09'N, 79°44'W) in the Republic of Panama (Figure 2.2). I worked in a 500 ha area on Barro Colorado with an extensive trail system (Figure 2.3a). Barro Colorado (1500 ha) was formed in 1914 by the flooding of Gatun Lake for the construction of the Panama Canal. The island has a long history of ornithological study (e.g., Chapman 1929, Eisenmann 1952, Willis and Eisenmann 1979). In Soberania, I worked in a 200 ha area of study encompassing "Limbo Plot," a 100 ha study plot, also with an extensive trail system (Figure 2.3b; Robinson et al. 2000). The Limbo basin lies

within 22,000 ha of continuous forest, approximately 8 km east of Barro Colorado (Robinson et al. 2000). I collected data during the wet season from May 2003 to August 2003, and the dry season from January 2004 to April 2004.

The vegetation of Barro Colorado and Soberania is tropical moist forest (Holdridge 1967) with an average annual rainfall of 2600 mm, 90% of which falls during the wet season (May – December). The average daily temperature is 27°C (Leigh 1999).

Army Ants: Background

Two species of Neotropical army ants forage in swarms, forming a dense carpet of ants along the forest floor and sub-canopy: *Eciton burchelli* and *Labidus praedator* (Formicidae: subfamily Ecitoninae, tribe Ecitonini). While traversing the forest floor in an advancing fan-like raid, these army ants flush leaf-litter arthropods (Rettenmeyer 1963). Escaping arthropods provide an accessible and abundant foraging resource for birds (Willis 1974).

E. burchelli follows a ca. 35-day rhythm governed by a regular endogenous cycle. Two distinct life cycle phases, nomadic and statary, are synchronized to brood development (Schneirla 1933). During the nomadic phase (11-14 days), the entire colony moves to a new temporary nest (bivouac) site nearly every night after foraging each day. In the statary phase, the colony first nests in a protected site for about three weeks once larvae from the previous cycle have pupated. Halfway through the statary phase, the queen lays a new cohort of worker eggs (Schneirla 1971). During the statary phase, the ants have less brood to feed and only raid three days out of five (Willis 1967). Once the new workers eclose from their pupal cases and the eggs hatch, the colony begins another

nomadic cycle (Schneirla 1971). When a colony grows to a critical size, the queen lays a reproductive brood and the colony divides into two (Schneirla 1971) or occasionally three parts (J. Touchton, *personal observation*). About one of every three colonies also divides at the end of the dry season (Franks 1982). If colonies fall below a threshold size where they can no longer raid efficiently enough to meet their food requirements, they shrink slowly and may die.

Three independent estimates have been made of the number of *E. burchelli* colonies on Barro Colorado, and all approximate 50 colonies on the island, (i.e., ca. 3 per 100 ha) (Schneirla 1949, Willis 1967, Franks 1982). Less is known about *L. praedator*, as this species generally only forages above ground when water fills subterranean soil cavities in the wet season. It rarely appears above ground in the dry season (Willis 1967). *E. burchelli* swarms are therefore a much more predictable foraging resource for ant-following birds. *E. burchelli* is the focal ant species in my study.

Ant-following Birds: Background

The 45-55g ocellated antbird dominates regular ant-followers in Central America (Willis 1974). During the 1960s, Willis (1973) studied the natural history and rapid decline of ocellated antbirds on Barro Colorado (Table 2.3a). Ocellated antbirds were extirpated on Barro Colorado by 1978 (Willis and Eisenmann 1979). The critical event causing this loss may have been a severe dry spell in 1968 (Willis 1974, Willis and Eisenmann 1979). No concurrent population studies of ocellated antbirds were performed on the mainland from 1960-1970. In the 1990s, density estimates of ocellated antbirds on the mainland were higher than original estimates on Barro Colorado in the

early 1960s (Table 2.3a). The 28-33g bicolored antbird is subordinate to the ocellated antbird; it has also been studied extensively on Barro Colorado (Willis 1967). It too declined in the 1960s but did not suffer extirpation (Table 2.3a). The 16-20g spotted antbird is considered a facultative ant-follower and is subordinate to both bicolored and ocellated antbirds (Willis 1972). Density estimates of spotted antbirds remained relatively constant on Barro Colorado during Willis' study on Barro Colorado (Willis 1972), and in Soberania since the late 1960s (Table 2.3a).

Foraging Resources

Army Ant Colony Abundance

E. burchelli colonies were located by walking both on and off trails in both study sites. Each study area was monitored continuously and regularly each field season to locate new colonies entering the area. Once a colony was located, it was monitored daily and its movements tracked nightly to new bivouac sites during the nomadic phase. Colonies were tracked until they were lost or no longer needed for study. In all,13 colonies were monitored on Barro Colorado and 13 in Soberania.

E. burchelli colony density was estimated by a weekly census of a 100 ha plot in each study site (Figure 2.3). During the wet season, the census lasted eight weeks on Barro Colorado and six weeks in Soberania. In the dry season, the census lasted five weeks on Barro Colorado and seven weeks in Soberania. Each plot consisted of 17 lines marked with flagging tape 100 meters apart north to south, and 200 meters apart east to west. Flags were placed every 10 meters on each line. The lines in the plot were walked

from 1400h to 1700h to increase chances of seeing a column of ants (by the afternoon, they had traveled further from their overnight bivouac).

Flushed Arthropod Abundance

I estimated flushed arthropod abundance at ant swarms in both sites during the wet and dry seasons. To sample arthropods, 0.62m by 0.40m sampling quadrats were placed on the leaf litter three meters in front of the center of approaching ant swarms. The observer sat on stools 0.38m in height next to the quadrat. When ants came within one meter of the front edge of the quadrat, the observer scored all arthropods either flushed into or out of the quadrat for the next ten minutes. Arthropods were identified to taxonomic order or family. Ten minutes allowed the entire depth (1-2 meters) of the swarm front to pass through the quadrat, as the ant colony progresses at a rate of ca. 0.25m per minute (Willis 1967). This procedure was replicated three to five times per day per nomadic swarm between 0900h and 1100h.

The quadrats were constructed of 0.025m in diameter white PVC tubing connected by corner joints. The corner joints held the tubing off the ground, allowing the raiding army ants to pass underneath. These dimensions produced a fairly large quadrat that allowed us to score all movements of arthropods consistently. All observers were trained to score arthropods within a 90% precision rate. We observed no avoidance behavior towards the quadrats by the army ants or arthropods.

Ant-following Birds

Ant-following birds were captured with two to three 6 m mist-nets placed along the entire front of moving ant swarms (Swartz 1995) ant then marked over a period of two days at each newly discovered colony. All mist-netting occurred between 0700h and 1400h. Captured birds were fitted with a unique combination of a single aluminum and two to three colored celluloid bands. Additional banding was performed as needed when the ants entered a new territory with un-banded ant-followers.

Population densities of focal species

Adult populations of bicolored and ocellated antbirds were estimated in the study areas during both the wet (2003) and dry (2004) season from swarm attendance. As bicolored and ocellated antbirds are obligate ant-followers, I assumed that they were always at swarms. Thus, my estimates are conservative. If some individuals foraged elsewhere, I underestimated these densities.

Because spotted antbirds are thought to follow army ant swarms only facultatively (less than 50% of the time; Willis and Oniki 1978), population density estimates could not be generated using the same method as for bicolored and ocellated antbirds. During this study, D. Robinson estimated population density of spotted antbirds on Barro Colorado by territory mapping in a 50 ha area. He generously provided these estimates (Table 2.3a). For a mainland density estimate for spotted antbirds, I used Strysky's (2003) numbers from 1998 – 2000 in the 100 ha Limbo plot. Again, this estimate was generated by mapping the movements of known individual (Table 2.3a). As is customary

for territory mapping, no error was assumed and any unmarked birds in the mapped area were assumed to be single individuals.

Microhabitat use of ant swarms

E. burchelli colonies were visited daily for 1 – 4h between 0700h and 1200h, the period of greatest bird activity (Willis 1967). If the colony was swarming, one or two observers stood at least five meters to the side of and behind the swarm front. Individuals of all species of birds present were then identified by their band combinations. If band combinations could not be read or bands were absent, the number of individuals per species was estimated using sightings of species and/or counts of species-specific calls. At the end of the observation period, the ant swarm width was estimated by a tape measure to estimate the available foraging space for the birds. If a colony was not swarming upon arrival, it was checked for activity until 1400h.

Behavior at swarms

Marked bicolored antbirds were observed at ant swarms between 0700h and 1200h at both sites and seasons. Continuous watches were performed on focal individuals for 5-25 minutes divided into five-minute segments. Individuals were observed sequentially at a swarm until all possible marked bicolored antbirds had been watched. Individuals were observed only once per season. Observations ceased during heavy rain as all bird and ant activity stopped.

Activity levels, foraging rates, and numbers of aggressive interactions by bicolored antbirds were scored during observations. Activity rates were counts of the

numbers of hops and flights 3 to 10 meters long per minute. Flights > 10 m were not included in analyses here because they usually entailed the focal bird flying out of view of the observer and leaving the swarm. Foraging rates were estimated from the number of prey captured during an observation. Prey length and prey order or family were scored when possible. For analysis, prey were scored as small (0.5 - 1 x bill length) and large (>1 x bill length). Although prey smaller than half the length of the bird's bill were also consumed, they were not analyzed due to their small contribution to the overall biomass consumed by the birds. Aggression took the form of supplanting attacks where a dominant bird physically hit a subordinate, driving it off its perch, and passive displacements where the subordinate moved away from an approaching dominant. Supplantings and displacements were combined for analysis.

Statistical analyses and data presentation

Foraging Resources

I used two-way analysis of variance (ANOVA) to test for the effects of the independent factors site and season on the mean number of army ant colonies per 100 ha and the mean swarm width of the colonies. Army ant colony density means were generated from weekly census means, and the mean swarm width of each colony was estimated from daily measurements per colony.

Numbers of flushed arthropods were converted to dry biomass following Gruner (2003). I compared the dry biomass of the flushed arthropod communities at army ant swarms between sites and seasons with a two-way crossed analysis of similarity (ANOSIM) with site and season as factors, using the PRIMER software package (Clarke and Gorley 2001). ANOSIM is a test built on a nonparametric permutation procedure

combined with a general randomization approach (Clarke and Warwick 1994). The ANOSIM test uses the ratio of the mean within group to between group distances to calculate the test parameter Global *R*, which falls between 0 and 1. Values approaching 1 indicate similarity where values approaching 0 indicate dissimilarity. To determine site and seasonal differences for each arthropod group, I performed a two-way MANOVA, followed by two-way ANOVA with Fischer's least significant difference (LSD) post-hoc tests.

Ant-following bird population abundances

I estimated adult population densities of bicolored and ocellated antbirds in the study areas during both the wet (2003) and dry (2004) season using Bowden's Model Estimation (Bowden 1993) in Program NOREMARK (White 1996). The Bowden Model Estimation is a mark-recapture analysis that uses the number of banded birds, the number of banded bird bird sightings, and the number of unbanded bird sightings to estimate the total bird density using the sampled area and its 95% confidence intervals. Heterogeneity of sighting probabilities is assumed. I added a 400-meter border to the study areas to account for the large home ranges of these species (Willis 1967, 1973) and then calculated the density per 100 ha from the Bowden Estimate.

Ant-following bird use of ant swarms and behavioral interactions

I examined the mean number of all ant-following birds present at ant swarms and their total mean biomass per swarm with two-way ANOVAs. Sites and seasons were the two factors. Biomass data were square-root transformed to normalize the data. I then

used a two-way MANOVA followed by two-way ANOVA with LSD post-hoc tests (Appendix 2.2) to explore differences in attendance of the four species groups of birds at ant swarms between sites and seasons. The composition of attendant birds at ant swarms varied daily. Every new ant swarm was considered an independent unit for analyses.

Bicolored antbird foraging rates, activity rates, and aggressive interactions at ant swarms were analyzed with two-way MANCOVA. Observation length was included as a covariate. These data are presented as mean rates (activities per minute). Data on foraging rates and aggressive interactions were rank transformed prior to running the analyses to meet the assumptions of MANCOVA (Zar 1991). After each MANCOVA, I used two-way ANCOVAs with LSD post-hoc tests to help ascertain which variables were responsible for significant main effects. ANOVA tables are in Appendices 2.3 and 2.4.

Preferences for flushed arthropod prey was estimated by calculating selection ratios for each prey item (proportion of occurrence in diet/relative biomass in flushed arthropod community (Manly et al. 2000). A standardized selection ratio over 0.14 here indicates the respective prey item is preferred, while a selection ratio less than 0.14 indicates avoidance (Manly et al. 2000). To test for differences in prey preference at swarms between sites and seasons, selection ratios for each prey item were compared using chi-squared tests (after Manly et al. 2002).

RESULTS

Foraging resources

E. burchelli colony density varied strongly across seasons. On average, colony density in the dry season was nearly double the density in the wet (Table 2.1). The mean

swarm width of *E. burchelli* colonies, however, did not differ reliably from season to season, although averaged 26% wider in Soberania than on Barro Colorado (Table 2.1).

Four taxa dominated the flushed arthropods at ant swarms. Tettigoniidae made up over 40% of the biomass, followed by Gryllidae (ca. 32%), large Araneida (ca. 18%), and Blattodea (ca. 7%). The composition of flushed arthropods at swarms differed between seasons (ANOSIM, Global R = 0.36, p < 0.01), but not sites (ANOSIM, Global R = 0.0, p > 0.05). Specifically, samples averaged 44% grams of dry weight more arthropods in the wet season due to higher numbers of Tettigoniidea, Araneida, and Blattodea (Table 2.2). Gryllidae and Isopodea, however, were 2.3 and 10 times less dense in the wet season than the dry, respectively (Table 2.2). I examine preference of these arthropods by the birds later.

Population responses of focal ant-followers

Overall densities for bicolored and spotted antbirds have changed since the 1960s on Barro Colorado. I estimated the bicolored antbird density on Barro Colorado to be 12.6 individuals per 100 ha, 66% higher than Willis' 1961 estimate, an increase of ca. 150 g/100 ha (Table 2.3b). This difference could be statistically significant if Willis estimated densities of bicolored antbirds with similar accuracy and precision to my study. After the extinction of ocellated antbirds in the late 1970s, spotted antbird density on Barro Colorado appeared to remain constant at 45 – 50 individuals per 100 ha until the mid-1990s, when numbers began to rise (Table 2.3a). According to recent estimates, spotted antbird density apparently has risen by 44% on Barro Colorado since the mid-1990s, an increase of ca. 350 g/100ha (Table 2.3a, D. Robinson *personal comm.*). The

combined increase in biomass of bicolored and spotted antbirds per 100 ha more than doubles the loss in biomass (ca. 200 g/100 ha) by ocellated antbirds.

In Soberania, densities of ocellated, bicolored, and spotted antbirds have remained more constant over time, but they differ from Barro Colorado. In Soberania, I estimated numbers of ocellated antbirds to be 80% higher than on Barro Colorado before their decline there (Table 2.3b). Again, assuming that previous estimates contained a similar amount of error as my estimates, this difference would be significant. My density estimate for bicolored antbirds in Soberania is nearly double that on Barro Colorado . (Table 2.3b). In contrast, however, recent estimates of spotted antbirds in Soberania (Strysky 2003) are 16% less than on Barro Colorado, or ca. 180 g/100 ha less (Table 2.3a, D. Robinson *personal comm.*).

Use of ant swarms

Although the total number of individual birds and biomass at ant swarms on Barro Colorado could not be compared to the 1960s, differences in swarm attendance by bicolored and spotted antbirds were apparent. The number of bicolored antbirds at swarms on Barro Colorado was 30% higher than in the 1960s (Table 2.4). Spotted antbirds attended swarms on Barro Colorado more than twice as often as they did in the 1960s (Table 2.4).

The combined number of individual birds at ant swarms did not differ between Barro Colorado and Soberania, but the combined biomass did. Biomass was ca. 30% less per swarm on Barro Colorado than in Soberania (Table 2.5). This biomass difference reflects site differences in species composition of the ant-following bird community

(Figure 2.4). On Barro Colorado there were, on average, 27% fewer of the large bicolored antbird per swarm then in Soberania, but 140% more of the small spotted antbird per swarm (Figure 2.4).

Relative proportion biomass per species group differed at swarms on Barro Colorado compared to Soberania. The small spotted antbirds accounted for 20-25 percent of the total biomass at ant swarms on Barro Colorado but only 7-10 percent in Soberania (Figure 2.5; Kruskal Wallis, $\chi^2 = 84.69$, df = 1, p < 0.001, n = 196). The large ocellated antbird accounted for 10-15 percent of the total biomass at ant swarms in Soberania, equal to the difference in biomass of spotted antbirds between Barro Colorado and Soberania (Figure 2.5). Thus, on Barro Colorado, spotted antbirds have increased in number at swarms, filling the "gap" left by the absence of ocellated antbirds. I will suggest below that dominance relations between the species help to explain these patterns.

Ant-following bird communities were similar between the wet and dry seasons at ant swarms (Table 2.5). Despite this overall similarity, there were some differences within the species groups. Nearly 40% more spotted antbirds attended swarms in the dry season than in the wet (Figure 2.4). The obligate ant followers, however, were more abundant at swarms in the wet season with 16% more bicolored antbirds, and 8% more ocellated antbirds (Figure 2.4).

Behavioral interactions at swarms

Foraging

The overall foraging rates of bicolored antbirds did not differ between sites and seasons (Figure 2.6). Slightly more (44%) small prey, however, were captured in Soberania as compared to Barro Colorado (Figure 2.6a).

Prey preferences of bicolored antbirds were similar between sites (Table 2.6a). The standardized selection ratios indicate that bicolored antbirds typically selected similar prey (i.e., Tettigoniidae, Blattodea, and large Araneida) in both sites. Bicolored antbirds in Soberania also selected weakly for Coleoptera (Table 2.6a). Despite preference for similar prey between sites, the strength of the selection ratios varied. For example, bicolored antbirds on Barro Colorado selected the three most preferred prey items (Tettigoniidae, Blattodea, and large Araneida) more strongly than in Soberania (Table 2.6a).

Slightly more prey items were selected for in the dry season than the wet season. For example, Blattodea were not selected in the dry season (Table 2.6b). Of the prey items selected, selection ratios were significantly higher in the dry season than the wet (Table 2.6b). In the dry season, large prey (Tettigoniidae, Blattodea, and large Araneida) were less abundant than in the wet (Table 2.2). (We did not detect any small Blattodea in our sampling.) Although they were consistently abundant, small Gryllidea and small Araneida were not preferred by bicolored antbirds (Table 2.6b).

Aggressive interactions

Overall rates of aggression involving bicolored antbirds differed between Barro Colorado and Soberania (MANCOVA, $F_{6,147} = 4.08$, p = 0.001). There were 43% more interspecific aggressive interactions on Barro Colorado (Table 2.7 a). Bicolored antbirds

also supplanted spotted antbirds three times as often on Barro Colorado as in Soberania (Table 2.7 a). The directions of arrows in Figure 2.8 illustrate the direction of aggression either from or to bicolored antbirds on Barro Colorado and in Soberania 2003-2004, and on Barro Colorado 1960-1961 (Willis 1967). The proportion and targets of aggressive interactions involving bicolored antbirds on Barro Colorado in the 1960s strongly resembles those in Soberania 2003 – 2004. In contrast, fewer current aggressive interactions occur with other bicolored antbirds on Barro Colorado, where a higher proportion of aggression involves spotted antbirds (Figure 2.7).

I expected both interspecific and intraspecific aggressive interactions to increase during the dry season due to lower abundances of preferred arthropods. Levels of aggression involving bicolored antbirds did vary seasonally (MANCOVA, $F_{6,147} = 5.83$, p < 0.001). Intraspecific aggression, however, did not change (Table 2.7 b). Aggression towards spotted antbirds by bicolored antbirds was higher in the dry season, but aggression involving all other species was higher in the wet season (Table 2.7 b).

Activity

Bicolored antbirds were slightly more active in Soberania than on Barro Colorado (MANCOVA, $F_{2,151} = 4.58$, p = 0.012), and they were more active in the dry season (MANCOVA, $F_{2,151} = 4.59$, p = 0.012) (Figure 2.8). Bicolored antbirds hopped 16% more often in Soberania than on Barro Colorado, and 39% more in the dry season than in the wet season (Figure 2.8a). Bicolored antbirds also flew 27% more often at swarms in Soberania and 50% more during the dry season (Figure 2.8b).
DISCUSSION

Below, I discuss the numerical and behavioral responses of the ant-following clinger guild on Barro Colorado Island, Panama, several generations after the loss of their dominant competitor, the ocellated antbird. I elaborate on possible mechanisms behind density and biomass compensation at the population level, and at the microhabitat level by abundances at ant swarms. I further discuss direct and indirect behavioral interactions as they may relate to population abundances, and how seasonal variation may influence these interactions.

Effects of competition on the abundance of members of the "clinger" guild

Population estimates on Barro Colorado from 2003-2004 suggest that the loss of ocellated antbirds has led to compensatory gains in the absolute abundance of bicolored and spotted antbirds. Density estimates for these two guild members exceed 1961 estimates by about 40-60%. This amounts to a gain in combined biomass of nearly double that from the loss of biomass incurred through the extirpation of ocellated antbirds from Barro Colorado (Table 2.3). If, however, biomass is scaled to account for differences in food consumption rates of differing body sizes (Walsburg 1983), bicolored and spotted antbird combined biomass compensatory responses at the population level have been measured in competitor removal experiments, complete or over-density and biomass compensation has rarely been documented (Rodda and Dean-Bradley 2002). Most studies have revealed under-compensation (Hairston 1981, Holbrook and Schmitt 1995, Robertson 1996, Munday et al. 2001).

The over-compensation in density at the population level observed here could be an artifact of the timing of the initial density estimates on Barro Colorado. Willis (1974) documented a decline of ocellated antbirds from 1961 to 1971. Bicolored antbird density also declined in the 1960s, but appeared to stabilize in the early 1970s (Willis 1974). Spotted antbirds, on the other hand, maintained a similar density throughout the 1960s (Willis 1974). It is possible that the initial population density estimates generated by Willis (1974) for these guild members occurred after ocellated and bicolored antbirds already had begun to decline on Barro Colorado. Willis (1974) states that, in the 1960s, numbers of bicolored and ocellated antbirds were as high or higher on the mainland than on Barro Colorado. Estimates from the mid 1990s and this study document higher numbers of ocellated and bicolored antbirds in Soberania than were on Barro Colorado during the 1960s. It remains possible that ocellated and bicolored antbirds have always been less numerous on Barro Colorado than in Soberania.

Several competitor removal experiments have failed to demonstrate complete density compensation (Schoener 1983, Gurevitch et al. 1992). Often, long periods are needed for density compensation to occur, particularly for long-lived organisms. Surfperch under-compensated in density after one generation of competitive release (Schmidt and Holbrook 1990). Two generations have been suggested as a suitable time scale to measure such population responses (Yodzis 1988). A maximum compensatory response in damselfish took four generations, however, and was only apparent after complete population turnover (Robertson 1996). Complete population turnover has also been proposed as a minimum time frame to assess population stability (Connell and Sousa 1983).

Bicolored and spotted antbirds on Barro Colorado took over 20 years to increase in abundance following the extirpation of ocellated antbirds. These species of antbirds are known to reach ages of at least 12 and 15 years (Willis 1983). By 1994, these populations may have undergone a complete turnover with only slight increases in abundances (Robinson 1999). There are several possible explanations for the delay in population increases by bicolored and spotted antbirds on Barro Colorado, including fluctuations in foraging resources, recruitment limitation, and slow behavioral shifts. If such fluctuations were extreme, they could exacerbate the time required for population abundances to increase.

Fluctuations in foraging resources may be responsible for not only the initial declines of ocellated and bicolored antbirds, but also for slow increases in bicolored and spotted antbird density on Barro Colorado. The abundance of ant-following birds may be closely coupled to army ant colony density. In Cocha Cashu, Peru, forest flooding influenced the availability of army ants, which could have affected adult survival of ant-following birds (Willson 2004). *E. burchelli* colony density was similar between Barro Colorado and Soberania in this study (Tables 2.1), but was lower than previous estimates for Barro Colorado (Schneirla 1949, Willis 1967, Franks 1982). The population of *E. burchelli* has been proposed to be one of the most stable on Barro Colorado (Franks 1982). However, my *E. burchelli* density estimates indicate that numbers may fluctuate more than suggested by Franks (1982). Climatic fluctuations may play a role here. Repeated food shortages following unusual seasonal extremes have caused famine for some species on Barro Colorado (Leigh 1999). S. Powell (*personal comm.*) noted fewer large colonies and evidence of colony fission on Barro Colorado in 2002 following the

harsh dry season of 2001. Willis (1974) also found it difficult to locate *E. burchelli* colonies on Barro Colorado in 1968 following an extremely dry year.

High nest predator densities on Barro Colorado may hinder recruitment in bicolored and spotted antbirds and thus slow increases in population abundance. According to Glanz (1982, 1990) and Sieving (1992), common mammalian nest predators are more abundant on Barro Colorado than in Soberania. Experiments using artificial nests suggested that ant-following birds, including spotted and bicolored antbirds, experienced higher levels of nest predation on Barro Colorado than in Soberania (Sieving 1992). The validity of artificial nest studies, however, has been questioned (review in Moore and Robinson 2004). Nevertheless, low juvenile recruitment in obligate ant-following birds in Peru contributed to large population fluctuations there (Willson 2004). Nest predation may ultimately be one reason why bicolored antbirds have not been able to increase to greater densities on Barro Colorado.

The abundance of guild members at ant swarms

My results suggest that ocellated antbirds reduce the spotted antbird swarm use by forcing them to the periphery (zone C; Figure 2.1). More than twice as many spotted antbirds foraged at ant swarms on Barro Colorado as they did on Barro Colorado in the 1960s and in Soberania during this study. I did not expect spotted antbirds to display density or behavioral compensation at swarms. Spotted antbird swarm attendance was expected to be limited, as they were previously only known to forage at ant swarms when they passed through their territories. Usually, there were only two or three individual spotted antbirds per swarm (Willis 1972). Given there was a similar composition of

attendant ant-followers on Barro Colorado in the 1960s as I observed in Soberania, spotted antbirds will have compensated for 100% of the proportion of biomass missing at swarms on Barro Colorado after the extirpation of ocellated antbirds (Figure 2.5).

Bicolored antbirds may also limit ant swarm use by spotted antbirds. The number of bicolored antbirds per swarm was higher in Soberania than on Barro Colorado (Table 2.4). Despite this fact, mean numbers of bicolored antbirds at swarms on Barro Colorado in the 1960s were lower than in this study while numbers of spotted antbirds per swarm were similar to those in Soberania today. Thus, ocellated antbirds may have more influence on swarm use by spotted antbirds than bicolored antbirds.

Behavioral responses in relationship to abundance of guild members

Ocellated antbirds could limit spotted antbird swarm use through either direct or indirect interactions. Willis (1972) noted that spotted antbirds maintain a sufficient distance from ocellated antbirds that they are rarely supplanted or displaced by them. Bicolored antbirds, however, actively supplant spotted antbirds away from prime foraging spaces at ant swarms (represented by zone B in Figure 2.1; Willis 1972). My observations from Soberania confirm these observations (Figure 2.7). It thus seems plausible that ocellated antbirds limit spotted antbird swarm use indirectly, possibly through interactions with bicolored antbirds in zones A and B (Figure 2.1). Such competitor induced behavioral plasticity has also been shown to occur with larval green frogs (Relyea 2000).

Bicolored antbirds behaved differently at swarms on Barro Colorado and in Soberania, suggesting that other changes have occurred on Barro Colorado since the loss

of ocellated antbirds. Bicolored antbirds still preferred and captured large prey items on both Barro Colorado and in Soberania, yet they foraged on smaller prey more frequently in Soberania than on Barro Colorado. This result suggests that some bicolored antbirds in Soberania are foraging in poorer locations (zones B or C; Figure 2.1) at swarms than on Barro Colorado where bicolored antbirds may continuously forage in zone A (figure 2.1). Rates of intraspecific aggression were similar between sites, but the number of flights by bicolored antbirds at swarms was higher in Soberania than on Barro Colorado. Bicolored antbirds maintain areas at swarms by displacing or supplanting subordinate birds that come within 2m (Willis 1967, J. Touchton personal observation). More often, however, subordinate birds simply avoid dominants; thus supplanting or displacement need not occur. The frequent flights by bicolored antbirds at swarms in Soberania suggests that birds have to change their foraging locations more often than on Barro Colorado. These changes in location may be in response to ocellated antibrds coming and going from swarms and taking over the most profitable foraging areas when they do so. These behavioral differences in bicolored antbirds suggest that profitable foraging locations for spotted antbirds in zone B, for example (Figure 2.1), are available at swarms on Barro Colorado but not in Soberania.

Shifts in microhabitat use following competitive release are generally immediate (review in Schoener 1983, Holbrook and Schmidt 1995, Griffis and Jaeger 1998). For example, information gathering (e.g., learning, particularly of reliable information) affected the nature of competitive interactions between three coexisting hummingbird species (Sandlin 2000). Williams and Batzli (1979) demonstrated that red-bellied woodpeckers utilize forest they are normally excluded from by red-headed woodpeckers,

following removals of the latter species. During less productive years, red-headed woodpeckers also vacate the forested area where the two species competed. Perhaps the information red-bellied woodpeckers obtained over the years supported such rapid shifts in behavior when their dominant competitor was absent.

The short duration of many studies may not have revealed delays in behavioral adaptations allowing for shifts in microhabitat use. Bicolored and spotted antbirds took at least ten years to display recognizable behavioral shifts on Barro Colorado. Willis did not report significant changes in microhabitat use by bicolored or spotted antbirds during his work in the 1960s (Willis 1972, 1974). The decline of bicolored antbirds on Barro Colorado may have contributed to an increase in use of army ant swarms by spotted antbirds. It is possible that spotted antbirds took several years to learn that space at ant swarms was sufficiently reliable to leave their territories to look for these swarms.

Seasonal impacts on microhabitat use

Seasonal limitation in foraging resources is known to affect species interactions within guilds (Terborgh 1983). Seasonal variation in the number of army ant colonies and leaf litter arthropods (Levings and Windsor 1982, Table 2.2) may therefore affect seasonal differences in behavior of ant-following birds. The greater number of ant colonies and longer foraging periods in the dry season may compensate for the fact that there are fewer flushed arthropods during this time. Afternoon rains generally interrupt army ant foraging behavior in the wet season (J. Touchton *personal observation*), forcing ant-following birds to "fill-up" in the morning. Greater numbers of ocellated and bicolored antbirds were present at swarms during the wet season in the morning. More

intensive foraging by obligate ant-followers at swarms in the wet season could explain the smaller numbers of spotted antbirds at swarms during this time.

Increased competition for swarm space in the wet season may not be the only reason why spotted antbirds attended swarms more in the dry season. During the dry season, spotted antbirds are not restricted to a nest area, allowing them to travel further to ant swarms. Although flushed leaf-litter arthropods are less abundant at ant swarms in the dry season, they are also less abundant away from swarms (Levings and Windsor 1982).

CONCLUSION

This study suggests that interspecific competition actively maintains structure in this tropical guild by limiting the use of shared resources and setting overall population density. Following the prolonged absence of a dominant guild member, density compensation may have occurred through delayed direct and indirect interactions between remaining guild members. Surprisingly, complete population turnover occurred before evidence of density compensation was detectable. Delayed behavioral adaptations of guild members could have contributed to the delay in density compensation. Other factors, such as recruitment limitation could have also prevented more immediate density compensation. Moreover, seasonal variation in resource levels and variability in life history parameters of guild members probably influenced the strength of competitive interactions. Long-term experiments and comparative studies measuring population abundances and behavioral interactions are thus important to fully understand the role of competition in the maintenance and re-structuring of multi-species tropical guilds.

Table 2.1: Mean number of E. burchelli colonies per 100 ha, mean width of swarms per colony (meters), and two-way ANOVA results. Factors: a) site; Barro Colorado Island (BCI) and Soberania National Park (SNP), and b) season; Wet and Dry.

	E. burchelli c	olonies	per 10	0 ha	Swarm width of colonies (m)			
-	Mean ± SE	F	df	P	Mean ± SE	F	df	Р
a) SITE	•••••••••••••••••••••••••••••••••	•i						
BCI	2.08 ± 0.18	0.00	1 22	0.214	9.60 ± 0.51	7 52	1 16	0.01/
SNP	2.62 ± 0.35	0.88	1,22	0.214	12.21 ± 0.85	1.52	1,10	0.014
† BCI (1961)	3.17				6.00			•
b) SEASON								
WET	1.71 ± 0.13	10.8	1 77	<0.001	10.56 ± 1.27	0.98	1 16	0 337
DRY	3.08 ± 0.29	10.8	1,22	<0.001	11.13 ± 0.48	0.70	1,10	0.557
c) SITE X SEAS	ON	2.45	1, 22	0.131		0.50	1, 16	0.490

WIIIIS

	BCI	SNP	Two-way ANOVA	
a) 511 E	n = 134	n = 170	F	P
Tettigoniidae	52.03 ± 12.61	41.01 ± 10.63	0.22	0.641
Blattodea	6.51 ± 1.03	8.19 ± 1.35	0.09	0.771
Araneida > 0.5 cm ^a	14.43 ± 2.32	18.88 ± 2.86	2.92	0.088
Araneida < 0.5 cm^{b}	4.71 ± 0.42	3.66 ± 0.28	7.30	0.007
Gryllidae	29.52± 3.47	35.32 ± 3.85	0.19	0.667
Coleoptera	2.27 ± 0.42	1.56 ± 0.32	2.47	0.117
Lepidoptera	0.09 ± 0.06	0.43 ± 0.12	7.30	0.007
Isopodea	2.61 ± 0.50	2.48 ± 0.47	0.00	0.984
TOTAL	117.67±13.52	113.54 ± 12.2		
b) SEASON	WET	DRY	Two-way A	NOVA
b) SEASON	n = 100	n = 204	F	Р
Tettigoniidae	77.92 ± 19.06	30.15 ± 7.50	5.33	0.022
Blattodea	11.33 ± 1.37	5.55 ± 1.11	29.33	<0.001
Araneida > 0.5 cm ^a	30.86 ± 4.62	10.08 ± 1.48	21.31	<0.001
Araneida < 0.5 cm ^b	6.83 ± 0.48	2.79 ± 0.23	91.60	<0.001
Gryllidae	12.81 ± 1.91	42.55 ± 3.63	25.68	<0.001
Coleoptera	1.80 ± 0.42	1.91 ± 0.33	0.00	0.965
Lepidoptera	0.28 ± 0.09	0.28 ± 0.12	0.03	0.857
Isopodea	0.36 ± 0.18	3.59 ± 0.48	27.69	<0.001
TOTAL	145.10 ± 20.48	100.78 ± 8.86		

Table 2.2: Mean dry biomass (mg) of flushed arthropods per quadrat between a) sites(Barro Colorado: BCI, and Soberania: SNP) and b) seasons (wet and dry). Two-wayANOVA results on the ranked data are presented.

^aSite X Season, p<0.05

^bSite X Season, p<0.001

	Date	Surveyor			Species			
		· · · · · · · · · · · · · · · · · · ·	Ocellated	antbird	Bicolored an	tbird	Spotted	antbird
a)			Ind./100 ha	g/100 ha	Ind./100 ha	g/100 ha	Ind./100 ha	g/100 ha
BCI	1961	Willis (1974)	3.8	193.8	7.6	228.0	46.4	788.8
-	1970	Willis (1974)	0.3	15.3	3.2	96.0	45.2	768.4
	1994	Robinson (1999)	0.0	0.0	4.0	120.0	48.0	816.0
	2003	D. Robinson (pers.comm	.)				66.7	1133.9
SNP	1968	Karr (1971)			20.0	600.0		
	1994	Robinson et al. (2000)	8.0	408.0	24.0	720.0	50.0	850.0
	1998 - 2000	Strysky (2003)	-				56.0	952.0
b)			Ocellated	antbird	Bicolored antbird			
U)			Ind./100 ha	g/100 ha	Ind./100 ha	g/100 ha		
BCI	2003	This study	0.0	0.0	12.6 (11.1-14.3)	378.0	- .	
	2004	This study	0.0	0.0	13.0 (11.1-15.1)	390.0		
SNP	2003	This study	6.8 (5.9 -7.4)	346.8	21.9 (20.1-23.8)	657.0		· ·
	2004	This study	7.0 (4.8 - 8.7)	357.0	24.4 (22.0 - 27.1)	732.0		

Table 2.3: Population density (mean number and grams per 100 ha) for ocellated, bicolored, and spotted antbirds on Barro Colorado (BCI) and in Soberania (SNP) from a) other studies and b) this study. C.I.'s were generated from Bowden's Model Estimator.

<u> </u>	······································	Ocellated			Bicolored			Spotted		
Site	Date	Mean ± SE	Max	Ν	Mean ± SE	Max	Ν	Mean \pm SE	Max	Ν
DCI	1960-64	2.9	12	448	4.1	15	1116	1.8	8	428
BCI	this study	0	0	85	5.3 ± 0.24	10	85	5.5 ± 0.32	14	85
SNP	this study	1.4 ± 0.12	5	108	6.8 ± 0.29	16	108	2.3 ± 0.16	6	108

Table 2.4: Mean number and maximum number of ocellated, bicolored, and spotted antbirds per ant swarm on Barro Colorado (BCI) and in Soberania (SNP). Historical data for BCI from 1960-1964 are from Willis (1967, 1972, 1973).

	Individu	als per	swarm		Total biom	ass per s	warm (g)
	Mean ± SE	F	df	P	Mean ± SE	F	df	Р
a) SITE						· · · ·		
BC	14.87 ± 0.60		1 180	0.870	416.53 ± 18.80	13.03	1 189	<0.001
SNF	14.31 ± 0.51	0.03	1, 109	0.870	541.87 ± 24.07	15.05	1, 107	NO.001
b) SEASON								
WET	14.04 ± 0.73	0.50	1 100	0.440	455.02 ± 30.35	0.03	1 180	0.760
DRY	14.74 ± 0.46	0.39	1, 109	0.440	497.44 ± 19.38	0.95	1, 107	0.700
c) SITE X SEA	SON	3.61	1, 189	0.060		1.37	1, 189	0.244

Table 2.5: Mean numbers of all birds counted per ant swarm and mean total biomass of all birds per ant swarm for a) sites (Barro Colorado: BCI, and Soberania: SNP) and b) seasons (WET and DRY).

Table 2.6: Estimates of the selection ratios (relative occurrence of arthropods in the diet/relative abundance of flushed arthropods available) of bicolored antbirds a) between sites (BCI and SNP) and b) between seasons (WET and DRY). A standardized selection index > 0.14 indicates preference and is depicted in bold. Results from χ^2 test of differences between selection ratios between a) sites and b) seasons are reported. χ^2 values are Bonferroni adjusted. Statistically significant different differences are in bold (P < 0.05).

·	Propo	rtion	Propo	rtion	Selec	tion	Standa	rdized	γ^2
a) SITE	in D	Diet	in Sa	nple	Rat	io	Selection	n Index	λ
-	BCI	SNP	BCI	SNP	BCI	SNP	BCI	SNP	
Tettigoniidae	9.79	8.40	1.13	2.46	8.65	3.41	0.46	0.31	12.28
Blattodea	24.97	23.04	6.65	10.85	3.76	2.12	0.20	0.20	17.55
Araneida >0.5 cm	21.81	23.70	6.65	11.29	3.28	2.10	0.18	0.19	10.01
Araneida <0.5 cm	15.11	18.82	48.80	35.31	0.31	0.53	0.02	0.05	12.32
Gryllidae	18.29	16.77	19.66	30.54	0.93	0.55	0.05	0.05	10.30
Coleoptera	6.47	7.17	4.53	4.05	1.43	1.77	0.08	0.16	0.69
Other	3.56	2.10	12.59	5.50	0.28	0.38	0.02	0.04	0.49
N	350	488	748	751		•			
	Proportion		Propo	rtion	Selec	tion	Standa	rdized	$\sqrt{2}$
b) SEASON	in D	Diet	in Sa	mple	Rat	tio	Selectio	n Index	×.
-	WET	DRY	WET	DRY	WET	DRY	WET	DRY	
Tettigoniidae	6.01	10.31	1.93	1.70	3.11	6.06	0.35	0.37	7.94
Blattodea	12.92	27.31	11.80	6.92	, 1.09	3.94	0.12	0.24	78.12
Araneida >0.5 cm	31.85	19.34	14.51	5.68	2.20	3.41	0.25	0.21	11.81
Araneida <0.5 cm	32.68	12.23	51.84	36.44	0.63	0.34	0.07	0.02	20.53
Gryllidae	9.92	20.45	8.70	34.62	1.14	0.59	0.13	0.04	7.19
Coleoptera	0.00	8.56	3.68	4.65	0.00	1.84	0.00	0.11	50.36
Other	4.81	1.80	7.54	9.99	0.64	0.18	0.07	0.01	6.92
N	300	538	526	973					·

	BCI	SNP	Two-w	ay ANCC	VA
a) SITE	N = 69	N = 88	F	df	Р
To:					
Bicolored	0.05 ± 0.01	0.09 ± 0.02	1.15	1, 152	0.284
Spotted ^a	0.06 ± 0.01	0.02 ± 0.01	9.17	1, 152	0.003
Other	0.02 ± 0.01	0.01 ± 0.01	0.85	1, 152	0.357
From:					
Bicolored	0.05 ± 0.01	0.09 ± 0.02	1.15	1, 152	0.284
Spotted	0.01 ± 0.01	0.00	0.72	1, 152	0.398
Ocellated	0.00	0.02 ± 0.01	9.14	1, 152	0.003
Other	0.01 ± 0.01	0.02 ± 0.01	2.847	1, 152	0.094
	Wet	Dry	Two-w	ay ANCC	VA
D) SEASON	N = 48	N = 109	F	df	Р
То:			<u></u>	······································	<u></u>
Bicolored	0.09 ± 0.02	0.07 ± 0.01	2.16	1, 152	. 0.143
Spotted ^a	$0.01 \pm .01$	0.05 ± 0.01	9.95	1, 152	0.002
Other	0.03 ± 0.02	0.01 ± 0.004	10.94	1, 152	0.001
From:				,	
Bicolored	0.09 ± 0.02	0.07 ± 0.01	2.16	1, 152	0.143
Spotted	0.00	0.01 ± 0.004	2.97	1, 152	0.087
Ocellated	0.01 ± 0.003	0.01 ± 0.01	0.92	1, 152	0.339
Other	0.02 ± 0.01	0.01 ± 0.01	6.65	1, 152	0.011

Table 2.7: Mean rates of aggression \pm SE (per minute) directed TO species groups by bicolored antbirds or received by bicolored antbirds FROM species groups. Mean rates reported are between a) sites (BCI and SNP) and between b) seasons (WET and DRY). Results from two-way ANCOVA are presented with site and season as factors and observation length as a covariate. N = number of observations.

^aSite X Season; p < 0.05



Figure 2.1: Spatial partitioning at an ant swarm. The greatest abundance of arthropods occurs in zone A, where the swarm front drives arthropods from the leaf litter, here, occupied by the dominant ocellated antbird. Zone B, still an area of high arthropod activity, is occupied by the subordinate bicolored antbird. Surrounding zone B is zone C, occupied by the small subordinate spotted antbird, considered a facultative ant follower. Vertical partitioning of resources at ant swarms also occurs. In zone D, a plain-brown woodcreeper forages on invertebrates flushed upwards by the ants. E represents the bivouac, the army ant nest location, while the arrow depicts the direction of forward movement by the ant swarm. *Illustration by James N. M. Smith*



Figure 2.2: Study area in the Republic of Panama. Focal sites were Barro Colorado Island, and surrounding the Limbo plot in Soberania National Park.





Figure 2.3: Study areas in a) Barro Colorado, and b) Soberania. Light gray areas depict study area, while the 100 ha census plots are designated by dark gray.

a)





Figure 2.4: Mean numbers of individual spotted, bicolored, and ocellated antbirds, and all other species attending ant swarms during the dry (black) and wet (gray) season. a) Barro Colorado (BCI), b) Soberania (SNP). N = 189 swarms. Error bars represent 95% CI's of the mean. Two-way ANOVA results are given in Appendix 2.2; * Site: p<0.05; † Season: p<0.05; ‡Interaction (Site X Season): p<0.05.



Figure 2.5: Percent of total biomass at ant swarms of spotted, bicolored, and ocellated antbirds, and all others species for both Barro Colorado (BCI; black hatched) and Soberania (SNP; gray hatched) over both seasons.







Figure 2.6: Foraging rates per minute by bicolored antbirds during both season on Barro Colorado (BCI) and in Soberania (SNP) during the dry (black) and wet (gray) seasons; a) small prey (0.5-1.0 x bill length), b) large prey (>1.0 x bill length). N = 152observations. Two-way ANOVA results given in Appendix 2.3; * Site: p<0.05; † Season: p<0.05; ‡Interaction (Site X Season): p<0.05.

· a)



Figure 2.7: Percentage of aggressive interactions (supplanting or displacing) made by or received by bicolored antbirds on a) Barro Colorado (BCI) 2003-2004, b) Soberania (SNP) 2003-2004, and c) BCI 1960-1961 (Willis 1967). The direction and width of the arrows indicate the direction of and strength of aggression, respectively. Bicolored (BCAB); Spotted (SPAB); Ocellated (OCAB); Other (OTHER).









a)

LITERATURE CITED

2

Armstrong, R. A., and R. McGehee. 1976. Coexistence of 2 competitors on one resource. Journal of Theoretical Biology **56**:499-502.

Chapman, F. M. 1929. My tropical air castle. Appleton-Century, New York.

- Chappell, M. A. 1978. Behavioral factors in altitudinal zonation of chipmunks (Eutamias). Ecology **59**:565-579.
- Chesson, P. 2000b. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics **31**:343-366.
- Clarke, K. R., and R. N. Gorley. 2001. PRIMER v5: User manual/tutorial. PRIMER-E, Plymouth, UK.
- Clarke, K. R., and R. M. Warwick. 1994. Similarity-based testing for community pattern - the 2-way layout with no replication. Marine Biology **118**:167-176.
- Cody, M. L. 1974. Competition and the structure of bird communities. Monographs in Population Biology 7. Princeton University Press, Princeton, New Jersey.
- Cody, M. L., and J. M. Diamond. 1975. Ecology and the evolution of communities. Harvard University Press, Cambridge, Massachusetts.
- Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. Science **199**:1302-1310.
- Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos **35**:131-138.
- Connell, J. H. And Orias, E. 1964. The ecological regulation of species diversity. The American Naturalist **98**:399-414.
- Connell, J. H. And W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist **121**:789-824.

Dobzhansky, T. Evolution in the tropics. American Scientist 38: 209-221.

- Eisenmann, E. 1952. Annotated list of birds of Barro Colorado Island, Panama Canal Zone. Smithsonian Institution, Washington, D.C.
- Franks, N. R. 1982. Ecology and population regulation in the army ant *Eciton burchelli*. In E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D.C.

- Glanz, W. E. 1982. The terrestrial mammal fauna of Barro Colorado Island: censuses and long-term changes. Pages 455-468 in E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. The ecology of a tropical forest: seasonal rhythms and longterm changes. Smithsonian Institution Press, Washington, D.C.
- Glanz, W. E. 1990. Neotropical mammal densities: how unusual is the community on Barro Colorado Island, Panama? Pages 287-313 in A. Gentry, editor. Four Neotropical rain forests. Yale University Press, New Haven, Connecticut.
- Griffis, M. R., and R. G. Jaeger. 1998. Competition leads to an extinction-prone species of salamander: Interspecific territoriality in a metapopulation. Ecology **79**:2494-2502.
- Gruner, D. S. 2003. Regressions of length and width to predict arthropod biomass in the Hawaiian Islands. Pacific Science **57**:325-336.
- Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A metaanalysis of competition in field experiments. American Naturalist 140:539-572.
- Hairston, N. G. 1981. An experimental test of a guild salamander competition. Ecology **62**:65-72.
- Holbrook, S. J., and R. J. Schmitt. 1995. Compensation in resource use by foragers released from interspecific competition. Journal of Experimental Marine Biology and Ecology **185**:219-233.

Holdridge, L. R. 1967. Life zone ecology, San Jose, Costa Rica.

- Hubbell, S. P. 2001. The unified neutral theory of species abundance and diversity. Princeton University Press, Princeton, New Jersey.
- Karr, J. R. 1971. Ecological, behavioral, and distributional notes on some central Panama birds. Condor **73**:107-111.
- Leigh, E. G., Jr. 1999. Tropical forest ecology. Oxford University Press, New York, New York.
- Leigh, E. G., Jr. 1982. Introduction: the significance of population fluctuations. Pages 435-440 *in* E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D.C.
- Levings, S. C., and D. M. Windsor. 1982. Seasonal and annual variation in litter arthropod populations. *In* E. G. Leigh, Jr. And D. M. Windsor, editors. The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes. Smithsonian Inst. Press, Washington, D. C.

- Lotka, A. J. 1932. The growth of mixed populations: two species competing for a common food supply. Journal of the Washington Academy of Sciences 22:461-469.
- MacArthur, R. H. And R. Levins. 1967. Limiting similarity convergence and divergence of coexisting species. American Naturalist **101**:377-385.
- MacArthur R. H. 1958. Population ecology of some warblers in northeastern coniferous forests. Ecology **39**:599-619.
- MacNally, R. C. 1983. On assessing the significance of interspecific competition to guild structure. Ecology **64**:1646-1652.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Martin, P. R. And T. E. Martin. 2001. Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. Ecology **82**:189-206.
- May, R. M., and R. H. Macarthur. 1972. Niche overlap as a function of environmental variability. Proceedings of the National Academy of Science (USA) **69**:1109-1113.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs patterns and importance. Ecological Monographs **65**:21-74.
- Moore, R. P., and W. D. Robinson. 2004. Artificial bird nests, external validity, and bias in ecological field studies. Ecology **85**:1562-1567.
- Munday, P. L., G. P. Jones, and M. J. Caley. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology 82:2177-2189.
- Oaten, A., and W. W. Murdoch. 1975. Switching, functional response, and stability in predator-prey systems. American Naturalist **109**:299-318.
- Paine, R. T. 1992. Food-web analysis through field measurement of per-capita interaction strength. Nature **355**:73-75.
- Palmer, T. M., M. L. Stanton, and T. P. Young. 2003. Competition and coexistence: Exploring mechanisms that restrict and maintain diversity within mutualist guilds. American Naturalist 162:S63-S79.
- Rastetter, E. B., and G. I. Ågren. 2002. Changes in individual allometry can lead to species coexistence without niche separation. Ecosystems 5:789-801.
- Relyea, R. A. 2000. Trait-mediated indirect effects in larval anurans: Reversing competition with the threat of predation. Ecology **81**:2278-2289.

- Relyea, R. A., and K. L. Yurewicz. 2002. Predicting community outcomes from pairwise interactions: integrating density- and trait-mediated effects. Oecologia 131:569-579.
- Rettenmeyer, C. W. 1963. Behavioral studies of army-ants. University of Kansas Science Bulletin 44:281-465.
- Robertson, D. R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology 77:885-899.
- Robinson, W. D. 1999. Long-term changes in the avifauna of Barro Colorado Island, Panama, a tropical forest isolate. Conservation Biology **13**:85-97.
- Robinson, W. D. 2001. Changes in abundance of birds in a Neotropical forest fragment over 25 years: a review. Animal Biodiversity and Conservation 24:51-65.
- Robinson, W. D., J. D. Brawn, and S. K. Robinson. 2000. Forest bird community structure in central Panama: Influence of spatial scale and biogeography. Ecological Monographs **70**:209-235.
- Rodda, G. H., and K. Dean-Bradley. 2002. Excess density compensation of island herpetofaunal assemblages. Journal of Biogeography **29**:623-632.
- Roughgarden, J. 1974. Species packing and the competition function with illustrations from coral reef fish. Theoretical Population Biology 5:163-186.
- Sandlin, E. A. 2000. Foraging information affects the nature of competitive interactions. Oikos **91**:18-28.
- Schmitt, R. J., and S. J. Holbrook. 1990. Population responses of surfperch released from competition. Ecology **71**:1653-1665.
- Schneirla, T. C. 1933. Studies on army ants in Panama. Journal of Comparative Psychology 15:267-299.
- Schneirla, T. C. 1949. Army-ant life and behavior under dry-season conditions. Bulletin of the American Museum of Natural History **94**:7-81.
- Schneirla, T. C. 1971. Army ants: a study in social organization. W. H. Freeman, San Francisco, California.
- Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist **122**:240-285.
- Sieving, K. E. 1992. Nest predation and differential insular extinction among selected forest birds of Central Panama. Ecology **73**:2310-2328.

SPSS. 2003. SPSS statistical software. Eleventh edition.

- Styrsky, J. N. 2003. Life-history evolution and population dynamics of a Neotropical forest bird (*Hylophylax naevioides*). Ph.D. Dissertation. University of Illinois, Urbana, IL.
- Swartz, M. B. 1997. Behavioral and population ecology of the army and *Eciton burchelli* and ant-following birds. Ph.D. Dissertation. University of Texas, Austin.
- Terborgh, J. 1983. Five new world primates: a study in comparative ecology. Princeton University Press, Princeton, New Jersey.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey.
- Walsberg, G. E. 1983. Avian ecological energetics. Pages 161-220 in D. S. Farner, J. R. King, and K. C. Parkes, editors. Avian Biology. Academic Press, New York.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083-1100.
- White, G. C. 1996. NOREMARK: population estimation from mark-resighting surveys. Wildlife Society Bulletin 24:50-52.
- Wiens, J. A. 1992a. The ecology of bird communities volume 1: Foundations and patterns. Harvard University Press, Cambridge.
- Wiens, J. A. 1992b. The ecology of bird communities volume 2: Processes and variations. Harvard University Press, Cambridge.
- Williams, J. B., and G. O. Batzli. 1979. Competition among bark-foraging birds in Central Illinois Experimental-Evidence. Condor 81:122-132.
- Willis, E. O. 1967. The behavior of bicolored antbirds. University of California Publications in Zoology **79**.
- Willis, E. O. 1972. The behavior of spotted antbirds. Ornithological monographs 10. The American Ornithologists' Union, Washington, D.C.
- Willis, E. O. 1973. The behavior of ocellated antbirds. Smithsonian Contributions to Zoology 144.
- Willis, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecological Monographs 44:153-169.
- Willis, E. O. 1983. Longevities of some Panamanian forest birds, with note of low survivorship in old spotted antbirds (Hylophylax-Naevioides). Journal of Field Ornithology 54:413-414.

- Willis, E. O., and E. Eisenmann. 1979. A revised list of birds of Barro Colorado Island, Panama. Contributions to Zoology **291**.
- Willis, E. O., and Y. Oniki. 1978. Birds and army ants. Annual Review of Ecology and Systematics 9:243-263.
- Willson, S. K. 2004. Obligate army-ant-following birds: a study of ecology, spatial movement patterns, and behavior in Amazonian Peru. Ornithological Monographs
 53. The American Ornithologists' Union, Washington, D.C.
- Wright, S. J., C. Carrasco, O. Calderon, and S. Paton. 1999. The El Niño Southern Oscillation, variable fruit productions, and famine in a tropical forest. Ecology 80:1632-1647.
- Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology **69**:508-515.

		Occurre	nce at E. burch	<i>ielli</i> swarms	per season §
Species †	$Mass(g) \ddagger \overline{F}$	Barro Co	lorado Island	Soberania I	National Park
· · · · · · · · · · · · · · · · · · ·		Wet	Dry	Wet	Dry
Tinamidae					
Tinamus major	1160		VR		VR
Accipitridae					
Leucopternis semiplumbea	278	VR	VR		
Leucopternis albicollis	736	VR			
Harpagus bidentatus fasciatus	185	VR	_		
Accipiter superciliosus fontanieri	100				VR
Falconidae					·
Micrastur ruficollis interstes	179	VR			
Micrastur semitorquatus naso	650			VR	VR
Cuculidae					
Neomorphus geoffroyi salvini	340			U	U
Momotidae					
Momotus momota	105			VR	VR
Baryphthengus martii	162	R	R	R	R
Electron platyrhynchum	62	R	R	R	R
Bucconidae					
Malacoptila panamensis	44	R	R	R	R
Furnariidae					
Philydor fuscipennis				VR	VR
Xenops minutus	11	VR			
Sclerurus guatemalensis	34	VR	VR	VR	VR
Dendrocolaptidae					
Dendrocincla fuliginosa	41	С	С	С	С
Dendrocincla homochroa	41				VR
Deconychura longicauda	24				VR
Clyphorhynchus spirurus	15			VR	VR
Dendrocolaptes certhia	68		VR	U	U
Xiphyorhynchus guttatus	47	С	С	С	С
Xiphorhynchus lachrymosus	51	R	R	R	R

Appendix 2.1: Frequency of species observed at or near ant swarms on Barro Colorado and in Soberania during both wet and dry seasons.

Appendix 2.1: contined

		Occurrenc	e at E. burch	<i>elli</i> swarms p	<i>elli</i> swarms per season §		
Species †	Mass(g) ‡ I	Barro Colo	orado Island	Soberania N	lational Park		
		Wet	Dry	Wet	. Dry		
Thamnophilidae							
Cymbilaimus lineatus	37			VR	VR		
Thamnophilus punctatus	22	С	С	. C	С		
Myrmotherula fulviventris	10	$^{\circ}$ U	U	R	R		
Myrmotherula axillaris	8	U	U	R	R		
Microrhopias quixensis	8	U	U	R	R		
Myrmeciza exsul	27	С	С	VR	,		
Hylophylax naevioides	17	Α	А	С	С		
Gymnopithys leucaspis	30	А	А	А	А		
Phaenostictus mcleannani	51			С	С		
Formicarius analis	57			VR	VR		
Hylopezus perspicillatus	42			VR	VR		
Pipridae							
Manacus vitellinus	17 ·		•	R	R		
Pipra mentalis	15	R	R	R	R		
Troglodytidae							
Henicorhina leucosticta	17 .			R	R		
Cyphorhinus phaeocephalus	25			U	U		
Sylviinae							
Microbates cinereiventris	12	R ·	R				
Polioptila plumbea	7	VR	VR	,			
Thraupinae			1		• •		
Eucometis penicillata	30	С	C	U	<u>U</u>		

† Species names and sequence follow Ridgely and Gwynne (1989)

‡ Mass (g) follow Robinson et al. (2000)

§ VR: very rare, only a few sightings; R: rare, sightings < 25% of swarms; U: uncommon, sightings 20-50% of swarms; C: common, > 75% sightings in small numbers; A: abundant, always present in large numbers

	<u> </u>	F	df	P
MANOVA				
	Site	56.42	4, 186	<0.001
	Season	10.94	4, 186	<0.001
	Site X Season	6.94	4, 186	<0.001
ANOVA				
Spotted antbirds				
	Site	66.10	1, 189	<0.001
	Season	19.53	1, 189	< 0.001
	Site X Season	5.60	1, 189	0.019
Bicolored antbirds				
	Site	16.56	1, 189	<0.001
	Season	7.00	1, 189	0.009
	Site X Season	3.20	1, 189	0.075
Ocallated anthirds				
Ocentated antonus	Site	134.44	1, 189	<0.001
	Season	7.01	1, 189	0.009
	Site X Season	7.01	1, 189	0.009
				,
Other	Site	3.95	1, 189	0.048
	Season	2.32	1, 189	0.130
	Site X Season	3.79	1, 189	0.053

Appendix 2.2: Results of two-way MANOVA for overall effects of site and season on the individuals per swarm at ant swarms of four main groups: spotted, bicolored, ocellated, and all other antbirds and between subject effects from two-way ANOVA.

		F	df	Р
MANCOVA				
	Site	2.18	2, 151	0.117
	Season	1.38	2, 151	0.256
	Site X Season	1.32	2, 151	0.271
ANCOVA				
Small Prey				
	Site	3.96	1, 152	0.048
	Season	2.24	1, 152	0.136
	Site X Season	0.10	1, 152	0.753
Large Prey				
	Site	0.05	1, 152	0.832
	Season	1.05	1, 152	0.306
	Site X Season	2.24	1, 152	0.137

Appendix 2.3: Results of two-way MANCOVA for foraging rates of bicolored antbirds at ant swarms and two-way ANCOVA results of the response variables, small and large prey. Factors: site and season; Covariate: observation length.

U

		F	df	Р
MANCOVA				s
	Site	4.58	2, 151	0.012
	Season	4.59	2, 151	0.012
	Site X Season	0.32	2, 151	0.725
ANCOVA				
Hops				
	Site	3.01	1, 152	0.085
	Season	6.36	1, 152	0.013
	Site X Season	0.46	1, 152	0.499
Flights				
	Site	8.66	1, 152	0.004
	Season	6.13	1, 152	0.014
	Site X Season	0.42	1, 152	0.520

Appendix 2.4: Results of two-way MANCOVA for main activity rates of bicolored antbird, and the effects of the response variables hops and flights, at ant swarms by two-way ANCOVA. Factors: site and season; Covariate: observation length.

CHAPTER 3: GENERAL CONCLUSIONS

Summary of thesis

My primary objective in this study was to test if interspecific competition maintains the structure of a tropical avian guild, either through direct or indirect interactions. I explored both numerical and behavioral compensatory responses, several generations following the loss of a dominant competitor from a specialized guild of antfollowing birds. I document three new results suggesting that competition influences the structure of this avian guild.

First, following the sustained absence of a dominant competitor, the ocellated antbird, the remaining guild members completely compensated in biomass density. Although data on population abundances of this guild were only collected intermittently before my study, evidence of density compensation only became apparent following complete population turnover. Second, compensatory use of microhabitat (ant swarms) was also observed. Unexpectedly, the subordinate spotted antbird exhibited the largest compensatory response. Spotted antbirds doubled in number at ant swarms on Barro Colorado Island, compensating for the relative proportion of missing biomass from ocellated antbirds. Bicolored antbirds, which are dominant to spotted antbirds, did not differ in rates of foraging, aggression with conspecifics, and activity levels at ant swarms. Rates of aggression between bicolored and spotted antbirds, however, increased. Ocellated antbirds have rarely been observed to directly supplant spotted antbirds. Thus, limited swarm use by spotted antbirds likely resulted from avoidance of ocellated antbirds by spotted antbirds, and indirect competitive pressure by ocellated antbirds,

mediated through their direct interactions with bicolored antbirds. Third, life-history characteristics such as limited mobility during the breeding season, in addition to seasonally varying levels of competition for resources, influenced the interaction strength between guild members and the use of resources.

ć

Avenues for future research

Spatial dynamics

Often, population responses are coupled to shifts in territory sizes in birds (Newton 1998) but less is known about how shifts in abundance affect home range sizes. Indeed, my conclusion that spotted antbirds increased in abundance on Barro Colorado since the 1990s was based on territory size (D. Robinson, *personal communication*). However, I observed pairs of spotted antbirds following army ant swarms for several consecutive days, far outside of what would be considered territorial boundaries by Willis' (1972) criteria. For birds or species that hold loose territories, such as obligate ant-followers, little is known about how density or behavioral compensation may influence space use. Home range sizes of obligate ant-followers in Cocha Cashu, Peru, also increased during an early rainy season. In that case, flooding of the forest floor reduced the area that was suitable for foraging (Willson 2004).

An expansion in home range by spotted antbirds on Barro Colorado as a result of behavioral compensation leads to another interesting question. Increased foraging at ant swarms by spotted antbirds on Barro Colorado, and its corollary increased distances traveled to follow ant swarms, challenges the notion that these birds are only facultative ant-followers (i.e., they forage at ant swarms only when passing through their territory).
If spotted antbirds on Barro Colorado begin to more obligately follow ant swarms, will their territory structure break down as the need to hold loose territories increases in order to decrease agonistic aggression at ant swarms with conspecifics? A shift in territoriality could affect population abundances. Greenberg and Gradwohl (1986) hypothesized that year-round territoriality is one proximate cause of population stability in tropical birds. Support for this hypothesis was provided by Willson (2004), who documented population declines in three non-territorial ant-following birds, while population of strictly territorial species remained stable.

Role of competition in species guilds

The idea of competition as a driving force behind community structure currently receives little focus because of the past criticism that many studies testing the idea lacked alternative hypotheses (Wiens 1992). More recent experimentally rigorous studies nevertheless have supported the notion of the importance of competition to guild structure through observed density compensation following species removals: particularly in damselfish (Robertson 1996), surfperches (Schmitt and Holbrook 1990), herpetofaunal assemblages (Rodda and Dean-Bradley 2002). These studies are further supported by this study on a tropical avian guild of ant-followers. In a study of gobies (*Gobiodon*), however, a variety of mechanisms in addition to competition were proposed to affect guild structure (Munday et al 2001). Competition is also thought to impact local community structure in less isolated systems. Species compensation, rather than density compensation, was observed in a species rich guild of desert rodents following local extinction of guild members (Goheen et al. 2005).

64

We thus have evidence of competition in a variety of taxa and environmental settings. Despite this experimental evidence for the importance of competition in these particular cases, we lack predictive power for when and what guilds might experience competition as a structuring factor, and to what degree. For example, are other tropical guilds influenced by competitive interactions similarly to the ant-followers and can we predict that the same pattern may not be revealed in temperate communities? Does the degree of specialization found within communities influence the nature of competitive forces? How does climatic stability and fluctuations in predators or parasites influence interactions among species? These questions will require a systematic body of work, including long-term observations and experimental approaches in a variety of environments and species guilds. We may then begin to predict the compensatory responses and lasting impacts in communities following periodic disturbances or species loss.

LITERATURE CITED

Goheen, J. R., E. P. White, S. K. M. Ernest, and J. H. Brown. 2005. Intra-guild compensation regulates species richness in desert rodents. Ecology 86:3 567-573.

Greenberg, R. and J. Gradwohl. 1986. Constant density and stable territoriality in some tropical insectivorous birds. Oecologia **69**:618-625.

Munday, P. L., G. P. Jones, and M. J. Caley. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. Ecology **82**:2177-2189.

Newton, I. 1998. Population limitation in birds. Academic Press. New York, New York.

Robertson, D. R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology 77:885-899.

Rodda, G. H., and K. Dean-Bradley. 2002. Excess density compensation of island herpetofaunal assemblages. Journal of Biogeography **29**:623-632.

Schmitt, R. J., and S. J. Holbrook. 1990. Population responses of surfperch released from competition. Ecology **71**:1653-1665.

Wiens, J. A. 1992. The ecology of bird communities volume 2: Processes and variations. Harvard University Press, Cambridge.

Willis, E. O. 1972. The behavior of spotted antbirds. Ornithological monographs 10. The American Ornithologists' Union, Washington, D.C.

Willson, S. K. 2004. Obligate army-ant-following birds: a study of ecology, spatial movement patterns, and behavior in Amazonian Peru. Ornithological Monographs
53. The American Ornithologists' Union, Washington, D.C.