

BEHAVIORAL ECOLOGY OF AMAZONIAN MIXED-SPECIES FLOCKS

By

Sean M. Williams

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Zoology–Doctor of Philosophy
Ecology, Evolutionary Biology, and Behavior–Dual Major

2017

ABSTRACT

BEHAVIORAL ECOLOGY OF AMAZONIAN MIXED-SPECIES FLOCKS

By

Sean M. Williams

Amazonian mixed-species flocks of birds are remarkable by virtue of their strength of interspecific association. In these flocks, individuals of different species associate with each other for the duration of their lives, i.e. during all daylight hours, 365 days of the year across many years. These obligate relationships provide a unique opportunity to study the behavioral ecology of dependent interspecific relationships. I break my thesis into three chapters. First, I ask whether the relationship between two obligatorily flocking species (nuclear antshrike and antwren species) is symmetrical and whether transient species (non-obligate flocking species) are equally attracted to the nuclear species. Are the transient species equally attracted to the two nuclear species? And are the two nuclear species equally attracted to each other? This first question was necessary to ask before my other questions because I needed to know which species are following other species and which species are being followed. Then, I ask whether the behavior of a single species (the same antshrike species I determined was mostly being followed in the first question) can predict the space use of the whole flock and what environmental and behavioral variables explain the space use. Finally, I ask whether a particular context-dependent vocalization of the antshrike might serve as a mechanism of interspecific cohesion of the flock. After having spent hundreds of hours studying the space use of flocks in order to define the spatial distribution of flocks within their territories, this last question followed naturally since the mechanism of interspecific cohesion was central to the coordination of the movement of the flock through space.

In resident Amazonian mixed-species flocks, the pattern of attraction of transient species to nuclear antshrikes and antwrens, and the pattern of heterospecific attraction between the nuclear species, are undocumented. Patterns of attraction can help elucidate the nature of interspecific relationships, i.e. whether they are mutualistic, commensal, or parasitic. We played antshrike and antwren vocalizations to flocks and observed how many transient species approached the playbacks, whether antshrikes and antwrens were attracted to each others' playbacks, and how strongly they responded to the playbacks. More transient species were attracted to antshrike vocalizations than antwren vocalizations and more transient species were attracted to antwren than control vocalizations. Antshrikes and antwrens approached each others' playback significantly more often than they approached control playbacks; antwrens responded significantly more strongly to antshrike vocalizations than antshrikes did to antwren vocalizations. The primary reason transients are attracted to antshrikes may be the reliable alarm calling of the antshrikes, and the primary reason transient species are attracted to antwrens may be that antwrens serve as an indicator of a flock. Finally, antshrikes and antwrens likely confer benefits to each other, but those benefits may not be symmetrical.

Investigating the drivers of space use is critical for understanding the ecology of a species. The drivers of space use patterns of multi-species groups have been studied seldom, although many avian species participate in mixed-species flocks throughout the world. We characterized the space use patterns of mixed-species flocks in Amazonian Peru and investigated the drivers of those patterns. We predicted that foraging and anti-predation behavior, i.e. attack rate, vigilance rate, and surrounding vegetation density of the "leader" Dusky-throated Antshrike (*Thamnomanes ardesiacus*) would explain the space use patterns of the whole flock.

ACKNOWLEDGMENTS

Staff of the Asociación para la Conservación de la Cuenca Amazónica were essential in providing a comfortable place to live during the study. I thank the Dirección de Gestión Sostenible del Patrimonio de Fauna Silvestre of Peru for providing the permit (N° 150-2015-SERFOR-DGGSPFFS) necessary for this study. Fernando A. Pratolongo assisted in submitting the permit.

The National Science Foundation provided critical support through a graduate research fellowship. The Integrative Biology (formerly Zoology) Department, the Center for Latin American and Caribbean Studies, the Graduate School, and the Ecology, Evolutionary, Biology and Behavior Program at Michigan State University provided necessary financial support.

My advisor, Catherine A. Lindell has been my mental pillar tirelessly and pivotally. She has spent countless hours meeting with me, reading drafts, and even traveling with me to Peru. She has paid critical attention to the development of my scientific judgment and writing, which immeasurably has advanced my abilities as a coherent scientist. She has trusted my judgment on many occasions, for which I am extremely grateful and honored.

My graduate committee met with me multiple times over the years to provide critical insight and direction in the development of my thesis. Willingly, they have provided additional assistance outside of committee meetings despite their demanding schedules, and I thank Tom Getty, Peggy Ostrom, Bill Porter, and my advisor Catherine Lindell.

The remote jungle can be lonely, and so I thank especially Dara Adams, Gordon Ulmer, Pascual Flores, Tuco Yupanqui, Tim Perez, Patrick Campbell, Gideon Erkenwick, and Mini

Watsa for numerous lively dinner table discussions over the years. CICRA became a warm place in my heart in large part due to my friends' constant comraderie, eye-opening conversations, and mutual, sibling-like teasing.

Finally, my wife, Chloe Williams, has supported me 100% through and through, even when I was absent for several months on five separate occasions. She has always held a good temperament in sending me off to the jungle or happily welcoming me back home, despite sometimes shedding some tears on both occasions. She has read proposal drafts, driven me to the airport when I almost missed a flight, and travelled twice to Peru with me to explore the rainforest; she carried a great big smile through it all because she wanted to do these things for me. For this, I cannot express enough gratitude.

TABLE OF CONTENTS

LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
Chapter 1: Nuclear species in Peruvian mixed-species flocks are differentially attractive to transient species and to each other.....	
transient species and to each other.....	1
INTRODUCTION.....	1
METHODS.....	4
Study area.....	4
Flocks.....	4
Playback stimuli.....	5
Playback experiments.....	6
Statistical analyses.....	7
RESULTS.....	8
DISCUSSION.....	9
ACKNOWLEDGMENTS.....	14
LITERATURE CITED.....	15
Chapter 2: An environmental cue perceived by a single species explains the space use patterns of mixed-species flocks in Amazonian Peru.....	
patterns of mixed-species flocks in Amazonian Peru.....	21
INTRODUCTION.....	21
METHODS.....	23
Study area.....	23
Behavioral observations.....	24
Statistical analyses.....	25
RESULTS.....	27
DISCUSSION.....	29
LITERATURE CITED.....	33
Chapter 3: A context-specific vocalization serves as a mechanism of interspecific cohesion in mixed-species flocks.....	
cohesion in mixed-species flocks.....	40
INTRODUCTION.....	40
METHODS.....	42
Study area.....	42
Behavioral observations.....	42
Statistical analyses.....	45
RESULTS.....	45
DISCUSSION.....	48
LITERATURE CITED.....	52

LIST OF TABLES

Table 1.1. Parameter estimates of a generalized linear mixed model predicting the number of transient species attracted to the playback by playback treatment.....	8
Table 2.1. Analyses included observations from the four most common species found in three understory flocks at Los Amigos Biological Station, Madre de Dios, Peru in 2014.....	27
Table 2.2. Results of model selection for the ten models with the smallest ΔAIC . The models relate behavioral variables of individual flock members to the space use of the entire flock. The surrounding vegetation densities (veg), attack rates (att), and vigilance rates (vig) of Dusky-throated Antshrikes (DTAN), Bluish-slate Antshrikes (BSAN), White-flanked Antwrens (WFAN), and Long-winged Antwrens (LWAN) were added step-wise to a basal model with no behavioral variables. We ΔAIC as the minimum AIC subtracted from the AIC of the corresponding model; K is the number of included parameters; and w is the normalized model likelihood (Burnham and Anderson 2002).....	28
Table 3.1. Flight calls are almost always associated with flight and perched calls with being perched (Fisher's exact test: $df = 1$, $\chi^2 = 502$, $P < 0.001$).....	45
Table 3.2. Model results of the effect of the number of antshrike flight calls on the latency for an antwren species to fly in the direction of an antshrike. The z statistic is the Wald test, which tests whether the effect is 0.....	48

LIST OF FIGURES

Figure 1.1. Significantly more transient species were attracted to antshrike playback treatment than to the antwren treatment, which attracted significantly more transient species than the antthrush treatment. The thick line within the boxes indicates the mean number of species/individuals that approached, the bottom and top edges of the boxes indicate the first and third quartiles, and the whiskers indicate the 1.5x interquartile ranges. The “X” over BFAN indicates the mean, which lies outside the box. BFAN = Black-faced Antthrush, control treatment; DTAN = Dusky-throated Antshrike; LWAN = Long-winged Antwren.....	9
Figure 1.2. The four most common transient species to be attracted to the playback treatments were White-flanked Antwren, Red-crowned Ant-Tanager, Wedge-billed Woodcreeper, and White-eyed Antwren. BFAN = Black-faced Antthrush, control treatment; DTAN = Dusky-throated Antshrike; LWAN = Long-winged Antwren.....	10
Figure 1.3. Antshrikes and antwrens approached each others’ playback for a similar number of trials, but approached each others’ playback significantly more than antthrush playback (control). BFAN = Black-faced Antthrush, control treatment; DTAN = Dusky-throated Antshrike; LWAN = Long-winged Antwren.....	11
Figure 2.1. Home ranges (light gray plus dark gray areas), high use areas (dark gray areas), and low use areas (light gray areas) of three mixed species flocks (A, B, and C) at Los Amigos Biological Station, Peru in May-August 2014. The double black lines indicate a spatial gap of 650 m.....	29
Figure 3.1. The number of harsh calls given per flight increases with the distance flown (linear regression: $t = 9.33$, $df = 183$, $P < 0.001$). One minute after encountering an antshrike in Jun-Aug 2015-2016 at Los Amigos Biological Station, the number of calls in the first harsh call bout and the distance of the flight were recorded ($n = 185$). Distance was estimated visually after practice and validation of estimates. No antshrike was sampled more than once per day.....	44
Figure 3.2. A) Harsh calls were characterized by a quick (0.1 s), high-pitched “sping!” The harsh call starts at a low frequency (2 kHz), and increases sharply until it levels off at 7.5 kHz, and then decreases back down to 2 kHz, first sharply, then slowly. Sometimes the call is given at lower amplitude, but still follows the same pattern otherwise. B) Soft calls were characterized by a low-pitched (1-3.5 kHz), descending “bowr.” The soft call is a rapid trill (0.3 s) of about 30 syllables, which are short (0.01 s) and quickly rise, then fall. Over the entire call, each syllable of the trill begins at a slightly lower pitched than the last syllable, resulting in what sounds like running a finger over a comb. The harsh and soft calls were identified by ear and I became familiar with them over several field seasons. Recordings were made with a Roland R-26 recorder and Sennheisher ME 66 directional microphone with a sampling rate of 96 kHz and 24-bit waveform file format. These images were produced using the Raven Lite software (2007)...	46

Figure 3.3. The latency to fly toward the antshrike for the flight call treatment was significantly shorter than the perched call treatment in all three antwren species (GRAN = Gray Antwren, LWAN = Long-winged Antwren, WFAN = White-flanked Antwren). The latencies for the flight call treatment for Long-winged and White-flanked Antwrens was significantly shorter than the control treatments.....47

Chapter 1: Nuclear species in Peruvian mixed-species flocks
are differentially attractive to transient species and to each other

INTRODUCTION

Hundreds of species throughout the world participate in mixed-species flocks, defined as ≥ 2 species moving together for ≥ 5 minutes without a concentrated feeding source (Stotz 1993, Greenberg 2000, Cordeiro et al. 2015). The majority of research on mixed-species flocks has focused on passerine and near-passerine flocks in forests, where *nuclear species* almost always are found in flocks, and rarely away from flocks, and *transient species* temporarily join flocks (Jullien and Thiollay 1998, Sridhar et al. 2009). Typically, the nuclear species serve as leaders of the flock, i.e. they guide the flock's movements, and transient species follow the nuclear species (Hutto 1994). The formation of a flock each morning and cohesion of the flock likely depends on the presence of the nuclear species (Munn and Terborgh 1979, Hino 1998, Goodale and Kotagama 2005a).

At our field site in southern Amazonian Peru, the Dusky-throated Antshrike (*Thamnomanes ardesiacus*; hereafter, “antshrike”) and the Long-winged Antwren (*Myrmotherula longipennis*; hereafter, “antwren”) are nuclear flocking species. Each flock contains a breeding pair and sometimes fledglings of each of the nuclear species (Munn and Terborgh 1979). They are found in nearly all understory flocks, and almost never are they found away from flocks (Munn 1985, Jullien and Thiollay 1998, Martinez and Zenil 2012). Previously, antshrikes and antwrens have been placed into the dichotomous categories of leaders and followers, respectively (Terborgh et al. 1990, Martinez and Zenil 2012). Terborgh and Munn (1979) observed that the “antshrikes appeared to direct the flock's movements... one or another of these birds moved to and called from a spot 20-30 m from the current flock position. Other flock members almost invariably

followed these leads.” We sought to characterize the relationships of nuclear antshrikes and antwrens quantitatively by measuring the frequency of attraction to heterospecific playback (Hutto 1994, Goodale and Beauchamp 2010). The attraction patterns to heterospecific playback of the nuclear species should indicate whether the leader and follower roles of the nuclear species are changeable or rigid.

Transient species, which temporarily join and exit the flock, include woodcreepers, the Tawny-crowned Greenlet (*Tunchiornis ochraceiceps*), and other antbirds (Munn and Terborgh 1979). The nuclear and transient species composition of a flock, and where a species falls on the nuclear-transient spectrum, varies from flock to flock and geographically (Munn and Terborgh 1979, Gradwohl and Greenberg 1980, Jullien and Thiollay 1998). We addressed two facets of flock cohesion: 1) Are the transient species equally attracted to the two nuclear species? and 2) Are the nuclear species equally attracted to each other? Investigating these two questions helps to elucidate the nature of the relationship between the nuclear species and the transient species, and between the two nuclear species. If a species is attracted to another species, benefits of association likely exist. If a species is not attracted to another species, it is unlikely any benefit of association exists (Goodale and Kotagama 2005a, Goodale et al. 2011, Cordeiro et al. 2015).

Nuclear species commonly give alarm calls on which other species eavesdrop (Goodale and Kotagama 2005b, Goodale and Kotagama 2008). As a sally-gleaner amongst sparse vegetation, antshrikes search for distant (1-5 m) prey. They detect predators earlier than other flocking species and give loud alarm calls in the presence of a predator (Schulenberg 1983, Martinez and Zenil 2012). Antwrens and transient species may be attracted to antshrikes due to this anti-predation benefit (Jullien and Thiollay 1998). Antwrens, on the other hand, do not detect predators earlier than other flocking species or give loud alarm calls (Jullien and Thiollay 1998,

Martinez and Zenil 2012). It is possible both antwrens and antshrikes confer anti-predation benefits to flocking species, through the many-eyes effect (Pulliam 1973, Ale and Brown 2007), the dilution effect (Ale and Brown 2007), and/or the selfish herd effect (Beauchamp 2012). Given the known benefit that antshrikes confer, i.e. alarm-calling, antshrikes may be more attractive to other species than the antwrens. It is possible that antshrikes (*Thamnomanes* spp.) gain foraging benefits by kleptoparasitizing antwrens, although kleptoparasitism has not been documented for our focal antshrike species, the Dusky-throated Antshrike (Munn 1986, Thiollay 2003, Martinez and Zenil 2012).

Because antshrikes and antwrens are almost always found together, it is unclear whether transient species are attracted to antshrikes, antwrens or both, and whether antshrikes and antwrens are attracted to each other. Transient species and antwrens are known to benefit from associating with antshrikes by eavesdropping on antshrikes' alarm calls (Munn 1986, Martinez et al. 2016); potential benefits received by transient species and antshrikes from the antwrens are not as obvious, but might include the aforementioned anti-predation effects (Martinez and Zenil 2012). Documentation of attraction patterns of transient species to nuclear species and nuclear species to each other will help to indicate the likely direction of benefits.

We aim to address the following questions: are transient species attracted to antshrikes, antwrens, or both? Are antshrikes and antwrens attracted to each other? We hypothesize that the antshrikes confer greater overall anti-predator benefits than antwrens to other flocking species. We recorded the loudsongs of Dusky-throated Antshrikes, Long-winged Antwrens, and Black-faced Antthrush (*Formicarius analis*) as a control species. We played the recordings to flocks to test the following predictions: 1) More transient species should approach antshrike playback than antwren playback. 2) Antwrens should approach antshrike playback for more playback trials than

antshrikes approach antwren playback. We also recorded attraction strength by measuring the latency in seconds to approach playback and the proximity in meters of a species' approach to the playback device.

METHODS

Study area

Data were collected at Los Amigos Biological Station, Madre de Dios, Peru (12° 34' 38" S, 70° 05' 06" W) in from May to July 2015 during the dry season. The field site lies at 300 meters above sea level, among 1500 km² of primary rainforest along two rivers. Understory mixed-species flocks containing antshrikes and antwrens are abundant and present year-round, and are easily found by listening for the nearly constant vocalizations of flock members. Based on our observations from 2012 to 2015, the territories of the flocks are stable, and neighboring flocks have relatively little overlapping area, consistent with previous work (Martinez and Gomez 2013).

Flocks

A flock was defined as a group of birds foraging, gleaning or sally-gleaning insects, and moving together, i.e. maintaining a distance of 10 m or less between species, for five or more minutes (Moynihan 1962, Stotz 1993).

Flocks typically were composed of at least a pair of Dusky-throated Antshrikes and a pair of Long-winged Antwrens. In addition, there were often a pair of White-flanked Antwrens (*M. axillaris*), *Epinecrophylla* antwrens, Wedge-billed (*Glyphorynchus spirurus*), Elegant (*Xiphorhynchus elegans*) and/or Buff-throated Woodcreepers (*X. guttata*), an Olive-backed Foliage-gleaner (*Automolus infuscatus*), a Tawny-crowned Greenlet (*Tunchiornis ochraceiceps*), and a Red-crowned Ant-Tanager (*Habia rubica*). Twenty-five different flocks were subject to

three different experimental treatments, resulting in 75 experimental trials. Flocks received each treatment one time, and a flock received treatments at least ten days apart. The sequence of treatments used with a particular flock was randomly selected. Individuals used in multiple experiments over time from one area are likely the same individuals because territories are spatially stable, flocks are not known to travel outside their normal territory, territories have relatively little overlapping area, and flock membership is stable (Munn and Terborgh 1979, Koloff and Mennill 2013, Martinez and Gomez 2013). Four color-banded flocks at this field site over three years support these observations. Therefore, we are confident that individuals were not exposed multiple times to the same playback treatment.

Playback stimuli

Songs of five Dusky-throated Antshrikes, five Long-winged Antwrens, and five Black-faced Antthrushes were recorded at Los Amigos Biological Station using a Roland R-26 recorder and Sennheiser ME 66 directional microphone with a sampling rate of 96 kHz and 24-bit waveform file format. Recordings used in trials had loud (90 dB at 1 m) focal individual vocalizations and negligible noise from non-flocking species. Frequencies lower than 200 Hz and higher than 20,000 Hz were filtered out, and focal individual vocalizations were amplified to 90 dB at 1 m using the Raven Lite software (Charif et al. 2006). A portable speaker with an MP3 player was used at maximum volume for playback of files converted to .mp3 format from .wav format. This volume level simulated real volume levels of the three species (Williams, pers. obs.). Recordings that were used on a focal flock came from an individual bird at least 400 m away since flock territory sizes are up to 400 m across (Jullien and Thiollay 1998, Martinez and Zenil 2012, Williams, pers. obs.). A distance of 400 m assured that flocks did not hear recordings from their own flocks.

The vocalizations of Dusky-throated Antshrike and Long-winged Antwren were included in the experiment since they are the most common nuclear species (Munn and Terborgh 1979, Thiollay 2003). Black-faced Antthrush was chosen as the control because it is an abundant species found in every territory of mixed-species flocks, yet it does not participate in mixed-species flocks. Therefore, its vocalization should have had no effect on the flocking behavior of antshrikes and antwrens.

Playback experiments

Experiments were performed at least 45 min after sunrise to allow for adequate lighting for data collection, until no more than 6 hr after sunrise. We began the experiments by walking transects along trails and listening for flocking species' vocalizations. Once a flock containing at least a Dusky-throated Antshrike and Long-winged Antwren was located, we placed a portable speaker with an MP3 player 30 m from the nearest bird in the flock, although we did not yet play any vocalizations. While standing 1 m from the speaker, we conducted a point count for ten minutes centered on the speaker, and observed whether the flock moved from their location. If the flock changed locations during the pre-playback period, the speaker was moved a distance of 30 m from the flock, and the pre-playback period was restarted. Distance was estimated visually after practice and validation of estimates.

Then, we played the song and calls of a Dusky-throated Antshrike, a Long-winged Antwren, or a Black-faced Antthrush (*Formicarius analis*, control) for 10 min. Throughout the playback experiment, recordings were played once every 30 sec, which is a realistic frequency of singing (Williams, pers. obs.). During these 10 min pre-playback and playback periods, we recorded the species and sex of each individual that entered a 20-m radius circle around the speaker and the following behavioral response variables: 1) latency to approach the speaker, and 2) the closest

distance approached to the speaker. Only the closest and first individual of a species to approach the speaker were used to investigate the latency to approach and the closest distance approached. Before the start of trials, only the presence of the Long-winged Antwren and Dusky-throated Antshrike were confirmed to be present in the flock. We did not attempt a full inventory of all species in a flock, which can range over 30 individuals of 15 or more species, prior to the experiment since species compositions of flocks change frequently and inventories require time-expensive visual and aural scrutiny.

Statistical analyses

Statistics were performed using the R Statistical Software version 3.2.3 and RStudio version 0.99.489 (R Core Team 2015; RStudio Team 2015). We used the lmer and glmer functions of the lme4 package for linear mixed models and generalized linear mixed models following recommendations of Bolker et al. (2009) and Bates et al. (2015). In analyses of the effects of playback treatment type on 1) the number of approaching transient species, 2) the latency of antshrikes and antwrens to approach the speaker, and 3) the closest distance antshrikes and antwrens approached to the speaker, we defined treatment as a fixed effect, and flock and the specific playback recording within a treatment as random effects. A Gaussian distribution in a linear mixed model described the closest distance approached to the speaker by treatment. Poisson distributions were used in GLMMs for describing the number of approaching transient species and the latency to approach the speaker. For the GLMMs, we report Wald Z test statistics since our data were not overdispersed, following recommendations of Bolker et al. (2009). We used Pearson's chi-square tests to compare the likelihoods of antshrikes and antwrens approaching the speaker for the different playback treatments.

Individuals of the same species are non-independent of each other because they travel together. Similarly, only the number of species to approach the speaker was considered, rather than the number of individuals. Because the antwrens and antshrikes only responded to the control treatment one to two times and this did not meet the necessary sample size for the tests, we excluded the antthrush control treatment from analyses of approach times and distances due to the low sample size. Values reported in results are means \pm standard errors.

RESULTS

The antshrike treatment attracted significantly more transient species (3.44 ± 0.50 species) than the antwren treatment (2.00 ± 0.54 species; $z = 2.45$; $P < 0.035$), which attracted significantly more species than the control (antthrush) treatment (0.56 ± 0.30 species; $z = 4.47$, $P = < 0.001$; Table 1.1; Fig. 1.1). The commonest transient species to approach the playback were Wedge-billed Woodcreeper, White-flanked Antwren, White-eyed Antwren, and Red-crowned Ant-Tanager (Fig. 1.2).

Treatment	Estimate	Standard error	95% confidence interval	z	P
Black-faced Antthrush	-1.19	0.363	(-1.98, -0.54)	-3.29	0.002
Dusky-throated Antshrike	2.06	0.343	(1.43, 2.80)	6.00	<0.001
Long-winged Antwren	1.58	0.353	(0.93, 2.33)	4.47	<0.001

Table 1.1. Parameter estimates of a generalized linear mixed model predicting the number of transient species attracted to the playback by playback treatment.

Antwrens approached antshrike playback significantly more often than control playbacks ($\chi^2 = 46.15$; $P < 0.001$). Antshrikes approached significantly more antwren trials than control trials ($\chi^2 = 19.10$; $P < 0.001$). Antshrikes and antwrens approached heterospecific (excluding control) playback for a similar number of trials ($\chi^2 = 2.17$; $P = 0.14$; Fig. 1.3).

Antwrens approached the speaker sooner ($z = 3.46$; $P < 0.001$) and more closely ($t = 1.90$; $P = 0.034$) for antshrike playback than antshrikes approached for antwren playback.

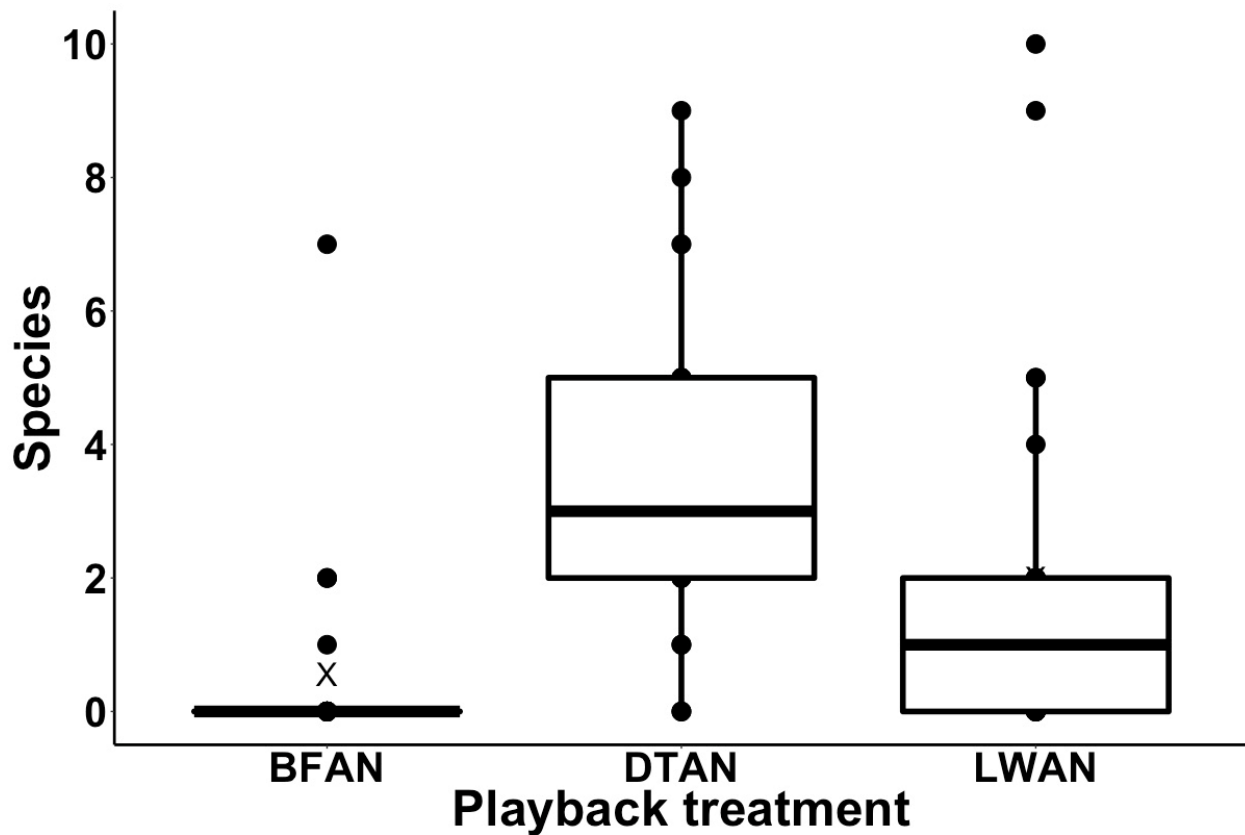


Figure 1.1. Significantly more transient species were attracted to antshrike playback treatment than to the antwren treatment, which attracted significantly more transient species than the antthrush treatment. The thick line within the boxes indicates the mean number of species/individuals that approached, the bottom and top edges of the boxes indicate the first and third quartiles, and the whiskers indicate the 1.5x interquartile ranges. The “X” over BFAN indicates the mean, which lies outside the box. BFAN = Black-faced Antthrush, control treatment; DTAN = Dusky-throated Antshrike; LWAN = Long-winged Antwren

DISCUSSION

As predicted, more transient species approached antshrike than antwren playback. These results are consistent with our hypothesis that antshrikes provide stronger anti-predation benefits than antwrens and so are more attractive to transient species. Antshrikes hyperopically scan vegetation for prey (Schulenberg 1983, Rosenberg 1993, Zimmer and Isler 2003). Common predators of flocking species are raptors, which ambush prey from a far distance (Robinson

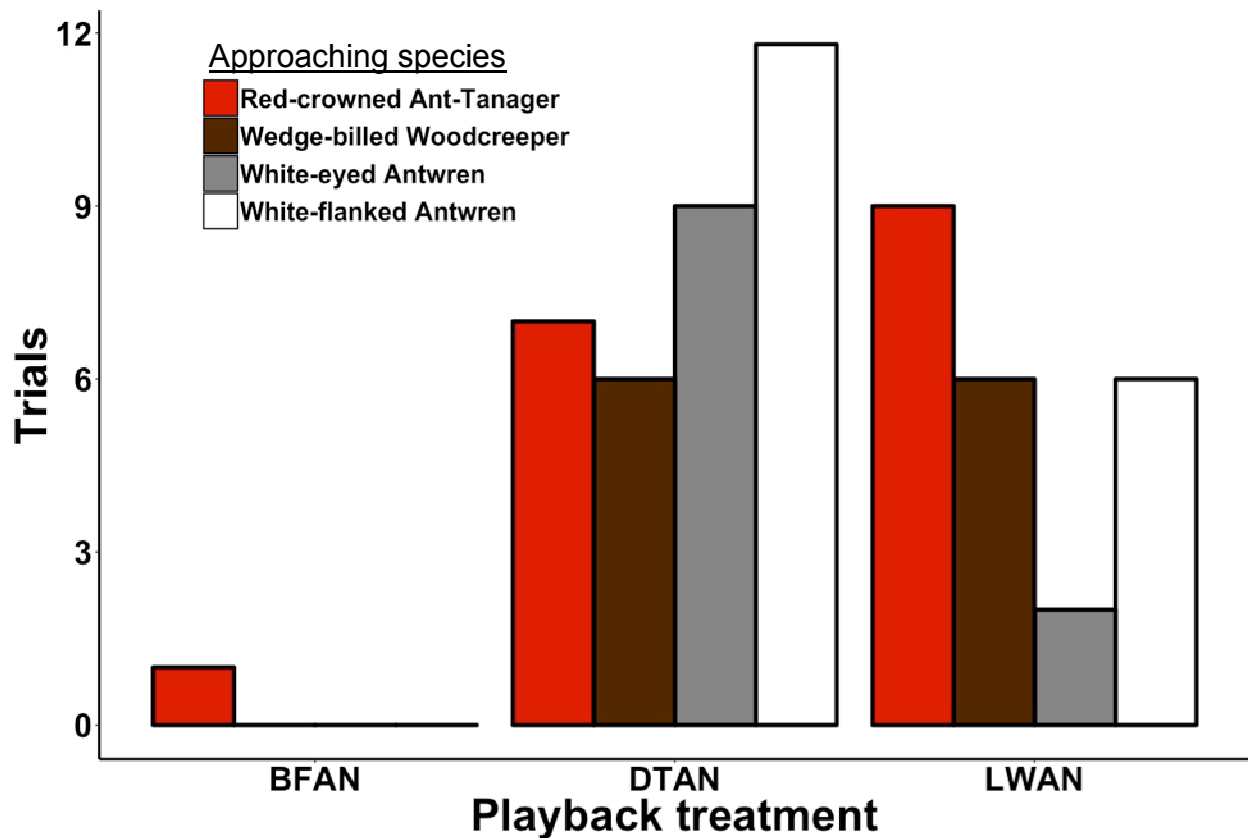


Figure 1.2. The four most common transient species to be attracted to the playback treatments were White-flanked Antwren, Red-crowned Ant-Tanager, Wedge-billed Woodcreeper, and White-eyed Antwren. BFAN = Black-faced Antthrush, control treatment; DTAN = Dusky-throated Antshrike; LWAN = Long-winged Antwren

1994). Hyperopic vision is effective at detecting distantly ambushing predators, and so antshrikes likely are predisposed to detect predators and give alarm calls (Jullien and Thiollay 1998, Martinez and Zenil 2012, Baigrie et al. 2014). Association with a flock containing antshrikes likely reduces predation risk for species that glean insects from nearby vegetation (Pomara et al. 2003, Sridhar et al. 2009, Martinez and Zenil 2012, Darrah and Smith 2013).

More transient species approached the speaker for antwren playback than control playback, and antshrikes approached for significantly more antwren playback trials than control trials. The attractiveness of antwren playback to antshrikes and transient species implies that antwrens

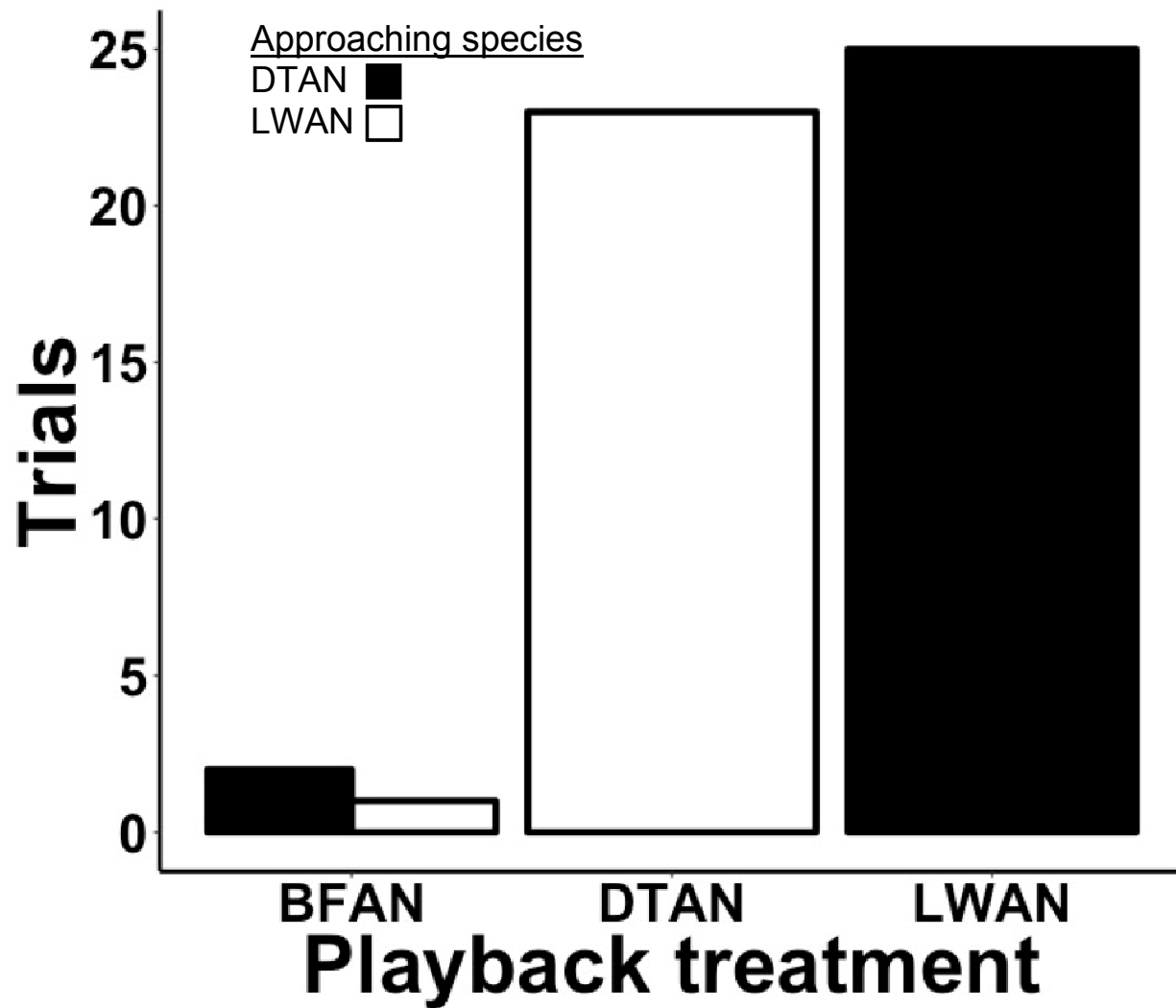


Figure 1.3. Antshrikes and antwrens approached each others' playback for a similar number of trials, but approached each others' playback significantly more than antthrush playback (control). BFAN = Black-faced Antthrush, control treatment; DTAN = Dusky-throated Antshrike; LWAN = Long-winged Antwren

confer some benefits to these other flocking species. At least four species of antwrens have been identified as nuclear species in Amazonian flocks (Munn and Terborgh 1979, Jullien and Thiollay 1998). Antwrens myopically search for gleanable insects from leaves and branches, and in contrast to antshrikes, antwrens do not give alarm calls (Munn and Terborgh 1979, Thiollay 2003). The nearly perpetual association of the antwrens with the antshrikes may have paved the way for transient species to use antwrens as an indicator of the presence of the beneficial alarm-calling of the antshrikes. The Orange-billed Babbler (*Turdoides rufescens*), for example, may serve as an indicator of a flock's presence (Goodale and Kotagama 2005a, b). Predation risk decreases by virtue of associating with other birds. Associating with more individuals may dilute predation risk (dilution effect), the scattering of many birds may inhibit a predator from focusing on a single individual (confusion effect), or the increase in the number of eyes may reduce the latency to become aware of a predator (many-eyes effect; Neill and Cullen 1974; Beauchamp 2003, Ale and Brown 2007, Beauchamp 2012). Additionally, associating with heterospecifics can lead to information transmission of foraging locations or other flock mates may flush prey (beater effect; Dolby and Grubb 2000, Hogstad 2009, Farine et al. 2015). Thus, in addition to antwrens serving as indicators of flock presence, they may provide these other benefits to other species.

Antshrikes approached antwren playback sometimes but not always (68% of trials), which suggests that context may influence heterospecific attraction for antshrikes. Antshrikes may gain foraging and anti-predatory benefits from flocking, and so temporarily low food resources and high predation risk could yield increased following of heterospecifics (Pomara et al. 2003, Dupuch et al. 2009, Hammerschlag et al. 2010, Darrah and Smith 2013). If food resources or predation risk are important drivers of heterospecific attraction for antshrikes, future studies

should record foraging and vigilance behavior before and after playback trials in order to investigate the contexts in which antshrikes respond to antwren playback. For example, if antshrikes have low foraging and high vigilance rates, i.e. if food resources are low or predation risk is high at a particular time or place in the territory, and antwrens provide some resource or anti-predation related benefit, antshrikes should be more likely to respond to antwren playback (Robinson and Holmes 1984, Morrison and Lindell 2011). Alternatively, future studies could augment food resources and predation risk and record propensity of the antshrikes to approach antwren playback before and after augmentation (Grubb 1987, Beauchamp 2004). The augmentation of food should decrease attraction propensity, while the augmentation of perceived predation risk should increase attraction to antwren playback.

If antshrikes always initiate flock movement, they likely accomplish this by moving away from flocking species rather than approaching them (Munn and Terborgh 1979, Strandburg-Peshkin et al. 2015). Therefore, since antshrikes approached a nuclear species more often than a control species in this study, they may not exclusively lead, but perhaps sometimes follow other flocking species. In addition, since antshrikes and transient species approached antwren playback more than control playback, the antwrens may lead some of the time instead of always following. The leading and following roles of antshrikes and antwrens may vary depending on context, and so likely vary across a spectrum (Gram 1998, Kotagama and Goodale 2004, Srinivasan et al. 2010) rather than falling into categories.

Interspecific interactions are key to maintaining biodiversity and conserving ecosystems (Cardinale et al. 2002, Soliveres et al. 2015). In ecosystems worldwide, the formation of mixed-species flocks hinges on the presence of nuclear species (Goodale et al. 2015). The removal of nuclear species may result in the disbanding of flocks, which likely results in reduced foraging

efficiency and/or increased predation risk for both nuclear and transient species. Thus, nuclear species possibly function as keystone species due to their disproportionately large effect on other species (Maldonado-Coelho and Marini 2004, Zhang et al. 2013).

The mutuality of the responses of antshrikes and antwrens to each others' playback suggests that they both receive some benefit from associating with each other. In other flocking systems, such as flocks centered around drongos or tits, there is likely always at least some benefit received by each species, often including anti-predation effects (Sridhar et al. 2009, Goodale et al. 2011), resulting in some level of mutual attraction. Future research should investigate the specific benefits antshrikes receive by associating with the flock, and the contexts in which antshrikes approach antwren playback.

ACKNOWLEDGMENTS

Staff of the Asociación para la Conservación de la Cuenca Amazónica were essential in providing a comfortable place to live during the study. F. A. Pratolongo assisted in submitting permits. D. Farine and E. Goodale provided critical insight in the development of this manuscript.

The National Science Foundation provided critical support during the early stages of this study. The Integrative Biology (formerly Zoology) Department, Center for Latin American and Caribbean Studies, the Graduate School, and the Ecology, Evolutionary, Biology and Behavior Program at Michigan State University provided additional support. The methods in this paper were in compliance with and have been approved by the Institutional Animal Care and Use Committee, AUF # 06/13-137-00.

LITERATURE CITED

LITERATURE CITED

- Ale, S. B. and J. S. Brown. 2007. The contingencies of group size and vigilance. *Evolutionary Ecology Research* 9:1263-1276.
- Baigrie, B. D., A. M. Thompson, and T. P. Flower. 2014. Interspecific signalling between mutualists: food-thieving drongos use a cooperative sentinel call to manipulate foraging partners. *Proceedings of the Royal Society of London B*:20141232.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1-48.
- Beauchamp, G. 2003. Group-size effects on vigilance: A search for mechanisms. *Behavioral Processes* 63:111-121.
- Beauchamp, G. 2004. Reduced flocking by birds on islands with relaxed predation. *Proceedings of the Royal Society of London B*:1039-1042.
- Beauchamp, G. 2012. Flock size and density influence speed of escape waves in semipalmated sandpipers. *Animal Behavior* 83:1125-1129.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulson, M. H. H. Stevens, and J. S. S. White. 2009. Generalized linear mixed-models: A practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24:127-135.
- Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415:426-429.
- Charif, R. A., D. W. Ponirakis, and T. P. Krein. 2006. *Raven Lite 1.0 User's Guide*. Cornell Laboratory of Ornithology, Ithaca, NY.
- Cordeiro, N. J., L. Borghesio, M. P. Joho, T. J. Monoski, V. J. Mkongewa, and C. J. Dampf. 2015. Forest fragmentation in an African biodiversity hotspot impacts mixed-species bird flocks. *Biological Conservation* 188:61-71.
- Darrah, A. and K. Smith. 2013. Comparison of foraging behaviors and movements patterns of the Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) traveling alone and in mixed-species flocks in Amazonian Ecuador. *Auk* 130:629-636.
- Dolby, A. S. and T. C. Grubb. 2000. Social context affects risk taking by a satellite species in a mixed-species foraging group. *Behavioral Ecology* 11:110-114.

- Dupuch, A., L. M. Dill, and P. Magnan. 2009. Testing the effects of resource distribution and inherent habitat riskiness on simultaneous habitat selection by predators and prey. *Animal Behavior* 78:705-713.
- Farine, D. R., L. M. Aplin, B. C. Sheldon, and W. Hoppitt. 2015. Interspecific social networks promote information transmission in wild songbirds. *Proceedings of the Royal Society of London B* 282:20142804.
- Goodale, E. and S. W. Kotagama. 2005a. Testing the roles of species in mixed-species bird flocks of a Sri Lankan rain forest. *Journal of Tropical Ecology* 21:669-676.
- Goodale, E. and S. W. Kotagama. 2005b. Alarm-calling in Sri Lankan mixed-species bird flocks. *Auk* 122:108-120.
- Goodale, E. and S. W. Kotagama. 2008. Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rain forest. *Behavioral Ecology* 19:887-894.
- Goodale, E., U. Goodale, and R. Mana. 2011. The role of toxic pitohuis in mixed-species flocks of lowland forest in Papua New Guinea. *Emu* 112:9-16.
- Goodale, E., P. Ding, X. Liu, A. Martinez, X. Si, M. Walters, and S. K. Robinson. 2015. The structure of mixed-species bird flocks and their response to anthropogenic disturbance, with special reference to East Asia. *Avian Research* 6:14.
- Gradwohl, J. and R. Greenberg. 1980. The formation of antwren flocks of Barro Colorado Island, Panama. *Auk* 97:385-395.
- Gram, W. K. 1998. Winter participation in Neotropical migrant and resident birds in mixed-species flocks in northeastern Mexico. *Condor* 100:43-53.
- Greenberg, R. 2000. Birds of many feathers: The formation and structure of mixed-species flocks of forest birds. Pages 521-558 *in* On the move: How and why animals travel in groups (S. Boinski and P. A. Garber, Editors) University of Chicago Press, Chicago, IL.
- Grubb, T. C. 1987. Changes in the flocking behavior of wintering English titmice with time, weather and supplementary food. *Animal Behaviour* 35:794-806.
- Hammerschlag, N., M. R. Heithaus, and J. E. Serafy. 2010. Influence of predation risk and food supply on nocturnal fish foraging distributions along a mangrove-seagrass ecotone. *Marine Ecology Progress Series* 414:223-235.
- Hino, T. 1998. Mutualistic and commensal organization of avian mixed-species foraging flocks in a forest in western Madagascar. *Journal of Avian Biology* 29:17-24.
- Hogstad, O. 2009. Winter flock coherence in Willow Tits- who decide what and why? *Ornis Norvegica* 32:190-201.

- Hutto, R. L. 1994. The composition and social organization of mixed-species flocks in a tropical deciduous forest in western Mexico. *Condor* 96:105-118.
- Jullien, M. and J. M. Thiollay 1998. Multi-species territoriality and dynamics of Neotropical forest understory bird flocks. *Journal of Animal Ecology* 67:227-252.
- Koloff, J. and D. J. Mennill 2013. The responses of duetting antbirds to stereo duet playback provide support for the joint territory defense hypothesis. *Ethology* 119:462-471.
- Kotagama, S. W. and E. Goodale. 2004. The composition and spatial organisation of mixed-species flocks in a Sri Lankan rainforest. *Forktail* 20:63-70.
- Maldonado-Coelho M., and M. A. Marini. 2004. Mixed-species bird flocks from the Brazilian Atlantic forest: The effects of forest fragmentation and seasonality on their size, richness and stability. *Biological Conservation* 116:19-26.
- Martinez, A. E. and J. P. Gomez. 2013. Are mixed-species bird flocks stable through two decades? *American Naturalist* 181:E53-E59.
- Martinez, A. E., J. P. Gomez, J. M. Ponciano, and S. K. Robinson. 2016. Functional traits, flocking propensity, and perceived predation risk in an Amazonian understory bird community. *American Naturalist* 187:000-000.
- Martinez, A. E. and R. T. Zenil. 2012. Foraging guild influences dependence on heterospecific alarm calls in Amazonian birds flocks. *Behavioral Ecology* 23:544-550.
- Morrison, E. B. and C. A. Lindell. 2011. Active or passive forest restoration? Assessing restoration alternatives with avian foraging behavior. *Restoration Ecology* 19:170-177.
- Moynihan, M. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. *Smithsonian Miscellaneous Collection* 143:1-140.
- Munn, C. A. 1985. Permanent canopy and understory flocks in Amazonia: species composition and population density. *Ornithological Monographs* 36.
- Munn, C. A. 1986. Birds that 'cry wolf.' *Nature* 319:143-145.
- Munn, C. A. and J. W. Terborgh. 1979. Multi-species territoriality in Neotropical foraging flocks. *Condor* 81:338-347.
- Neill, S. R. S. J. and J. M. Cullen. 1974. Effects on whether schooling by their prey affects the hunting behavior of cephalopods and fish predators. *Journal of Zoology* 172:549-569.
- Pomara, L. Y., R. J. Cooper, and L. S. Petit. 2003. Mixed-species flocking and foraging behavior of four Neotropical warblers in Panamanian shade coffee fields and forests. *Auk* 120:1000-

- Pulliam, H. R. 1973. On the advantages of flocking. *Journal of Theoretical Biology* 38:419-422.
- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Robinson, S. K. and R. T. Holmes. 1984. Effects of plant-species and foliage structure on the foraging behavior of forest birds. *Auk* 101:672-684.
- Robinson, S. K. 1994. Habitat selection and foraging ecology of raptors in Amazonian Peru. *Biotropica* 26:443-458.
- Rosenberg, K. V. 1993. Diet selection in Amazonian antwrens: Consequences of substrate specialization. *Auk* 110:361-375.
- RStudio Team. 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. <http://www.rstudio.com/>.
- Schulenberg, T. S. 1983. Foraging behavior, eco-morphology, and systematics of some antshrikes (Formicariidae: Thamnomanes). *The Wilson Bulletin* 95:505-521.
- Soliveres, C., C. Smit, and F. T. Maestre. 2015. Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning, and evolution of plant communities. *Biological Reviews* 90:297-313.
- Sridhar, H., G. Beauchamp, and K. Shanker. 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour* 78:337-347.
- Srinivasan, U., R. H. Raza, S. Quader. 2010. The nuclear question: Rethinking species importance in multi-species animal groups. *Journal of Animal Ecology* 79:948-954.
- Stotz, D. F. 1993. Geographic variation in species composition of mixed species flocks in lowland humid forests in Brazil. *Papeis Avulsos de Zoologia* 38:61-75.
- Strandburg-Peshkin, A., D. R. Farine, I. D. Couzin, and M. C. Crofoot. 2015. Shared decision-making drives collective movement in wild baboons. *Science* 348:1358-1361.
- Terborgh, J. 1990. Mixed-flocks and polyspecific associations: Costs and benefits of mixed groups to birds and monkeys. *American Journal of Primatology* 21:87-100.
- Terborgh, J. W., S. K. Robinson, T. A. Parker III, C. A. Munn, and N. Pierpont. 1990. Structure and organization of an Amazonian bird forest community. *Ecological Monographs* 60:213-238.
- Thiollay, J. M. 2003. Comparative foraging behavior between solitary and flocking insectivores

in a Neotropical forest: Does vulnerability matter? *Ornitologia Neotropical* 14:47-65.

Zhang, Q., R. Han, Z. Huang, and F. Zou. 2013. Linking vegetation structure and bird organization: Response of mixed-species bird flocks to forest succession in subtropical China. *Biodiversity and Conservation* 65:1965-1989.

Zimmer, K. J. and M. L. Isler. 2003. Family *Thamnophilidae* (typical antbirds). Pages 448-681 *in* Handbook of the birds of the world. Volume 8. Broadbills to tapaculos (J. del Hoyo, A. Elliot, and D. A. Christie, Editors). Lynx Edicions, Barcelona, Spain.

Chapter 2: An environmental cue perceived by a single species explains the space use patterns of mixed-species flocks in Amazonian Peru

INTRODUCTION

Determining the drivers of space use is critical for understanding a species' ecology and informing conservation efforts (Bodie *et al.* 2000, Krebs *et al.* 2007, Nathan *et al.* 2008, Haffner *et al.* 2009, Kearney & Porter 2009). While the drivers of space use of single individuals and monospecific groups are relatively well studied, few studies have examined drivers of space use of mixed-species groups (Garcia-Charton & Perez-Ruzafa 2001, Effenberger & Mouton 2007, Tolon *et al.* 2009, Anich *et al.* 2012, Potts *et al.* 2014), which are prevalent in avian communities (Greenberg 2000, Sridhar *et al.* 2009, Goodale *et al.* 2015).

Throughout the world, hundreds of species participate in mixed-species flocks, defined as ≥ 2 species moving together for >5 minutes (Stotz 1993, Bohorquez 2003, Nininuan 2004, Gordon & Harrison 2010). Recent research on mixed-species flocks has contributed to our knowledge of flock composition (Arbelaez-Cortes *et al.* 2012, Vanderduys *et al.* 2012), physical and behavioral similarities among flock participants (Sridhar *et al.* 2009, Srinivasan *et al.* 2010, Sridhar *et al.* 2012), and the stability of flocks over time (Martinez & Gomez 2013); few studies, however, have addressed factors that influence space use (but see Potts *et al.* 2014).

In single-species groups, the decisions of space use are typically made by one or a few individuals rather than collectively by all individuals (Morse 1970, Terborgh 1990, Plissner *et al.* 2000). For example, movements of olive baboons (*Papio anubis*) are initiated by a single individual when that individual moves in a highly directed manner (Strandburg-Peshkin *et al.* 2015). In wintering groups of unrelated Willow Tits (*Poecile montanus*), adults are more likely to lead than hatch-year birds (Hogstad 2009).

A mixed-species flock may function in a manner similar to a single-species group, i.e. a single species or individual may largely decide space use of the entire flock. In Amazonian mixed-species flocks, the Dusky-throated Antshrike (*Thamnomanes ardesiacus*; hereafter Dt antshrike) and the Long-winged Antwren (*Myrmotherula longipennis*; hereafter Lw antwren) are nuclear species, which are species nearly always found in a flock, and almost never away from a flock (Munn & Terborgh 1979, Greenberg 2000). Over 50 other transient species, e.g. Bluish-slate Antshrike (*T. schistogynus*) and White-flanked Antwren (*M. axillaris*), may associate with these flocks or not (Munn & Terborgh 1979, Terborgh 1990, Jullien & Thiollay 1998, Darrah & Smith 2013). Because transient species are found in the flocks inconsistently, we did not expect transient species to influence space use of the entire flock.

Organisms prefer to spend time in areas rich in resources and low in predation risk (Dupuch *et al.* 2009, Heithaus *et al.* 2009, Hammerschlag *et al.* 2010, Fraker & Luttbeg 2012). For example, the space use of Swainson's Warblers (*Limnothlypis swainsonii*) corresponded to the patchy spatial distributions of certain plants and habitat types that provided food and low predation risk (Anich *et al.* 2012). The distribution of animals often can be predicted by habitat characteristics (Schlaepfer *et al.* 2002, Battin 2004, Frei *et al.* 2013), which suggests that animals rely on habitat characteristics when making fine-scale space use decisions. For example, animals likely use vegetation density as an indicator of resource availability and predation risk (Orians & Wittenberger 1991, Caras & Korine 2009, Scheinin *et al.* 2012). Given that other species are attracted more often to Dt antshrikes than Lw antwrens (Williams & Lindell in press), the space use decisions of the flock may be driven, in large part, by the preferred habitat characteristics of the Dt antshrikes. Dt antshrikes typically scan sparsely vegetated areas for insects. Upon detecting a prey item, they sally-glean the prey from the vegetation (Schulenberg 1983, Thiollay

2003). Dt antshrikes may spend time in areas with low vegetation density because of high prey availability and low risk of predation. The Dt antshrikes may be largely responsible for the space use of multiple other species.

We investigated the following question: what are the mechanisms of space use of mixed-species flocks? We hypothesized that predation risk and resource availability are important drivers of the space use of the Dt antshrike, and that the space use patterns of Dt antshrikes would influence the space use patterns of the flock. In addition, influences of DT antshrikes on flock space-use should be greater than influences of any other species. In other words, a single species in mixed-species flocks may have a disproportionately large effect on the space use of many other species. We predicted that the foraging attack rate (a proxy for resource availability; Robinson & Holmes 1984, Pomara *et al.* 2003), vigilance rate (a proxy for predation risk; Caraco *et al.* 1980, Monús & Barta 2016), and surrounding vegetation density of the Dt antshrikes could explain the space use of the flock. Specifically, Dt antshrikes should have higher attack rates, lower vigilance rates, and lower surrounding vegetation density in high-use areas compared to low-use areas of the flock. Meanwhile, these rates and vegetation density should not vary for other species regardless of whether they are in high-use or low-use areas.

METHODS

Study area

Data were collected at Los Amigos Biological Station (12.568 S, 70.100 W) in May-Aug 2013-2014. Los Amigos is situated among 1500 km² of primary rainforest at 300 meters above sea level in eastern Madre de Dios, Peru. Understory mixed-species flocks containing antshrikes and antwrens are abundant and present year-round, and are easily found by listening for the nearly incessant vocalizations of flock members. Based on our observations from 2012-2015, the

territories of the flocks are stable, and neighboring flocks have relatively little overlapping area, consistent with previous work (Martinez & Gomez 2013). In May-Jul 2013 and May-Jun 2014, the first author SMW color-banded 26 individuals of four species from three flocks in terra firme habitat for individual recognition.

Behavioral observations

We entered each territory five minutes before dawn at a location where the flock was known to gather every morning. We followed a flock until six hours after dawn. Every twenty minutes we took geographic coordinates of the flock using a Garmin GPSMap 78 (Anich *et al.* 2012).

We opportunistically recorded behavioral observations of antshrikes and antwrens for as long as possible using a digital voice recorder while the birds were foraging. We considered birds to be flocking when they were actively moving along branches and gleaning or sallying insects, and maintaining a distance of 10 m or less between individuals for five or more minutes (Moynihan 1962, Stotz 1993). During a focal behavioral observation of an individual, we recorded the vegetation density, the attack rate, the vigilance rate, and GPS coordinates (Altmann 1974).

No more than one observation per hour was taken per color-banded individual in order to reduce non-independence of observations, following recommendations by Swihart & Slade (1985), Lair (1987), and Pechacek (2006). When collecting observations on non-banded individuals, we did not use an individual of the same species more than once per hour unless we were certain it was a different individual, based on plumage differences. The flocks typically moved 120-180 m per hour, although they sometimes moved over 300 m per hour. The territories were less than 300 m at the widest, and so flocks could have moved to any point in the territory within an hour. Therefore, the movements over one hour reflect choices by the flocks to

forage in preferred areas rather than being restricted by an ability to reach any location within a territory (Lair 1987).

The attack rate was defined as the number of attacks per unit time. The attack rate approximates the number of insects consumed and so the attack rate increases with prey availability (Robinson & Holmes 1984, Holmes & Schultz 1988, Pomara *et al.* 2003). Following recommendations of Remsen & Robinson (1990), we defined an attack as the action of the bill striking or picking up an object. The proportion of time spent vigilant has been used as a proxy of predation risk since vigilance increases with predation risk (Caraco *et al.* 1980, Lima & Dill 1990, Monús & Barta 2016). Birds were considered vigilant when the bill was held horizontally or pointed upward (Morrison & Lindell 2011).

Immediately following an observation, we visually estimated the vegetation density within a one-meter-radius sphere of the bird based on the percent of light that passed through the sphere, following recommendations of “foliage density” sampling by Remsen & Robinson (1990). A score of 0% indicated that all light passed through the sphere because there was no vegetation.

Although we observed >40 species in the flocks, only four species were common enough to obtain a sufficient number of observations to be included in the analyses. The four species used in the analyses were: the nuclear Long-winged Antwren, the nuclear Dusky-throated Antshrike, the transient White-flanked Antwren, and the transient Bluish-slate Antshrike.

Statistical analyses

The home range of the flock was defined as the 95% fixed-kernel home range, following recommendations of Worton (1989). A high use area was calculated using the inner 55% isopleths of the home range, and the low use area was defined as the area lying outside the high use area, but still within the home range. In other words, the flock spent 55% of its time in the

high use area, 40% of its time in the low use area, and 5% of its time outside of these areas. The 55% isopleth was chosen because it delineated hotspots of space use (pers. obs.). Isopleths of 50-60% are typically used for defining high use area (Samuel *et al.* 1985, Heupul *et al.* 2004, Anich *et al.* 2012). The home ranges, high use areas, and low use areas were calculated with the “kernelUD” and “getverticeshr” functions of the “adehabitatHR” package of the R Statistical Software, version 3.2.3 (Calenge 2006, R Core Team 2016). The smoothing parameters were chosen using least-squares cross-validation, following recommendations of Seamen *et al.* (1999).

To determine whether enough locations were sampled for home range kernel density estimation, we used the “rhr” package of the R Statistical Software, version 3.2.3 (Signer & Balkenhol 2015, R Core Team 2016). Home range asymptotes were reached for each flock after 50 locations, which is a typical number of sampling locations to reach an asymptote (Seamen *et al.* 1999, Anich *et al.* 2009).

We used a generalized mixed model with a binomial distribution and link logit function to investigate whether vegetation density, attack rate, and vigilance of each of the four species distinguished areas of high (within the 55% isopleths of the territories) or low (between the 55% and 95% isopleths of the territories) space use by the flocks. Flock and individual were considered random effects. A list of 28 candidate models was developed via stepwise selection. We calculated an Akaike Information Criterion (AIC), ΔAIC ($AIC_i - AIC_{min}$), and normalized model likelihoods (w) for each model. The behavioral variables, i.e. the surrounding vegetation density, attack rate, and vigilance rate of the focal species, i.e. the Dt antshrike, Bluish-slate Antshrike, White-flanked Antwren, and Lw antwren were added step-wise to a basal model with no behavioral variables. The full model included all three behavioral variables of all four species.

The best selected model was at least 2 AIC units lower than the model with the next lowest AIC score (Burnham & Anderson 2002). The directions and strengths of the effects of the predictor variables on the response variable were estimated with 95% confidence intervals. A strong effect was defined as an interval that did not include zero, an intermediate effect included zero but was not centered on zero, and a non-effect was centered on zero (Dugger *et al.* 2011, Bruggeman *et al.* 2015). The “glmer” function of the “lme4” package was used for modeling (Bates *et al.* 2015) and the “AICtab” function of the “bbmle” package was used for the model selection (Bolker & R Core Team 2016). All analyses were performed with the R Statistical Software, version 3.2.3 (R Core Team 2016). The estimates are reported \pm standard errors.

RESULTS

We collected, 134, 173, and 148 locations for each of the three flocks. Home range sizes were 6.74, 6.34, and 5.08, hectares, and high use areas were 2.04, 2.46, and 1.79 hectares, respectively (A, B, and C of Figure 2.1). We collected 346 behavioral observations from 26 individuals of four species (Table 2.1).

Species	Number of individuals	Number of observations in high use areas	Number of observations in low use areas	Total number of observations
Bluish-slate Antshrike	4	13	25	38
Dusky-throated Antshrike	7	68	36	104
Long-winged Antwren	9	88	51	139
White-flanked Antwren	6	24	24	48

Table 2.1. Analyses included observations from the four most common species found in three understory flocks at Los Amigos Biological Station, Madre de Dios, Peru in 2014.

Model	ΔAIC	K	w
veg.DTAN	0	4	0.53
veg.DTAN + att.DTAN	2.0	5	0.20
veg.DTAN + vig.DTAN	2.0	5	0.20
veg.DTAN + att.DTAN + vig.DTAN	4.0	6	0.073
veg.DTAN	10.9	4	0.0023
att.DTAN	11.2	4	0.0020
att.DTAN + vig.DTAN	12.8	5	0.00
att.BSAN + att.WFAN + att.LWAN	180.0	6	0.00
veg.BSAN + veg.WFAN + veg.LWAN	180.3	6	0.00
vig.BSAN + vig.WFAN + vig.LWAN	180.8	6	0.00

Table 2.2. Results of model selection for the ten models with the smallest ΔAIC . The models relate behavioral variables of individual flock members to the space use of the entire flock. The surrounding vegetation densities (veg), attack rates (att), and vigilance rates (vig) of Dusky-throated Antshrikes (DTAN), Bluish-slate Antshrikes (BSAN), White-flanked Antwrens (WFAN), and Long-winged Antwrens (LWAN) were added step-wise to a basal model with no behavioral variables. We ΔAIC as the minimum AIC subtracted from the AIC of the corresponding model; K is the number of included parameters; and w is the normalized model likelihood (Burnham and Anderson 2002).

Only one model was substantially supported ($< 2 \Delta AIC$), and this model ($w = 0.53$) contained the vegetation density surrounding the Dt Antshrike as the only fixed-effect predictor (Table 22.). The 95% confidence interval of the effect of vegetation density of the Dt Antshrike on the space use of the flock was (-8.53, -2.07). The ΔAIC of next two most likely models both were 2.0 and included the vegetation density of the Dt Antshrike and either the attack rate or vigilance rate of the Dt Antshrike. Random effects did not have a measureable effect on the variation of the space use of the flock.

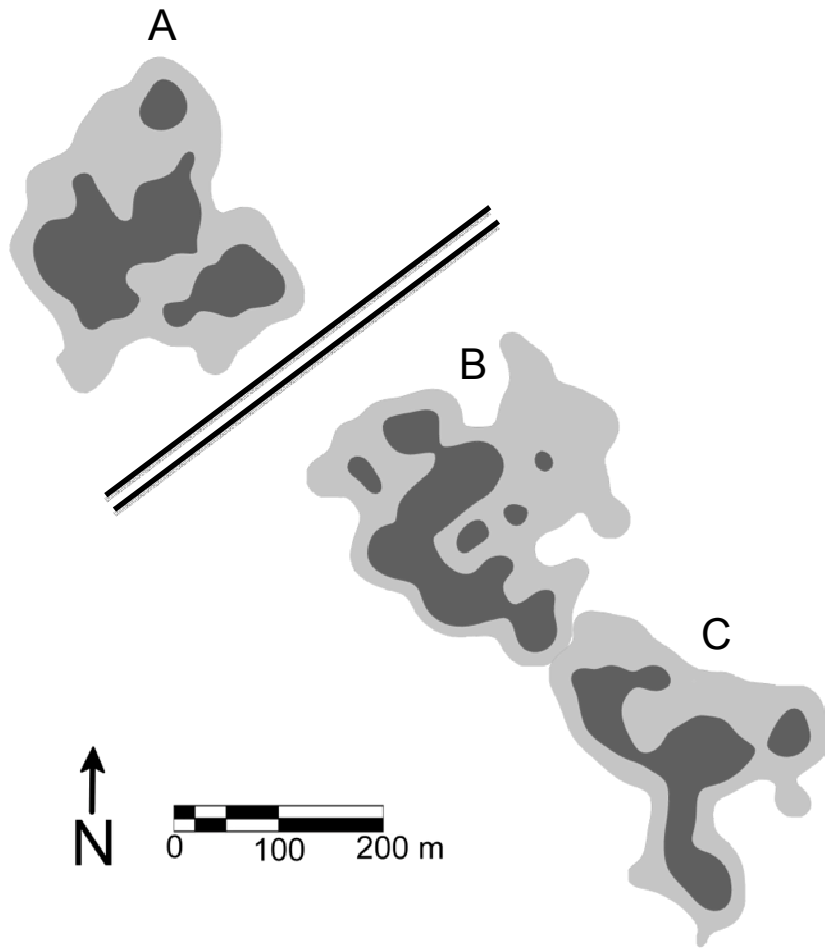


Figure 2.1. Home ranges (light gray plus dark gray areas), high use areas (dark gray areas), and low use areas (light gray areas) of three mixed species flocks (A, B, and C) at Los Amigos Biological Station, Peru in May-August 2014. The double black lines indicate a spatial gap of 650 m.

DISCUSSION

The results supported our prediction that the surrounding vegetation density of a single species, the Dusky-throated Antshrike, explained space use patterns of mixed-species flocks. DTAN attack and vigilance rates, in contrast, were not predictive. The areas in which the flocks spent the most time could be predicted by vegetation density of Dt antshrike foraging locations.

Dt antshrikes forage by perching in areas with low vegetation density and scanning distant vegetation (Schulenberg 1983, Thiollay 2003). They search for food hyperopically, which likely facilitates the detection of aerial predators, i.e. forest-falcons, which commonly barrage flocks. Dt antshrikes give loud alarm calls upon the detection of the forest-falcons. This alarm-calling is a likely mechanism for the strong attraction of antwrens to Dt antshrikes; the attraction of Dt antshrikes to Lw antwrens is not as strong (Martinez & Zenil 2012, Williams & Lindell in press). Dt antshrikes likely move to and spend time in areas with a low vegetation density since, from the perspective of the Dt antshrike, there are accessible prey and low predation risk. Other species then associate with the Dt antshrikes to gain anti-predation benefits (Martinez & Zenil 2012 Williams & Lindell in press). Therefore, the space use patterns of Dt antshrikes drive, at least in part, the space use patterns of the whole flock.

We predicted that Dt antshrikes would prefer to forage in areas that increased foraging efficiency and decreased predation risk. The results did not support our predictions that attack rate and vigilance rate of the Dusky-throated Antshrike predicted space use of the flock. Although predation risk and resource availability frequently are associated with space use patterns, other mechanisms, such as competition, may play a role in space use. Neotropical insectivorous birds, including antbirds, defend territories against floater individuals or territory intruders (Morton *et al.* 2000, Fedy & Stutchbury 2004). Floaters can constitute a large portion of the population and so the effect of floaters on behavioral adaptations of territory holders is likely underappreciated (Moreno 2016). Because antbirds are highly territorial, it is possible that Dt antshrikes spend time in areas with sparse vegetation in order to visually search for and chase away floaters or territory intruders (Stutchbury & Morton 2001). If this hypothesis is correct, the

simulated presence of intruding conspecifics (e.g. through playback) should cause Dt antshrikes to forage in sparsely vegetated areas more frequently than control Dt antshrikes.

Alternatively, we recognize that the behavioral variables we measured, attack rate and vigilance rate, are proxies for available food resources and predation risk, and therefore are imperfect measures of real-time food resource availability and predation risk (Robinson & Holmes 1984, Hutto 1990). It is possible that the actual success rate of capturing prey items and the actual predation risk were higher and lower, respectively, in the low vegetation areas compared to the high-vegetation areas but that our measures could not capture these differences.

Another species of antshrike, the Bluish-slate Antshrike, has been considered to perform a similar role to the Dusky-throated Antshrike in mixed-species flocks; they give raucous alarm calls in the presence of predators and are thought to be leaders of some flocks (Munn & Terborgh 1979, Munn 1985, Jullien & Thiollay 1998). Among the flocks used in this study, Bluish-slate Antshrikes occurred in two, but only intermittently, and when the Bluish-slate Antshrike and Dusky-throated Antshrike departed from each other, each antshrike continued to associate with a suite of other species. It is possible that the Bluish-slate Antshrike plays a role similar to the role of the Dusky-throated Antshrike and influences flock space use disproportionately compared to other flock species.

Other leader species around the world may dictate space use patterns of mixed-species flocks similar to the Dt antshrikes. Such leader species include Orange-billed Babblers (*Turdoides rufescens*) and Greater Racket-tailed Drongos (*Dicrurus paradiseus*) in Sri Lanka, Square-tailed Drongos (*Dicrurus ludwigii*) in Tanzania, Buff-rumped Thornbills (*Acanthiza reguloides*) in Australia, and Gray-cheeked Fulvettas in Taiwan (Chen & Hsieh 2002, Kotagama & Goodale 2004, Farine & Milburn 2013, Cordeiro *et al.* 2015). Drongos visually scan for insects in

sparsely vegetated areas, similar to the Dusky-throated Antshrike, and so flocks led by drongos may spend a disproportionate amount of time in sparsely vegetated areas relative to the available vegetation densities (Goodale & Kotagama 2005, Rocamora & Yeatman-Berthelot 2009). Some species may serve only as indicators of a flock's presence and not confer other benefits to flocking species (Goodale & Kotagama 2005). These species would likely not drive space use patterns of the flock since flocking species, after having found the flock, would experience no benefit from following the indicator species. Future studies should aim to predict habitat variables that are important to flocking species that attract other species, and investigate whether the space use patterns of the flock are associated with the habitat variables across the flock's home range.

LITERATURE CITED

LITERATURE CITED

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–267.
- Anich, N.M., Benson, T.J. & Bednarz, J.C. 2009. Estimating territory and home-range sizes: Do singing locations alone provide an accurate estimate of space use? *Auk* 126:626–634.
- Anich, N.M., Benson, T.J. & Bednarz, J.C. 2012. What factors explain differential space use within Swainson's Warbler (*Limnothlypis swainsonii*) home ranges? *Auk* 129:409–418.
- Arbelaez-Cortes, E. & Marin Gomez, O.H. 2012. The composition of mixed-species bird flocks in Alto Quindio, Colombia. *Wilson Journal of Ornithology* 124:572–580.
- Bates, D., M. Maechler, B. Bolker, & S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Battin, J. 2004. When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Conservation Biology* 18:1482–1491.
- Bruggeman, J. E., T. Swem, D. E. Andersen, P. L. Kennedy, & D. Nigro. 2016. Multi-season occupancy models identify biotic and abiotic factors influencing a recovering Arctic Peregrine Falcon *Falco peregrinus tundrius* population. *Ibis* 158:61–74.
- Bodie, J. R. & R. D. Semlitsch. 2000. Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtle. *Oecologia* 122: 138–146.
- Bohorquez, C. I. 2003. Mixed-Species bird flocks in a montane cloud forest of Colombia. *Ornitología Neotropical* 14:67–78.
- Bolker, B. & R Core Team. 2016. bbmle: Tools for General Maximum Likelihood Estimation. R package version 1.0.18.
- Burnham, K. P. & D. R. Anderson. 2002. Model selection and multi-mode inference. Springer Press, New York, New York.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197: 516–519.
- Caraco, T., S. Martindale, H. R. Pulliam. 1980. Avian flocking in presence of a predator. *Nature* 285:400–401.
- Caras, T., & C. Korine. 2009. Effect of vegetation density on the use of trails by bats in secondary tropical rain forest. *Journal of Tropical Ecology* 25:97–101.

- Chen, C., & F. Hsieh. 2002. Composition and foraging behavior of mixed-species flocks led by the Gray-cheeked Fulvetta in Fushan Experimental Forest, Taiwan. *Ibis* 144:317-330.
- Cordeiro, N. J., L. Borghesio, M. P. Joho, T. J. Monoski, V. J. Mkongewa, & C. J. Dampf. 2015. Forest fragmentation in an African biodiversity hotspot impacts mixed-species bird flocks. *Biological Conservation* 188: 61–71.
- Darrah, A. & K. Smith. 2013. Comparison of foraging behaviors and movements patterns of the Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) traveling alone and in mixed-species flocks in Amazonian Ecuador. *Auk* 130:629–636.
- Dugger, K. M, R. G. Anthony, & L. S. Andrews. 2011. Transient dynamics of invasive competition: Barred Owls, Spotted Owls, habitat, and the demons of competition present. *Ecological Applications* 21:2459-2468.
- Dupuch, A., L. M. Dill, & P. Magnan. 2009. Testing the effects of resource distribution and inherent habitat riskiness on simultaneous habitat selection by predators and prey. *Animal Behavior* 78:705-713.
- Effenberger, E. & P. L. N. Mouton. 2007. Space use in a multi-male group of the group-living lizard. *Journal of Zoology* 272:202-208.
- Farine, D. R. & P. J. Milburn. 2013. Social organisation of thornbill-dominated mixed-species flocks using social network analysis. *Behavioral Ecology and Sociobiology* 67:321-330.
- Fedy, B. C. & B. J. M. Stutchbury. 2004. Territory switching and floating in White-bellied Antbird (*Myrmeciza longipes*), a resident tropical passerine in Panama. *Auk* 121:486-496.
- Fraker, M. E. & B. Luttbeg. 2012. Predator-prey space use and the spatial distribution of predation events. *Behaviour* 149:555-574.
- Frei, B., J. W. Fyles, J. J. Nocera. 2013. Maladaptive habitat use of a North American Woodpecker in population decline. *Ethology* 119:377-388.
- Garcia-Charton, J. A. & A. Perez-Ruzafa. 2001. Spatial pattern and the habitat structure of a Mediterranean rocky reef local assemblage. *Marine Biology* 138: 917-934.
- Goodale, E., & S. W. Kotagama. 2005. Testing the roles of mixed-species bird flocks of a Sri Lankan rain forest. *Journal of Tropical Ecology* 21:669–676.
- Goodale, E., P. Ding, X. Liu, A. Martinez, X. Si, M. Walters, & S. K. Robinson. 2015. The structure of mixed-species bird flocks and their response to anthropogenic disturbance, with special reference to East Asia. *Avian Research* 6:14.
- Gordon, A. I., & N. M. Harrison. 2010. Observations of mixed-species bird flocks at Kichwa

- Tembo Camp, Kenya. *Ostrich* 81: 259-264.
- Greenberg, R. 2000. Birds of many feathers: The formation and structure of mixed-species flocks of forest birds. In *On the move: How and why animals travel in groups* (Boinski, S. & Garber, P.A., eds.), pp. 521–558, University of Chicago Press, Chicago, USA.
- Haffner, C. D., F. J. Cuthbert, & T. W. Arnold. 2009. Space use by Great Lakes Piping Plovers during the breeding season. *Journal of Field Ornithology* 80: 270-279.
- Hammerschlag, N., M. R. Heithaus, J. E. Serafy. 2010. Influence of predation risk and food supply on nocturnal fish foraging distributions along a mangrove-seagrass ecotone. *Marine Ecology Progress Series* 414:223-235.
- Heithaus, M. R., A. J. Wirsing, D. Burkholder, J. Thomson, & L. M. Dill. 2009. Towards a predictive framework for predator risk effects: The interaction of landscape features and prey escape tactics. *Journal of Animal Ecology* 78:556-562.
- Heupel, M. R., C. A. Simpfendorfer, & R. E. Hueter. 2004. Estimation of shark home ranges using passive monitoring techniques. *Environmental Biology of Fishes* 71:135-142.
- Hogstad, O. 2009. Winter flock coherence in Willow Tits- who decide what and why? *Ornis Norvegica* 32:190-201.
- Holmes, R. T., & J. C. Schultz. 1988. Food availability for forest birds: Effects of prey distribution and abundance on bird foraging. *Canadian Journal of Zoology* 66:720-728.
- Hutto, R. L. 1990. Measuring the availability of food resources, pp. 20-28 *in* Avian foraging: Theory, methodology, and applications (M. L. Morrison, C. J. Ralph, J. Verner, & J. R. Jehl, Jr., eds). *Studies of Avian Biology* 13.
- Jullien, M. & J. M. Thiollay 1998. Multi-species territoriality and dynamics of Neotropical forest understory bird flocks. *Journal of Animal Ecology* 67:227-252.
- Kearney, M. & W. Porter. 2009. Mechanistic niche modeling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:334-350.
- Kotagama, S. W. & E. Goodale. 2004. The composition and spatial organisation of mixed-species flocks in a Sri Lankan rainforest. *Forktail* 20:63-70.
- Krebs, J., E. C. Lofroth, & I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71: 2180-2192.
- Lair, H. 1987. Estimating the location of the focal center in red squirrel home ranges. *Ecology* 68:1092-1101.

- Lima, S. L., & L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68:619-640.
- Martinez, A. E., & Gomez, J. P. 2013. Are mixed-species bird flocks stable through two decades? *American Naturalist* 181:E53-E59.
- Martinez, A. E., & R. T. Zenil. 2012. Foraging guild influences dependence on heterospecific alarm calls in Amazonian birds flocks. *Behavioral Ecology* 23:544-50.
- Monús, F., & Z. Barta. 2016. Is foraging time limited during winter? – A feeding experiment with tree sparrows under different predation risk. *Ethology* 122:20-29.
- Moreno, J. 2016. The unknown life of floaters: The hidden face of sexual selection. *Ardeola* 63:49-77.
- Morrison, E. B. & C. A. Lindell. 2011. Active or passive forest restoration? Assessing restoration alternatives with avian foraging behavior. *Restoration Ecology* 19:170-177.
- Morse D. H. 1970. Ecological aspects of some mixed-species flocks of birds. *Ecological Monographs* 40: 119-168.
- Morton, E. S., K. C. Derrickson, & B. J. M. Stutchbury. 2000. Territory switching in a sedentary tropical passerine, the Dusky Antbird (*Cercomacra tyrannina*). *Behavioral Ecology* 11:648-653.
- Moynihan, M. 1962. The organization and probably evolution of some mixed species flocks of Neotropical birds. *Smithsonian Miscellaneous Collection* 143:1-140.
- Munn, C. 1985. Permanent canopy and understory flocks in Amazonia: species composition and population density. *Ornithological Monographs*: 36.
- Munn, C. & J. Terborgh. 1979. Multi-species territoriality in neotropical foraging flocks. *Condor* 81:338-347.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, & P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *PNAS* 105:19052-19059.
- Nininuan, S, P. D. Round, G. A. Gale. 2004. Structure and composition of mixed-species bird flocks in Khao Yai National Park. *Natural History Bulletin of the Siam Society* 52:71-79.
- Orians, G. H., & J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137:S29-S49.
- Pechacek, P. 2006. Foraging behavior of Eurasian Three-toed Woodpeckers (*Picoides tridactylus alpinus*) in relation to sex and season in Germany. *Auk* 123:235-246.

- Plissner, J. H., L. W. Oring, & S. M. Haig. 2000. Space use of Killdeer at a Great Basin breeding area. *Journal of Wildlife Management* 64:421-29.
- Pomara, L. Y., R. J. Cooper, & L. S. Petit. 2003. Mixed-species flocking and foraging behavior of four Neotropical warblers in Panamanian shade coffee fields and forests. *Auk* 120:1000-1012.
- Potts, J. R., K. Mokross, P. C. Stouffer, M. A. Lewis. 2014. Step selection techniques uncover the environmental predictors of space use patterns in flock of Amazonian birds. *Ecology and Evolution* 4:4578–4588.
- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Remsen, J. V. & S. K. Robinson. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. In *Avian foraging: theory, methodology, and applications* (M. Morrison, C. J. Ralph, J. Vemer, & J. Jehl, eds.), pp. 144-160.
- Robinson, S. K. & R. T. Holmes. 1984. Effects of plant-species and foliage structure on the foraging behavior of forest birds. *Auk* 101:672-84.
- Rocamora, G. J. & D. Yeatman-Berthelot. 2009. Family Dicruridae (drongos). Pages 172-226 in *Handbook of the birds of the world. Volume 14. Bush-shrikes to Old World sparrows* (J. del Hoyo, A. Elliot, & D. A. Christie, Editors). Lynx Edicions, Barcelona, Spain.
- Samuel, M. D., D. J. Pierce, & E. O. Garten. 1985. Identifying areas of concentrated use within the home range. *Journal of Animal Ecology* 54:711-719.
- Scheinin, M., S. Scyphers, L. Kuappi, K. L. Heck, K. Mattila. 2012. The relationship between vegetation density and its protective value depends on the densities and traits of prey and predators. *Oikos* 121:1093-1102.
- Schlaepfer, M. A., M. C. Runge, & P. W. Sherman. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17:474-480.
- Schulenberg, T. 1983. Foraging behavior, eco-morphology, and systematics of some antshrikes (Formicariidae: Thamnomanes). *The Wilson Bulletin* 95:505-21.
- Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739-747.
- Signer, J., & N. Balkenhol. 2015. Reproducible home ranges (*rhr*): A new, user-friendly R package for wildlife telemetry data. *Wildlife Society Bulletin* 39:358-363.

- Strandburg-Peshkin, A., D. R. Farine, I. D. Couzin, & M. C. Crofoot. 2015. Shared decision-making drives collective movement in wild baboons. *Science* 348:1358-1361.
- Sridhar, H., G. Beauchamp, K. Shanker. 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour* 78:337-47.
- Sridhar, H., Srinivasan U, Askins RA, Canales-Delgadillo, JC, Chen CC, Ewert DN, Gale GA, Goodale E, Gram WK, Hart PJ, Hobson KA, Hutto RL, Kotagama SW, Knowlton JL, Lee TM, Nizam BZ, Peron G, Robin VV, Rodewald AD, Rodewald PG, Thomson RL, Trivedi P, VanWilgenburg SL, & Shanker K. 2012. Positive relationships between association strength and phenotypic similarity characterize the assembly of mixed-species bird flocks worldwide. *American Naturalist* 180:777-790.
- Srinivasan, U., R. H. Raza, S. Quader. 2010. The nuclear question: Rethinking species importance in multi-species animal groups. *Journal of Animal Ecology* 79:948-954.
- Stotz, D. F. 1993. Geographic variation in species composition of mixed species flocks in lowland humid forests in Brazil. *Papeis Avulsos de Zoologia* 38:61-75.
- Stutchbury, B. J. M. & E. S. Morton. 2001. Behavioral ecology of tropical birds. Academic Press: San Diego, California.
- Swihart, R. K., & N. A. Slade. 1985. Testing for independence of observations in animal movements. *Ecology* 66:1176-1184.
- Terborgh, J. 1990. Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. *American Journal of Primatology* 21:87-100.
- Thiollay, J. M. 2003. Comparative foraging behavior between solitary and flocking insectivores in a Neotropical forest: Does vulnerability matter? *Ornitologia Neotropical* 14:47-65.
- Tolon, V., S. Dray, A. Loison, A. Zeileis, C. Fischer, E. Baubat. 2009. Responding to spatial and temporal variations in predation risk: Space use of a game species in a changing landscape of fear. *Canadian Journal of Zoology* 87: 1129-1137.
- Vanderduys, E. P., A. S. Kutt, J. J. Perry, & G. C. Perkins. 2012. The composition of mixed-species bird flocks in northern Australian savannas.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-68.

Chapter 3: A context-specific vocalization serves as a mechanism of interspecific cohesion in mixed-species flocks

INTRODUCTION

Interspecific associations are key to the structure and function of communities (Cardinale et al. 2002, Hooper et al. 2005, Soliveres et al. 2015). Interspecific associations require a mechanism of communication to promote the proximity of individuals. For example, plants attract seed-dispersing ants via chemical cues (Youngsteadt et al. 2008), and client fish stiffly pose by standing on their heads or tails when soliciting the removal of ectoparasites from cleaner gobies (Côté et al. 1998).

The mechanisms responsible for maintaining interspecific cohesion within mixed-species flocks are poorly understood, but likely involve contact calls (Munn and Terborgh 1979, Wiley 1980, Greenberg 2000). Individuals within monospecific groups frequently produce context-specific contact calls as a mechanism of group cohesion (Ficken et al. 1978, Janik and Slater 1998, Trillmich et al. 2004, Kondo and Watanabe 2009, Husemann et al. 2014, Mumm et al. 2014). Interspecific associations are particularly prevalent in avian communities, and birds traveling in groups often communicate aurally (Greenberg 2000, Bohorquez 2003, Nininuan et al. 2004). Therefore, contact calls may serve as a mechanism of cohesion in multi-species groups.

In Amazonian mixed-species flocks, the Dusky-throated Antshrike (*Thamnomanes ardesiacus*, hereafter antshrike) and the Long-winged Antwren (*Myrmotherula longipennis*) are virtually always associated with each other (Munn and Terborgh 1979, Jullien and Thiollay 1998). They are often accompanied by a White-flanked Antwren (*M. axillaris*), Gray Antwren (*M. menetriesii*), and one to a few ovenbird species (Furnariidae). Flock participants primarily

benefit from associating with the antshrikes by eavesdropping on alarm calls given by antshrikes in the presence of a predator (Jullien and Thiollay 1998, Martinez and Zenil 2012). Secondary benefits accrued from participating in the flock might include the dilution effect, many-eyes effect, or confusion effect, which should reduce the likelihood of predation (Neill and Cullen 1974, Beauchamp 2003, Ale and Brown 2007, Beauchamp 2012).

Some vocalizations delivered by the antshrikes are linked to certain actions. Wiley (1980) noted that “explosive ‘kseaa’” vocalizations (hereafter flight calls) are given at the onset of the flight, and are rarely given while perched. Another common vocalization of the antshrike is a low-pitched “bowr” (hereafter “perched call”) that is given while the antshrike is perched (Williams, pers. obs.). I investigated the potential linkage of flight and perching of the antshrikes with particular vocalization types through designed observations of individuals in mixed-species flocks. In addition, I assessed whether the number of flight calls given by an antshrike is proportional to the length of the flight. Since flight calls may be linked with flying, antwrens may move toward these calls in order to maintain proximity to the antshrikes. Antwrens should not fly toward perched calls since the antwrens should already be near the antshrikes while the antshrikes are stationary and giving perched calls.

Studying the mechanisms of interspecific cohesion can contribute to our understanding of how animals perceive and use environmental information in their own decisions (Schmidt et. al 2010). Amazonian mixed-species flocks represent a uniquely stable interspecific relationship in which many species gain information from one species (Terborgh 1990). Through investigating the mechanism of cohesion in these flocks, we can explain how a species perceives and uses information gained from heterospecifics to maintain the association with heterospecifics.

I hypothesized that antwrens use flight calls of the antshrikes to cohere to the antshrikes. I predicted that the latency for antwrens to approach the antshrike 1) is shorter after an antshrike flight call than after a non-vocal control treatment or a perched call control treatment and 2) is inversely related to the number of flight calls in a bout.

METHODS

Study area

Behavioral observations were collected at Los Amigos Biological Station (250-350 meters above sea level) in the Madre de Dios department, Peru (12.568° S, 70.100° W) in Apr-Jul 2014, May-Jul 2015, and Jun-Aug 2016. The climatic conditions are characterized by 25-33°C and 80-100% humidity. Annual rainfall averages 1500-2300 mm, and a dry season occurs between April and September (Pitman 2010). The 1500 m² of protected habitat around the field site consists of mostly primary terra firme forest, some secondary forest, palm swamps, dense bamboo patches, and floodplain forests. In the primary forest, the understory and subcanopy vegetation is dense, and the canopy height is 40-60 m. The tree species composition of the primary forest is extremely diverse, although some common, characteristic trees include *Parkia pendula*, *Cecropia* spp., and *Bertholletia excelsa*.

Behavioral observations

A flock was defined as at least two species of birds maintaining a distance of 10 m or less between species, for five or more minutes (Moynihan 1962, Stotz 1993). If an individual was farther than 10 m from a flocking individual, it was not considered to be participating in the flock.

The three focal species of antwren were the Long-winged, Gray, and White-flanked Antwrens. The three species are congeners, entirely insectivorous, forage by gleaning foliage,

and are susceptible to similar predators. They differ by the vertical stratification of understory in which they forage and slightly by their diet (Munn and Terborgh 1979, Rosenberg 1993).

All observations of focal individuals were made opportunistically (Altmann 1974). Data were taken between 45 minutes and 6 hours after sunrise. I recorded multiple flight and perched calls from at least 10 individuals. Recordings were made with a Roland R-26 recorder and Sennheiser ME 66 directional microphone with a sampling rate of 96 kHz and 24-bit waveform file format. Spectrograms of the calls were examined using the Raven Lite software (Figure 3.1; Charif et al. 2006).

Two distinct vocalization types were given frequently by the antshrikes (Figure 3.1). In order to determine whether certain vocalizations were associated with certain actions, I recorded the first vocalization type after encountering an antshrike, and whether the bird was flying or perched during the vocalization. Flight was defined as any time the antshrike changed positions and opened its wings. An antshrike was considered perched when its wings were closed and its feet were wrapped around a branch. No individual antshrike was sampled more than once per day.

One type of vocalization was significantly associated with flying and the other type was associated with perching (Table 3.1). Therefore, we named these two vocalization types the “flight call” and the “perched call.”

I considered an antwren to be cohering to the antshrikes only when the antwren flew toward the antshrikes. In order to test the prediction that the latency for an antwren to fly toward an antshrike is shorter for flight calls than for control treatments, I collected behavioral data on the

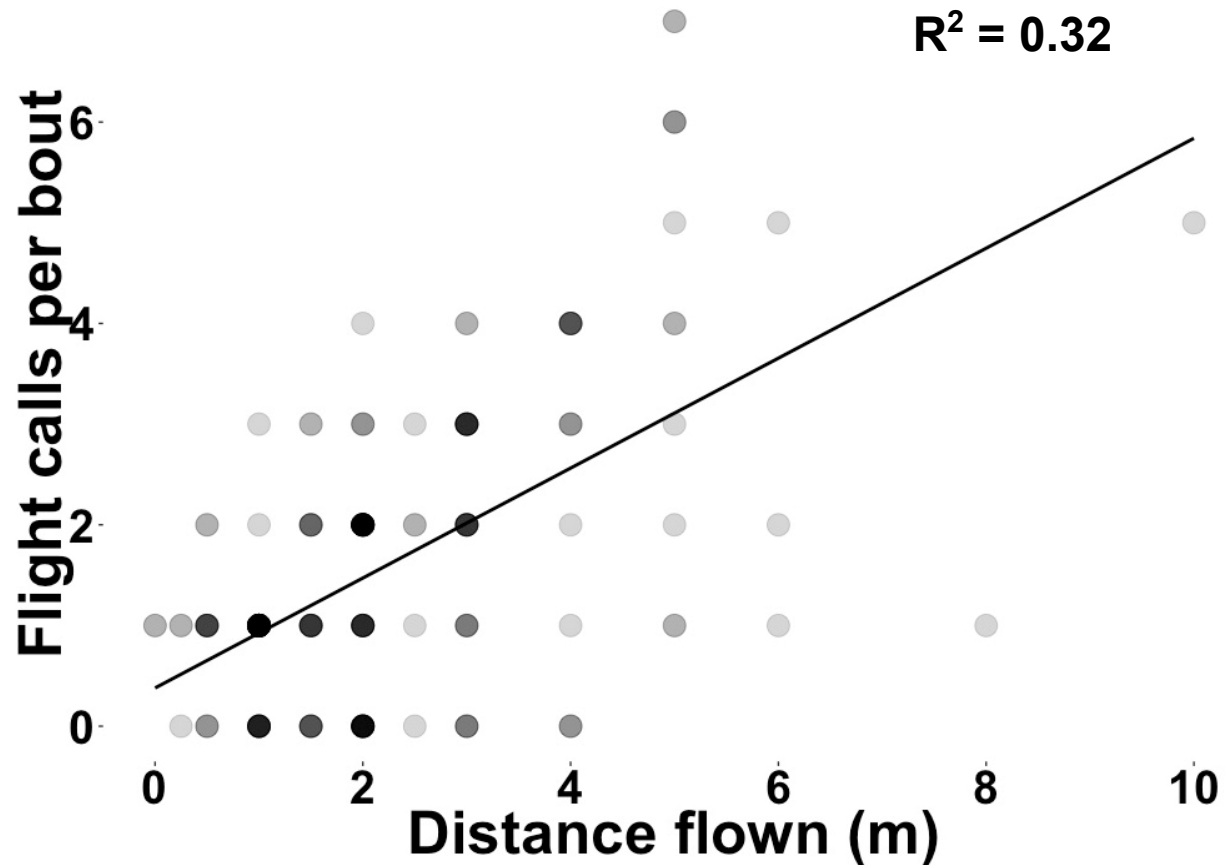


Figure 3.1. The number of flight calls given per bout increases with the distance flown (linear regression: $t = 9.33$, $df = 183$, $P < 0.001$), based on field observations in June-Aug 2015 and 2016. Paler circles represent fewer observations (as few as one) and darker circles represent more observations (as many as 28).

antwrens in the context of three treatments, i.e. two controls and the test treatment. A control treatment should have no effect on the latency for an antwren to fly toward the antshrike. For a non-vocal control treatment, I recorded the latency in seconds for the antwren to fly toward the antshrike at least one minute after visually detecting the antwrens, i.e. without regard to vocalizations of the antshrike. For the perched call control treatment, I recorded the latency for the antwren to fly toward the antshrike after a perched call. If the antwrens do not approach the antshrikes as a response to the perched call, the perched call control treatment should not differ from the non-vocal control treatment. Finally, for the flight call test treatment, I recorded the

Call type	Flight	Perched	# observations	# individuals
Flight call	271	4	275	54
Perched call	0	150	150	45

Table 3.1. Flight calls are almost always associated with flight and perched calls with being perched (Fisher's exact test: $df = 1$, $\chi^2 = 502$, $P < 0.001$).

latency for the antwren to fly toward the antshrike after a flight call. In addition, I noted the number of flight calls in the bout, which is defined as one or more calls given in succession, separated in time by no more than one second from the previous call.

A flight toward an antshrike was defined as the antwren opening its wings and moving a minimum distance of 0.5 m and a maximum angle of 30° away from the antshrike, with 0° being directly toward the antshrike. No antwren was sampled more than once per day.

Statistical analyses

In order to test the prediction that antwrens respond differently to different treatments, I used a generalized linear mixed-model with a Poisson distribution and log link function to model the latency for the antwrens to fly toward the antshrikes as a function of treatment, i.e. flight call, perched call control, and non-vocal control (Bolker et al. 2009). To model the latency for the antwrens to fly toward the antshrikes as a function of the number of flight calls, I used a generalized linear mixed-model with a Poisson distribution and log link function. A randomly assigned identification number for individuals was a random effect in each of the models.

I used the R Statistical Software version 3.2.3 and RStudio version 0.99.489 (R Core Team 2016; RStudio Team 2016).

RESULTS

Antshrikes gave flight calls almost exclusively while in flight, and perched calls exclusively while perched (Table 3.1). In addition, the number of flight calls was significantly positively associated with the distance of the flight of the antshrike (Figure 3.2).

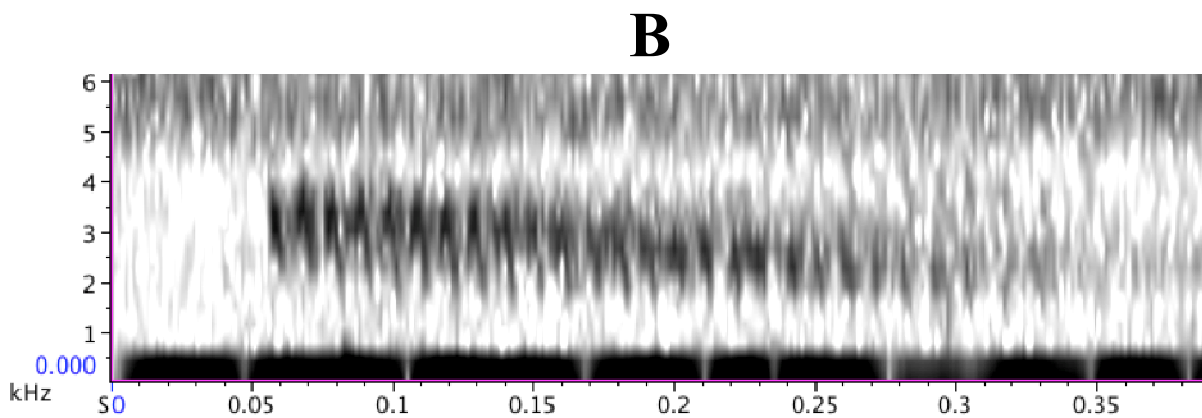
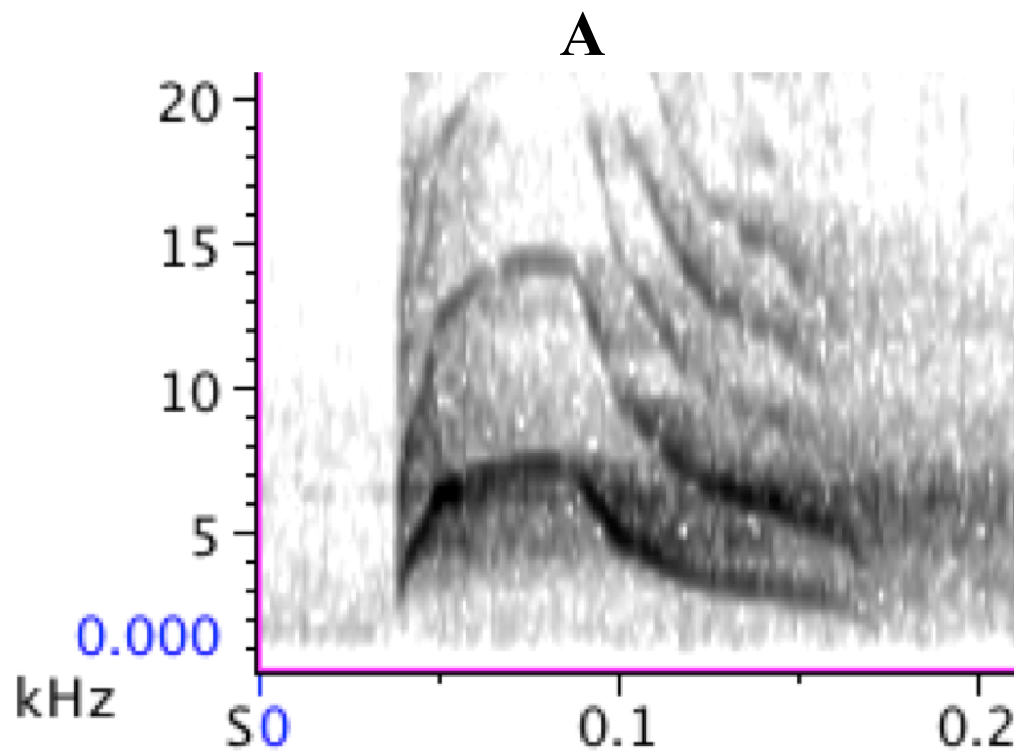


Figure 3.2. A) Flight calls were characterized by a quick (0.1 s), high-pitched “sping!” The flight call starts at a low frequency (2 kHz), and increases sharply until it levels off at 7.5 kHz, and then decreases back down to 2 kHz, first sharply, then slowly. Sometimes the call is given at lower amplitude, but still follows the same pattern otherwise. B) Perched calls were characterized by a low-pitched (1-3.5 kHz), descending “bowr.” The perched call is a rapid trill (0.3 s) of about 30 syllables, which are short (0.01 s) and quickly rise, then fall. Over the entire call, each syllable of the trill begins at a slightly lower pitched than the last syllable, resulting in what sounds like running a finger over a comb.

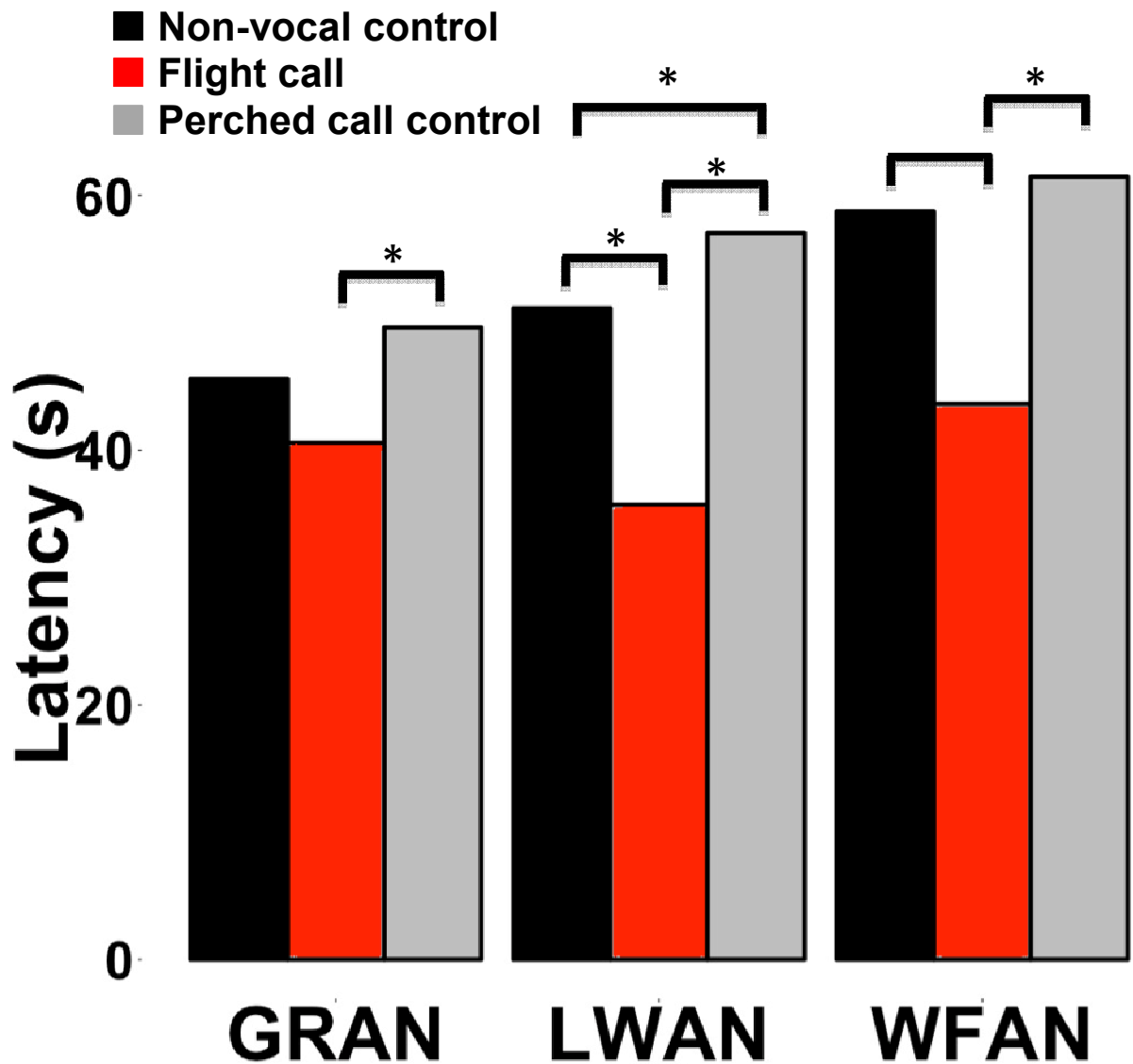


Figure 3.3. The latency to fly toward the antshrike for the flight call treatment was significantly shorter than the perched call control in all three antwren species (GRAN = Gray Antwren, LWAN = Long-winged Antwren, WFAN = White-flanked Antwren). The latencies for the flight call treatment for Long-winged and White-flanked Antwrens was significantly shorter than the control treatments.

The latencies for Gray, White-flanked, and Long-winged Antwrens to fly toward an antshrike were significantly lower for flight calls than for both control treatments (Figure 3.3). The one exception was that the latency for Gray Antwren was not significantly different between the

flight and non-vocal control treatment. In addition, the latency for the non-vocal control of the Long-winged Antwren was significantly lower than for the perched call control.

As the number of flight calls increased, the latency to fly toward the antshrike significantly decreased for Gray ($z = -7.2$, $P < 0.001$), White-flanked ($z = -5.1$, $P < 0.001$), and Long-winged Antwrens ($z = -17$, $P < 0.001$; Table 3.2). There was no effect of the individual on the latency to fly toward the antshrike.

Species	Estimate	z	P
Long-winged Antwren	-0.21	-17	<0.0001
White-flanked Antwren	-0.085	-5.1	<0.0001
Gray Antwren	-0.18	-7.2	<0.0001

Table 3.2. Model results of the effect of the number of antshrike flight calls on the latency for an antwren species to fly in the direction of an antshrike. The z statistic is the Wald test, which tests whether the effect is 0.

DISCUSSION

The flight call treatment had a significant negative effect on the latency of three antwren species to fly toward the antshrike compared to the control treatments, as predicted. Therefore, antwrens likely cohere to antshrikes by approaching the antshrikes after hearing flight calls. The antwrens likely associate the flight calls with antshrikes flying since the two behaviors are so strongly associated (Table 3.1). If the antwrens are predisposed to associate with the antshrikes, the antwrens should move toward the flight calls of the antshrikes in order to maintain their proximity.

An alternative explanation for the antwrens to fly toward the antshrikes is that the antwrens can see that the antshrikes are flying, and so they follow the antshrikes. Visual cues are common among birds, so this explanation is potentially viable (Sallabanks 1993, Bitton and Doucet 2016). The low light levels of rainforest understory and the drab, non-UV reflecting gray and brown coloration of antshrikes and antwrens produce little contrast of antshrikes and antwrens against

background coloration; thus visual communication may not have been strongly selected in these species (Gomez and Théry 2007, Schulenberg et al. 2007). Anderson et al. (2015) found that detectability of visual cues in rainforest is significantly hindered after 10 m due to obscuring by vegetation, but detectability of aural cues does not decline until after 40 m. Antshrikes give loud, piercing contact calls that can be heard from at least 30 m away (by humans; Wiley 1980, Williams, pers. obs.). Antwrens eavesdrop on antshrike alarm calls, so there is precedent for the hypothesis that aural cues serve as a mechanism of cohesion between antshrikes and antwrens (Jullien and Thiollay 1998, Martinez and Zenil 2012). Even if visual cues play some role in interspecific cohesion, aural cues likely serve as an important mechanism of cohesion; redundancy is common in nature (Møller and Pomiankowski 1993, Uetz et al. 2009).

The latency for the Long-winged Antwren to fly toward an antshrike was greater for the perched call control than the non-vocal control, which was not predicted. If flight calls function as a mechanism of cohesion, it is possible that the antwrens use other calls as mechanisms of cohesion. The perched call was only ever given in the context of the antshrike being perched. At our field site, the Long-winged Antwren is the only antwren that is found with the antshrike all or nearly all the time (Williams and Lindell in review). The Long-winged Antwrens likely know that the antshrikes give the perched calls only while perched. The antwrens may perceive the calls as anchoring the antshrikes to the current location of the flock, and so the antwrens may be more likely to stay in their current location than what would be expected at a random moment in time, i.e. the non-vocal treatment.

Within the flight call treatment, the latency of the antwrens to fly toward the antshrike was negatively associated with an increasing number of flight calls within a call bout, as predicted. Interspecific communication among birds sometimes encodes contextual information. For

example, White-browed Scrubwrens (*Sericornis frontalis*) and Superb Fairy-Wrens (*Malurus cyaneus*) mutually eavesdrop on each other's alarm calls. Both species are mutually more likely to flee in response to the heterospecific alarm call when the alarm call bout contains more calls, which indicates a greater risk of predation (Fallow and Magrath 2010). In a similar vein, the antwrens likely interpret the variation in the number of flight calls within a bout as a reliable indicator of the distance flown by the antshrike (Fig. 1). The antwrens may be more likely to fly toward the antshrikes sooner when they hear a greater number of flight calls because there is a greater likelihood of the antwrens losing their proximity to the antshrikes if the antshrikes fly a longer distance.

In multi-species associations, species may communicate deliberately with each other, or eavesdrop for information on food and predators (Dolby and Grubb 1998, Suzuki 2012, Fallow et al. 2013, Baigrie et al. 2014, Farine et al. 2015). For example, alarm vocalizations are given in certain contexts, on which heterospecifics eavesdrop for their benefit (Shriner 1999, Magrath et al. 2007, Wheatcroft and Price 2013). Interspecific acoustic eavesdropping and active signaling most commonly occur around alarm calling species (Westrip and Bell 2015). Is the flight call from the antshrikes eavesdropped upon by antwrens, or are the flight calls an active signal directed toward the antwrens? Westrip and Bell (2015) argue that in order to classify interspecific communication as eavesdropping or active signaling, it is necessary to determine whether the benefits received by the signaler, i.e. the antshrike, depend on whether the receiver, i.e. the antwren, responds. The antshrikes may accrue some anti-predation benefits from associating with the antwrens through the many eyes effect, the dilution effect, or the confusion effect (Beauchamp 2003, Ale and Brown 2007, Beauchamp 2012), although these benefits have not been demonstrated explicitly in our study species. Antshrikes sometimes approach antwren

vocalizations, which means that antshrikes likely receive some benefit from associating with antwrens, suggesting that the flight calling from the antshrikes can be considered active signaling (Williams and Lindell in press). Alternatively, it is possible that the antshrikes produce the vocalizations for conspecific communication and the antwrens eavesdrop. However, I observed 12 instances over three months of fieldwork in which only one antshrike and several antwrens were present. In every occasion, the antshrikes still produced the flight calls even in the absence of a conspecific, which is consistent with the hypothesis that the flight calls are an active signal directed toward heterospecifics.

Other species in the world may actively signal to heterospecifics as a mechanism of interspecific cohesion. For example, playback of drongo vocalizations (*Dicrurus*), which give alarm calls in the presence of predators, attract many flocking species (Goodale and Kotagama 2008, Cordeiro et al. 2015). However, it is unclear whether the drongos vocalizations are associated with flying or perching.

In conclusion, I found that the latency for antwrens to fly toward an antshrike is shorter after flight calls given by the antshrike than for perched calls and a non-vocal control. In addition, the latency shortens when there are more flight calls in a bout. The antwrens are likely responding to these calls differentially as a mechanism of cohering to the antshrike, which confers benefits to the antwrens. The antshrikes may be signaling the antwrens actively in order to gain anti-predation benefits associated with flocking, but further research is necessary to support this hypothesis. Overall, our results indicate that interspecific cohesion can be maintained by active signaling of a context-dependent vocalization.

LITERATURE CITED

LITERATURE CITED

- Ale, S. B. and J. S. Brown. 2007. The contingencies of group size and vigilance. *Evolutionary Ecology Research* 9:1263-1276.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267
- Anderson, A. S., T. A. Marques, L. P. Shoo, and S. E. Williams. 2015. Detectability in audio-visual surveys of tropical rainforest birds: The influence of species, weather and habitat characteristics. *PLoS ONE* 10:e0128464.
- Baigrie, B. D., A. M. Thompson, and T. P. Flower. 2014. Interspecific signalling between mutualists: food-thieving drongos use a cooperative sentinel call to manipulate foraging partners. *Proceedings of the Royal Society B*:20141232.
- Beauchamp, G. 2003. Group-size effects on vigilance: A search for mechanisms. *Behavioral Processes* 63:111-121.
- Beauchamp, G. 2012. Flock size and density influence speed of escape waves in semipalmated sandpipers. *Animal Behavior* 83:1125-1129.
- Bitton, P., and S. M. Doucet. 2016. Sympatric Black-headed and Elegant Trogons focus on different plumage characteristics for species recognition. *Animal Behaviour* 113:213-221.
- Bohorquez, C. I. 2003. Mixed-Species bird flocks in a montane cloud forest of Colombia. *Ornitología Neotropical* 14:67-78.
- Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415:426-429.
- Charif, R. A., D. W. Ponirakis, and T. P. Krein 2006. Raven Lite 1.0 User's Guide. Cornell Laboratory of Ornithology, Ithaca, NY.
- Cordeiro, N. J., L. Borghesio, M. P. Joho, T. J. Monoski, V. J. Mkongewa, and C. J. Dampf. 2015. Forest fragmentation in an African biodiversity hotspot impacts mixed-species bird flocks. *Biological Conservation* 188:61-71.
- Côte, I. M., C. Arnal, and J. D. Reynolds. 1998. Variation in posing behavior among fish species visiting cleaning stations. *Journal of Fish Biology* 53 (Supplement A):256–266.
- Fallow, P. M., and R. D. Magrath. 2010. Eavesdropping on other species: Mutual interspecific understanding of urgency information in avian alarm calls. *Animal Behaviour* 79:411-417.

- Fallow, P. M., B. J. Pitcher, and R. D. Magrath. 2013. Alarming features: birds use specific acoustic properties to identify heterospecific alarm calls. *Proceedings of the Royal Society B* 208:20122539.
- Farine, D. R., L. M. Aplin, B. C. Sheldon, and W. Hoppitt 2015. Interspecific social networks promote information transmission in wild songbirds. *Proceedings of the Royal Society of Biological Sciences- B* 282:20142804.
- Ficken, M. S, R. W. Ficken, and S. R. Witkin. 1978. Vocal repertoire of the Black-capped Chickadee. *Auk* 95:34-48.
- Gomez, D., and M. Théry. 2007. Simultaneous crypsis and conspicuousness in color patterns: Comparative analysis of a Neotropical rainforest bird community. *American Natural* 149: S42-S61.
- Goodale, E. and S. W. Kotagama. 2008. Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rain forest. *Behavioral Ecology* 19:887-894.
- Greenberg, R. 2000. Birds of many feathers: The formation and structure of mixed-species flocks of forest birds. In *On the move: How and why animals travel in groups* (Boinski, S. and Garber, P.A., eds.), pp. 521-558, University of Chicago Press.
- Dolby, A. S. and T. C. Grubb. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. *Animal Behavior* 56:501-509.
- Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti... et al. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3-35.
- Husemann, M., W. Ulrich, and J. C. Habel. 2014. The evolution of contact calls in isolation and overlapping populations of two white-eye congeners in east Africa (Aves, Zosterops). *BMC Evolutionary Biology* 14:115.
- Kondo, N. and S. Watanabe. 2009. Contact calls: Information and social function. *Japanese Psychological Research* 51:197-208.
- Janik, V. M. and P. J. B. Slater. 1998. Context-specific use suggests that bottlenose dolphins signature whistles are cohesion calls. *Animal Behaviour* 56:829-838.
- Jullien, M. and J. M. Thiollay. 1998. Multi-species territoriality and dynamics of Neotropical forest understory bird flocks. *Journal of Animal Ecology* 67:227-252.
- Magrath, R. D., B. J. Pitcher, and J. L. Gardner. 2007. A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. *Behavioral Ecology* 18:944-951.
- Martinez, A. E., and R. T. Zenil. 2012. Foraging guild influences dependence on heterospecific

- alarm calls in Amazonian birds flocks. *Behavioral Ecology* 23:544-50.
- Møller, A. P. and A. Pomiankowski. 1993. Why have birds got multiple sexual ornaments. *Behavioral Ecology and Sociobiology* 32:167-176.
- Moynihan, M. 1962. The organization and probably evolution of some mixed species flocks of neotropical birds. *Smithsonian Miscellaneous Collection* 143:1-140.
- Mumm, C. A., M. C. Urrutia, and M. Knornschild. 2014. Vocal individuality in cohesion calls of giant otters, *Pteronura brasiliensis*. *Animal Behavior* 88:243-252.
- Munn, C. and J. Terborgh. 1979. Multi-species territoriality in neotropical foraging flocks. *Condor* 81:338-347.
- Neill, S. R. S. J. and J. M. Cullen. 1974. Effects on whether schooling by their prey affects the hunting behavior of cephalopods and fish predators. *Journal of Zoology* 172:549-569.
- Nininuan, S, P. D. Round, G. A. Gale. 2004. Structure and composition of mixed-species bird flocks in Khao Yai National Park. *Natural History Bulletin of the Siam Society* 52:71-79.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rosenberg, K. V. 1993. Diet selection in Amazonian antwrens: Consequences of substrate specialization. *Auk* 110:361-375.
- RStudio Team. 2016. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. <http://www.rstudio.com/>.
- Sallabanks, R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology* 74:1326-1336.
- Schulenberg, T., D. F. Stotz, D. F. Lane, J. P. O'Neill, and T. A. Parker. 2007. *Birds of Peru*. Princeton University Press: Princeton, New Jersey, USA.
- Shriner, W. M. 1999. Antipredator responses to a previously neutral sound by free-living adult golden-mantled ground squirrels, *Spermophilus lateralis* (Sciuridae). *Ethology* 105:747-757.
- Soliveres, C., C. Smit, and F. T. Maestre. 2015. Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning, and evolution of plant communities. *Biological Reviews* 90:297-313.
- Stotz, D. F. 1993. Geographic variation in species composition of mixed species flocks in lowland humid forests in Brazil. *Papeis Avulsos de Zoologia* 38:61-75.

- Suzuki, T. N. 2012. Long-distance calling by the willow tit, *Poecile montanus*, facilitates formation of mixed-species foraging flocks. *Ethology* 118:10-16.
- Trillmich, J., C. Fichtel, and P. M. Kappeler. 2004. Coordination of group movements of Verreaux's sifakas (*Propithecus verreauxi*). *Behaviour* 141:1103-1120.
- Uetz, G. W., J. A. Roberts, and P. W. Taylor. 2009. Multimodal communication and mate choice in wolf spiders: Female response to multimodal versus unimodal signals. *Animal Behaviour* 78:299-305.
- Westrip, J. R. S. and M. B. V. Bell. 2015. Breaking down the species boundaries: Selective pressures behind interspecific communication in vertebrates. *Ethology* 121:725-732.
- Wheatcroft, D., and T. D. Price. 2013. Learning and signal copying facilitate communication among bird species. *Proceedings of the Royal Society B* 280:20123070.
- Wiley, R. H. 1980. Multispecies antbird societies in lowland forests of Surinam and Ecuador: Stable membership and foraging differences. *Journal of Zoology* 191:127-145.
- Youngsteadt, E., S. Nojima, C. Häberlein, S. Schulz, and C. Schal. 2008. Seed odor mediates an obligate ant-plant mutualism in Amazonian rainforests. *Proceedings of the National Academy of Sciences* 105:4571-4575.