

INTERSPECIFIC COMMUNICATION AND ITS CONSEQUENCES FOR THE  
ORGANIZATION OF PERMANENT MIXED-SPECIES BIRD FLOCKS

By

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To my mom

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INTERSPECIFIC COMMUNICATION AND ITS CONSEQUENCES FOR THE  
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Information use by animals has consequences for decision-making that can translate into community level patterns. My dissertation encompasses empirical approaches, using direct observations and experiments to evaluate animal behaviors and data on behavioral and morphological traits to understand community assembly of species in groups. In addressing these issues, I used mixed-species flocks of birds in the lowland forests of Northeastern Peru as my main study system, with additional data collected from field sites in Bolivia and French Guiana. I show that flock characteristics, such as the distribution of roosting sites, territory location and species composition remain unchanged over a 17 year period suggesting a high degree of environmental stability (Chapter 2). Stable and constant environments may lead to the evolution of complex communication between species in groups. I subsequently conduct experimental tests through playbacks as to whether information use is unidirectional or bidirectional among different species in flocks and find that information use is unidirectional: species respond to different cues, such as the songs and calls of only the one species that provides information on predators through alarm calling. The evidence that information use is centered around alarm calling heterospecifics led me to

experimentally test whether species respond differently to threat information as a function of their foraging guild. My results suggest that myopic birds indeed have stronger responses to alarm calls than flycatching birds which search for prey, and thus are more aware of predators, at a distance. I subsequently test to what extent different behavioral and morphological traits influence a species tendency to join flock and corroborate these results with experimental tests of how these traits may influence response to threat information given in alarm calls. I show that while body mass, foraging height and foraging strategy all influence a species tendency to participate in mixed species groups, foraging strategy alone explains responses to alarm information. These results suggest that information use in mixed species groups in forested habitats often centers around threat information provided by one or a few heterospecifics. The dependency on such information, as influenced by morphological traits such as foraging strategy will allow informed predictions as to the traits that influence the assembly of mixed species groups where perceived predation risk is high.

## CHAPTER 1 INTRODUCTORY REMARKS

Information use by animals occurs in many contexts, and has direct consequences for reducing uncertainty and influencing individual fitness (Wagner and Danchin 2010). Social information, in which animals receive information from other animals, is perhaps one of the most widespread contexts under which information gathering occurs (Danchin et al. 2004). Social groups provide some of the most concrete examples in which animals collect information about food or predators from other individuals (Alexander 1974). Some of the best examples of the use of social information occur through the formation of mixed species groups, which can range from fluid and dynamic to permanent and stable entities. As such, mixed-species animal groups are communities that provide a wonderful opportunity to understand the different scenarios under which species produce and receive information and how these mechanisms may lead to the organization of mixed-species groups. Indeed while much work has discussed the nature of information within groups (Seppanen et al. 2007) studies that quantify this aspect of communication are few (Goodale et al 2010). Understanding the degree to which species produce and receive information from each other is the basis for understanding how groups are structured. Quantifying the degree of symmetry of information flow between species can provide insight into the nature of species interactions that underlie group formation and may indicate the degree to which certain species disproportionately maintain group cohesion. From a conservation context, the latter may have important implications understanding how the loss of certain species may disproportionately affect communities.

Understanding the nature of cohesion of mixed species groups necessitates an understanding of the nature of producers and receivers of information and the degree to which species take on one or both of those roles (Goodale et al. 2010). Where species share common food resources or share traits that allow them to be equally vigilant against predators, information flow is expected to be bidirectional amongst species (Krebs 1973, Goodale and Kotagama 2008). However in many animal groups, species may disproportionately provide certain kinds of information such as alarm calling or mobbing of which other species may take advantage (Gaddis 1980, Nolen and Lucas 2009). While the extent to which information flow is bidirectional among species may indicate the nature of interactions within groups, there is still little information allowing us to predict what types of species might produce or receive such information. With the growing recognition of the importance of information transfer as a mechanism structuring communities, we must now determine which traits determine if species become producers of information, receivers of information or both (Seppanen et al. 2007, Goodale et al. 2010). To date, most research in this area has focused on the traits associated with species that produce and send information of different types to other species in a group. In contrast, few studies have examined the traits that determine the degree of dependence amongst species that are receivers (Goodale et al. 2010). Even less is known about complex communication such as deception, which has been hypothesized to occur in highly stable societies.

Neotropical mixed-species bird flocks have long been recognized for their stability and organization and complex communication among member species, including deception (Munn 1986, Greenberg 2000). Thus they provide an ideal system

to quantify the nature of information flow among different species in general and allow us to test the hypothesis that stability leads to complex communication such as symmetrical information flow (Munn and Terborgh 1979). The high diversity of species that join these flocks also provides an opportunity to evaluate the traits that allow species to be producers and receivers and thus the traits that might be responsible for the assembly of animal groups.

I use Amazonian systems to test the hypothesis of stability, the nature of information flow among groups and the traits that might influence the degree to which species are receivers that depend upon heterospecific threat information.

In Chapter 2 I revisit a field site where flock territories were documented previously on a well-established grid in Nouragues French Guiana. By sampling characteristics (roosting sites, territory locations) of these flocks during my visit, I was able to compare my estimates of those characteristics to those obtained in the original study and thus determine that these elements have barely changed over the 17 year period. These results provide the first test of stability across multiple generations in these societies. In my third chapter I evaluate the nature of information flow by determining whether species in permanent flocks respond to each other's cues. I did so by conducting playback experiments and measuring whether species are attracted to both vocalization cues and movement of other species in the flock. My fourth chapter tests whether a particular trait, foraging strategy, influences dependence on heterospecific threat information. I used playback experiments to measure how species respond to and resume normal activity in response to alarm calls from a heterospecific. I test this by looking at two separate flock systems from two different habitats. My final

chapter expands this analysis to an entire community by evaluating traits that influence the dependence of species on heterospecific threat information by assessing the response of a large number of species to the alarm calls of heterospecifics. Thus I evaluated the extent to which birds depend upon threat information as a function of behavioral traits such as foraging strategy, body size, foraging height, vegetation density and morphological traits such as body size.

The nature of information flow and use amongst different species in animal groups ultimately may influence the degree of cohesion and stability that characterize such a group. The results of these experiments will provide a mechanistic explanation of information flow and use and the underlying traits that may influence the dependence on heterospecific information. Understanding how specific traits underlie the nature of producers and receivers of social information will thus contribute to a predictive framework for how social information influences the organization of mixed species groups.

## CHAPTER 2 ARE MIXED-SPECIES BIRD FLOCKS STABLE THROUGH TWO DECADES?

### **Introduction**

Ecologists have hypothesized that constant environmental conditions through evolutionary time such as those presumed to exist in the tropics explain both high diversity and the maintenance of stable biological communities (Dobzhansky 1950; Pianka 1966). Despite this perception, studies of community stability (i.e. persistence in species composition and community structure through time) have mainly focused on non-tropical ecosystems (Ives and Carpenter 2007). The limited number of studies from the tropics has reported varying degrees of stability. Furthermore, most studies in the tropics focus on sessile plants and animals, presumably because they are easier to monitor through longer periods of time (Collins 1995; Condit 1995; Connell et al. 1997).

Studies of stability in mobile tropical animal communities are scarce, logistically challenging, and rarely include data from more than a few years. Early studies of tropical bird communities suggested stability in bird diversity, abundance and spatial distribution (Orians 1969, Ricklefs 1973, Greenberg and Gradwohl 1986; MacArthur 1972; Munn 1985; Murray 1985). However, studies using mist-nets have documented high variation in species composition and abundance over a 3-8 year period (Karr 1976; Karr 1982; Martin and Karr 1985; Loiselle and Blake 1992). Therefore the stability of highly mobile tropical bird communities remains poorly understood.

Mixed-species flocks are among the most fascinating natural history features of neotropical bird communities. Specifically, these flocks form socially complex

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aggregations that exhibit year round multi-species territoriality and partitioning of ecological roles including alarm calls and defense. These flocks occur throughout the Neotropics (Central America: Powell 1979; Greenberg and Gradwohl 1986; Amazonia: Munn and Terborgh 1979; Munn 1985; Guiana shield: Jullien and Thiollay 1998; Atlantic Forests of Brazil: Stotz 1993) and are among the most cohesive multi-species groups found in terrestrial vertebrates (Munn 1985). Amazonian flocks, for example, usually consist of a permanent group of five to ten species pairs or family groups of insectivores that defend a joint home range (Munn 1985). They are usually led by one or two “sentinel species” from the antbird genus *Thamnomanes* (Munn and Terborgh 1979; Jullien and Thiollay 1998). Sentinels, which appear to lead the flock as it moves, constantly vocalize and sound “alarm calls” in the presence of predators. Other members of the flock remain within several meters of the sentinels, and take advantage of alarm calls. Other members are usually perch-gleaning insectivores, many in the antwren genus *Myrmotherula*, that spend most of their time myopically searching for insects, often while probing their entire head into suspended, curled dead leaves and other dense clusters of leaves. Sentinels have been hypothesized to benefit from flushed insects and possibly stealing large prey items while distracting them with the use of “false” alarm calls (Munn 1986). Up to 65 other species join these flocks throughout the day within single forest bird communities, which means that they play a central role in the ecology of a large fraction of the resident bird community of neotropical forests (Munn and Terborgh 1979; Munn 1985; Jullien and Thiollay 1998).

Stability of the flocks in space and time may allow for the rise of evolutionary stable strategies such as the interdependence of flock members that flush insects and

the flycatcher foraging behavior of the “sentinels” that benefit from catching flushed prey (Munn 1986). Only one study, however, has documented territorial stability of mixed-species flocks. Greenberg and Gradwohl (1986) found that flocks in central Panama were stable in terms of territory occupancy and species composition over an eight-year period. Apart from this study most information on the stability of mixed species flocks is largely anecdotal, and opportunities to measure stable territories or home ranges and species composition over multiple generations would be useful in documenting the extent to which stability is widespread in this community module.

Jullien and Thiollay (1998) reported the home-ranges and roosting sites of 11 flocks occurring in the Nouragues field station in French Guiana in 1994. These flocks were located in a ~130 ha trail system of lowland *tierra firme* forest. Almost 20 years after Jullien and Thiollay (1998) originally mapped the home ranges and roosting sites of these flocks, the Nouragues station has maintained an environment free of human impact. Nevertheless, the forest is highly dynamic, with tree-fall gaps opening frequently but closing in short periods of about five years (P.M. Forget *personal comm.*). This suggests that the forest has a stable landscape composition free of large-scale disturbances, but retains the gap-phase dynamics typical of tropical forest communities (Brokaw 1985; Denslow 1987). The 20-year interval between the first study and the present is likely to comprise more than one generation of birds (Brawn et al. 1985, Blake and Loiselle 2008) giving us a unique opportunity to test whether flock features outlive the individuals that form them. Given that selection acts on individuals, the retention of the characteristics through different generations would allow us to make

inferences about the evolution of flocking behavior. Thus, Nouragues is an ideal site to document the stability of flock characteristics over a 20-year interval.

In this study, we quantify patterns of home range stability and the spatial distribution of mixed-species flocks by comparing samples of home ranges, the location and spatial distribution of roosting sites, and species composition of flocks from 1994 and 2011. We compared observed values of home range overlap, distance between roosting sites, dispersion between roosting sites and species similarity between the flocks in 1994 and 2011. We further constructed several null models to determine if such results are in fact the result of true community stability or random expectation. Quantifying such patterns will allow us to better understand the stability and distribution of tropical rainforest communities, and to understand the conditions under which such complex multi-species associations might have evolved.

### **Methods**

In October 2011, based on the home range and gathering site map by Jullien and Thiollay (1998), we located each of the eleven flocks by visiting grid locations where roosting sites were originally reported. We use the term roosting site instead of gathering site because we believe that species do not gather but actually spend the night in close proximity to each other at the site. Every day we found a flock in a roosting site most of the species were close together and we did not find evidence that species started to gather as the “sentinel” species started calling. Although *Thamnomanes antshrikes* often sang first, most species started singing at nearly the same time, and in some cases we located the flock by the call of a core species other than the sentinel. We arrived at sites reported on the map before dawn and located flocks by song identification of sentinel species. If the flock was located using the song

of other core species, we waited until we made visual contact with flock members to identify the sentinels and subsequently marked the coordinate locations of the flock roosting sites using a Garmin 60 csx GPS unit. Next, we followed the flock as closely as possible and recorded its location every 10 minutes and species composition over 30 minute intervals in the same day. We repeated this with each of 11 flocks based on roosting site locations established in the original study (Jullien and Thiollay 1998). We usually started the first interval at 6:30 am and followed the flock continuously until 5:00 pm. We followed seven flocks for 11 hours, one flock for 10.5 hours, two flocks for 10 hours and one flock for 9.5 hours for a total of 117 hours. Jullien and Thiollay (1998) followed the flocks for 937 hours. Color-banded individuals as in the original study would have helped us identify individual flocks allowing us to follow them for more than one day. Because we did not have marked individuals, however, we restricted sampling effort to one day per flock. However, we believe this has little effect on our study because we were testing for position of roosting site and flock territory and not territory size. To look at species occurrence, we recorded the % of the 11 flocks in which each species occurred. Birds were considered part of the flock if they were seen moving and feeding within 15m of other birds for at least 15min (see Jullien and Thiollay 1998).

### **Data Analysis**

Using Arc GIS v 9.3 (ESRI 2011), we digitized the map reported in the original paper (Figure 8 in Jullien and Thiollay 1998) and georeferenced it using our own data points from trail intersections and a grid layer provided by CNRS (Centre National de la Recherche Scientifique). We further reproduced the figure creating a digital map of roosting sites and flock territories. This allowed us to compare distances between 1994 and 2011 roosting sites, the average nearest neighbor distance and the percent overlap

of territories in 1994 and 2011. To determine statistical significance of each comparison, we constructed four null models: one for the distance between the 1994 and 2011 roosting sites, one for the average nearest neighbor at 1994 and 2011, and two different null models for the percentage overlap of territories. All of the following analyses regarding null models were constructed using ArcGIS except when noted. The p-value of all randomization tests was calculated by dividing the rank of the observed value in the null distribution by the number of randomizations made.

### **Null Model of Roosting Sites**

To establish whether the roosting sites we observed in 2011 were closer to those observed in 1994 than expected by chance we first calculated the distance from the roosting site reported in the original map (Jullien and Thiollay 1998) to the one recorded in 2011. We then built a null model in which we reconstructed 1000 random roosting sites within the 1994 flock home range and calculated the distance between each of these 1000 random roosting sites and the observed 1994 roosting site and built a null distribution of distance values. If smaller than expected by chance, then the observed distance will be smaller than most distances from the random distribution.

### **Null Models of Overlap of Home Range Points**

In this case we were confronted with biologically realistic null models that were either too relaxed or too restrictive. As a result we include both models here.

#### **Null model 1 (relaxed).**

First, we constructed polygons that matched the size of the home range of each flock in the one-day samples of 2011. Then, we constructed a polygon of the size of the 1994 eleven flock home-ranges combined. Next, we randomly placed the constructed 2011 polygon 1000 times each within the bigger polygon and calculated the amount of

overlap between flock *i* in 1994 and the 2011 random polygons. This resulted in a distribution of percent overlap between the 1994 and the 1000 2011 randomly placed polygons. We were interested in testing if the amount of observed overlap was greater than expected by chance; thus, we expected the observed value to be greater than the majority of overlaps generated randomly.

### **Null model 2 (restrictive)**

For this null model we used the same concept as in the previous one, but this time we randomly placed 1000 points within the 1994 home range of each flock and used those points as the centroid of 1000 polygons based on the size of the 2011 one-day sample. This null model might be more realistic than the first one because our searching for flocks was not random throughout the grid of the station but was systematically targeted to the home range that each flock occupied in 1994. However, it is also much more restrictive in that all the randomly placed polygons will be biased to have high degrees of overlap.

### **Nearest Neighbor Ratio (NNR) Analysis**

We used roosting sites from both 1994 and 2011 to test the hypothesis that flocks were evenly distributed in the space available. Roosting sites were spread over two habitat types that clearly influenced home range size (see Jullien and Thiollay 1998 and our own results below); thus, for this analysis, we only used eight of the roosting sites that were located in high mature forest (see Jullien and Thiollay 1998) habitat to remove this bias. We used the Average Nearest Neighbor distance tool in ArcGIS to compare the average nearest neighbor distances between roosting sites of the eight flocks. This analysis calculated the distance between each point in the data set and its nearest neighbor and determined if the points were clustered, random or overdispersed

in a given space. It is based on the ratio between observed and random average distance. A ratio greater than one means that points are more dispersed in space than expected by chance, which is the result we predicted. We set the area to which the points could be randomly placed to be the area of the grid that the eight flocks occupied. We further calculated standardized effect size (SES.NNR) of the NNR and associated p-values to test if flocks were overdispersed within the Nouragues station grid.

### **Comparison of Community Composition of Flocks**

We used the Bray-Curtis (BC) dissimilarity index to compare community composition between the flocks in 1994 and 2011. The BC index ranges from 0 (similar) to 1 (dissimilar) and measures similarity between two sets of samples (Krebs 1989). We then randomized 1000 times the community matrix for each time period keeping the number of species present in each period of time constant thus generating a null distribution of dissimilarity indices. We compared the observed dissimilarity index with the randomly generated distribution of values and calculated a p-value in the same way as previous null models. The randomizations were constructed using the picante package (Kembel et al. 2010) for R (R Development Core Team 2011) and the Bray Curtis index was calculated using vegan package (Oksanen et al. 2011).

## **Results**

### **Change in Roosting Sites**

Seven out of 11 roosting sites observed in 2011 were statistically identical to those observed in 1994 (Figure 2-1 and Table 2-1). Of the other four roosting sites, Flock 8 was the only flock where the roosting site was not closer or further than expected by chance from the 1994 sites (see p-values in Table 2-1).

## **Home Range Overlap**

Visually, the single day sample of home ranges observed in 2011 appeared to overlap greatly with the original home ranges from 1994 (Figure 2-1). This was confirmed using null model 1 where ten of the eleven flocks had a higher overlap than expected by chance (Table 2-1). However, null model 2, which is more restrictive, suggested that only three of the single-day samples in 2011 had a significantly higher overlap with the original home ranges observed in 1994 than expected by chance alone with two more showing a strong tendency in the same direction (Table 2-1). The other six flocks showed results in the direction of greater stability in space (higher overlap than expected), but their overlap could not be distinguished from a random expectation.

## **Roosting Site Distribution**

The results from the NNR analysis suggest that distribution of roosting sites was non-random for both periods of time (1994 and 2011). For 1994 and 2011 the NNR was higher than 1 suggesting that roosting sites were overdispersed in the Nouragues station grid (NNR 1994 = 1.7; NNR 2011 = 1.71). In fact, SES.NNR was positive and significant also suggesting the overdispersion in space of the roosting sites (ses.NNR 1994 = 3.79  $p < 0.001$ , ses.NNR 2011 = 3.85,  $p < 0.001$ ).

## **Community Composition**

Species composition was more similar than expected by chance when comparing samples from 1994 with 2011, suggesting that flocks are mainly composed of the same species in the two time periods (Observed BC index = 0.26, Mean Null BC index = .61, Null BC Standard Deviation = 0.047,  $p < 0.001$ , Figure 2-2, Appendix).

## Discussion

To our knowledge, our study provides evidence for the longest period of stability in space and composition documented for a Neotropical animal community. The strikingly similar position of territory and roosting-sites in 1994 and 2011 (Figure 2-1) was corroborated by statistical tests of these patterns against null models (Table 2-1). This stability almost certainly occurred across multiple generations of flocking species, which generally are thought to live between 2 - 4 years (Brawn et al. 1985; Blake and Loiselle 2008). At the Nouragues field site many of the birds that participated in the original flocks in 1994 were banded (Jullien and Thiollay 1998). However, in our sampling from 2011, none of the birds were banded suggesting that all of the almost identical home ranges and roosting sites were being used by different individuals. Thus, our study provides evidence of community stability through more than one generation, a limitation of most studies addressing these types of questions (Connell and Sousa 1983).

Theoretical models suggest that long-term environmental stability is required for the selection of traits that lead to evolutionary stable strategies (Maynard Smith and Price 1973). However, environmental stability may be altered in the forest by large-scale and local-scale disturbances that could potentially perturb animal communities in different ways. In humid lowland Amazonian rainforests, natural disturbances manifest themselves primarily as tree fall gaps within the forest matrix (Brokaw 1985; Denslow 1987). However, while gaps occur throughout the forest across a number of bird home ranges, they are generated in random fashion and on smaller scales than home ranges of flocks. The average home range size of flocks at the Nouragues station is 10.3 ha and tree fall gaps in Amazonian forests have been reported to vary between 0.001 and

0.4 ha (Uhl et al. 1988). Flock home ranges therefore may be large enough that they need not change in response to the most common form of disturbance. Because they are larger than tree fall disturbances generated by gap-phase dynamics, home ranges would naturally provide a constant environment and thus the conditions necessary for stability in territory position and species composition of the multi-species flocks.

At the same time, stability might have strong implications for the evolution of characteristics of birds in mixed-species flocks such as “sentinel” alarm systems and kleptoparasitism. The flycatcher foraging strategy of sentinels potentially allows them to be more vigilant and emit alarm calls in case of predation threat (Munn 1985; Sridhar et al. 2009; Martinez and Zenil 2012). In return, “sentinels” might take advantage of the alarm systems by sounding false calls to steal prey items from other flock members (i.e. kleptoparasitism: Munn 1986; Martinez and Gomez pers. obs.). The evolution of these complex behaviors and strong interdependence between sentinels and other members of the flock can only happen in a scenario of long-term stability in which the signal of selection for these behaviors is strong and constant during long periods of time (Futuyma and Moreno 1988).

The stability in composition of mixed flocks is consistent with results of several plant studies that report compositional stability in large plots throughout the Neotropics (see Condit 1995 for review). Evidence suggests that the Nouragues station shares this plant community stability with other large plots in the Neotropics (Sarhou et al. 2010). Thus, it is possible that flock stability evidenced here results from long-term stability in plant communities reflecting resource stability throughout the forest. In fact, the

maintenance of overdispersed roosting sites through time might suggest that resources are not only evenly distributed but stable through a period of time of almost 20 years.

Finally, this study hints that at least some tropical animal communities might have high stability through long periods of time. Nevertheless, questions about the mechanisms that drive this stability remain to be answered. Documenting the degree to which various systems might be stable despite environmental variation may provide insight into how communities may respond to human-induced environmental change.

Table 2-1. Observed and expected values for roosting sites and home range for 1994 and 2011

Flock	Roosting Site Distance Observed	Roosting Site Distance Null Model			Overlap Observed (%)	Overlap Null Model 1 (%)			Overlap Null Model 2 (%)		
		Mean	SD	P-value	Mean	SD	P-value	Mean	SD	P-value	
1	54.56	147.99	61.18	0.076	100.00	11.80	20.96	<.0001*	81.98	18.60	0*
2	29.66	140.21	51.16	0.016*	100.00	13.12	23.75	<.0001*	76.53	19.42	0*
3	14.38	150.45	56.83	0.007*	99.10	14.00	22.14	<.0001*	68.42	18.23	0.054
4	28.18	192.35	95.74	0.030*	65.60	10.42	19.90	0.038*	70.67	17.89	0.546
5	50.07	112.16	46.93	0.110	88.70	7.89	17.36	<.0001*	60.95	15.25	0.051
6	50.31	70.76	27.49	0.233	72.60	2.64	11.46	0.007*	65.68	17.18	0.332
7	60.51	93.12	35.06	0.006*	100.00	5.33	14.96	<.0001*	70.29	18.73	0*
8	99.27	95.84	36.29	0.504	71.20	4.97	15.62	0.014*	61.18	15.63	0.268
9	38.23	131.67	48.60	0.038*	96.80	11.43	20.37	<.0001*	77.53	19.26	0.297
10	46.02	160.84	63.00	0.034*	62.30	13.91	23.09	0.066	64.32	16.81	0.49
11	29.46	139.05	55.85	0.026*	69.80	9.95	21.31	0.028*	59.84	15.21	0.267

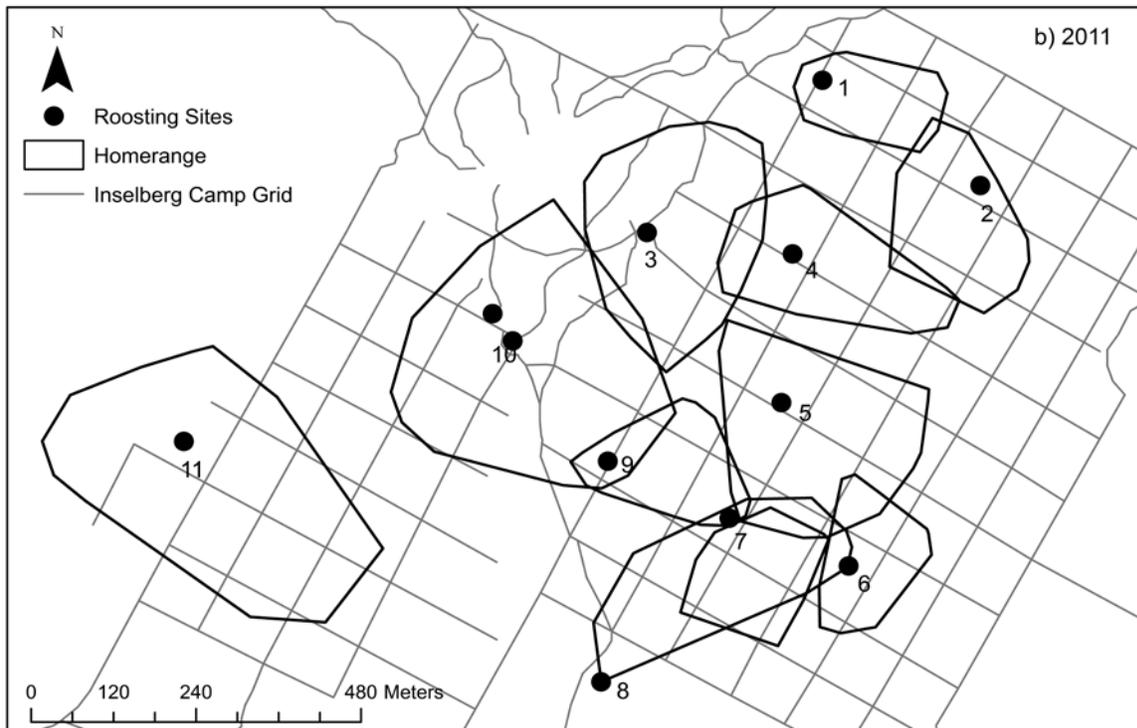
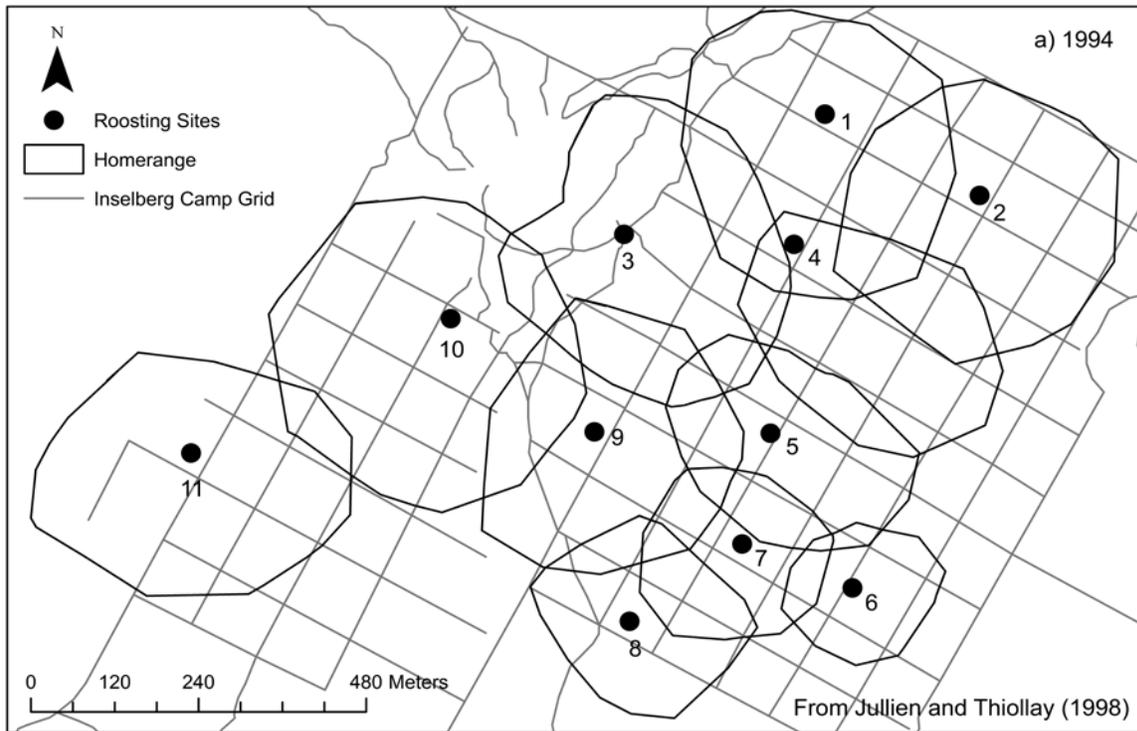


Figure 2-1. Maps showing the distribution of flocks and roosting sites in 1994 (a) and 2011 (b)

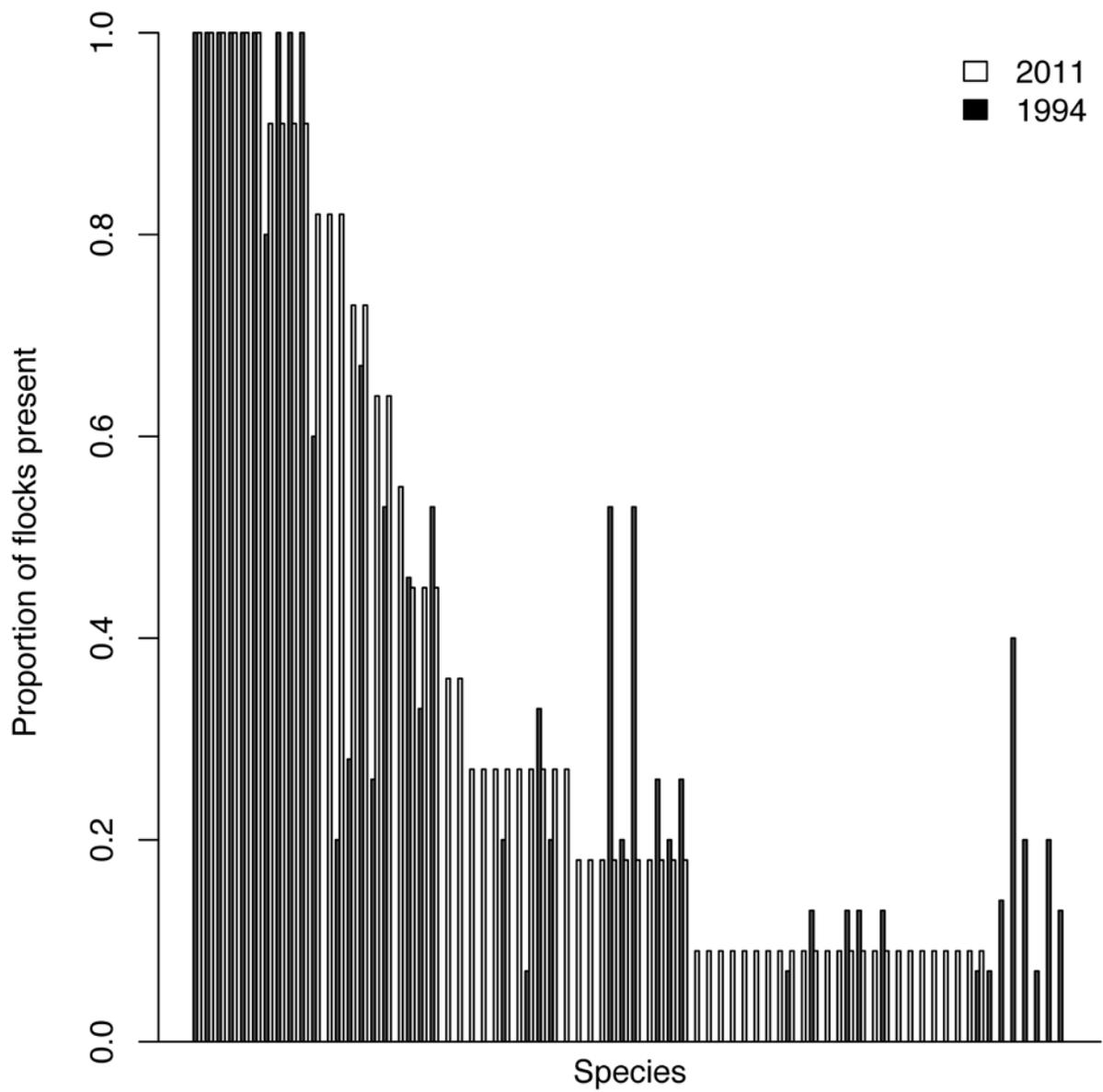


Figure 2-2. Bar plot showing the similarity in the abundance of species that compose the flocks in 1994 and 2011.

CHAPTER 3  
ASYMMETRICAL INFORMATION USE IN AMAZONIAN MIXED SPECIES FLOCKS  
POTENTIALLY REFLECTS ASYMMETRICAL BENEFITS FOR FLOCK MEMBERS

**Introduction**

A major challenge in animal ecology is to determine the evolution and maintenance of cooperative behavior (Boucher et al. 1982, Herre et al. 1999). Because communities and their environments are often dynamic, the conditions under which different species “choose” to cooperate in a mutualistic relationship have attracted much interest (Herre et al. 1999, Bronstein 2001). In mixed species animal groups, social information, gathering facts from other organisms, has been hypothesized to lead to mutual exploitation amongst both conspecific and heterospecific group members.

Social information amongst species can be used for predator vigilance and finding food resources and can potentially be viewed as two different types of information that organisms can either accumulate on their own or exploit from heterospecifics. Information about these types of resources is one hypothesized advantage underlying the formation of multi-species groups (Mönkkönen et al. 1996, Forsman et al. 1998b, Boinski and Garber 2000).

Social information becomes available to other group members through a number of ways. Numerous studies have evaluated the influence of both vocal and visual cues on heterospecifics when searching for food patches (Krebs 1973, Waite and Grubb 1988). Nine-spine sticklebacks, for example, have been experimentally shown to use foraging locations based on their observations of three-spine sticklebacks (Seppanen et al. 2007) and black-capped and chestnut-backed chickadees were shown to copy each other's foraging behavior based on successful foraging by heterospecifics (Krebs 1973). Vocal and visual cues have been used by individuals of different species or even

vertebrate classes as a warning against predators in mixed-species groups across a variety of taxa such as primates, birds, and ungulates (Boinski and Garber 2000, Rainey et al. 2004 and Sharpe et al. 2010). Because heterospecifics often exploit information from information providers, the providers must either learn to avoid exploitation or take advantage of resources provided by exploiters. Thus, the extent to which individuals respond to heterospecifics may reflect the degree of specialization in resources provided and thus the potential for trade of such resources amongst species living in groups.

Heterospecific information use between species can be bidirectional (multiple species send and receive information) or unidirectional (only one species provides information that is used by other species). The degree of directionality in response to heterospecific cues may have far-reaching consequences for the evolution of the hypothesized cooperation that underlies the organization of flocks. Bidirectional responses to heterospecific cues imply that interactions may be more mutualistic in the sense that individuals of several different species become “trade partners” that benefit from the resource that each provides. In Amazonian flocks for instance, it has been hypothesized that species in the antshrike genus *Thamnomanes*, provide threat information in the form of loud alarm calls in exchange for insects that can be flushed by species that provide no threat information (Munn 1986, Sridhar et al. 2012). Under this scenario species should respond to each other’s’ cues (anti-predator versus food-finding), which would be consistent with mutual information exploitation among group members. If responses to heterospecific cues are unidirectional (only one species responds to cues), on the other hand, then mixed-species groups may essentially

involve parasitic or commensal interactions in which individuals of some species exploit the information provided by others without providing any benefits. Amazonian flocks are stable mixed-species associations where members are more or less permanent and thus provide an ideal system for evaluating the directionality of information use and its consequences for the evolution of stable species interactions in mixed-species animal groups.

In this study I address the following questions: 1) To what extent do species within permanent mixed-species flocks in Amazonia differ in the extent to which they emit alarm calls? 2) To what extent do species respond to each other's cues (songs, calls, and mobbing) within these mixed-species flocks? If multiple species emit alarm calls then similar types of information may be mutually exploited amongst different species, and cooperation may result. If alarm calling is carried out predominantly by one species, then either flocking species that respond to alarm-calling birds unidirectionally exploit information in which only one species benefits from another or, non-alarm calling species provide cues that encode other types of information, such as where to forage. In the latter scenario alarm-calling species should respond to cues from other flocking species, which also would suggest mutual exploitation but for different types of information

## **Methods**

### **Study Site**

This project was conducted in the vicinity of the Madre Selva Biological Station, along the Rio Orosa, a blackwater tributary of the Amazon east of Iquitos, Peru, Dept of Loreto (Latitude 3,37'2"S, Longitude 72,14'8"W). This site has both secondary and primary forests. The primary forests have been selectively logged and hunted by

adjacent communities and apart from large game birds have a representative neotropical resident bird community. In these forests, understory flocks are composed of a simple core of three species, the sentinel antshrike *Thamnomanes saturninus*, the live-leaf gleaning antwren, *Myrmotherula axillaris*, and the dead-leaf gleaning antwren *Epinecrophylla haematonota*. Up to 62 other species join these flocks throughout the day as the flock moves throughout its home-range. These flocks are structurally simpler than the understory flocks studied by Munn and Jullien, which generally had two species of *Thamnomanes* and up to four species of *Myrmotherula*.

## **Recordings**

Alarm calls are one of the most widely investigated types of social cues that have been investigated in heterospecific information use. In this paper, I focus on other types of vocalizations that directly or indirectly may influence heterospecific behavior.

Heterospecifics may cue into songs and calls of other species that presumably lead to flock cohesion; I therefore used songs, calls and a fast call used by the three permanent flock members as they were the most common vocalizations used by flocks. Calls given at very high rates appear to function as mobbing vocalizations (pers. obs.), which have been shown to induce heterospecific responses (Hurd 1996, Templeton and Greene 2007, Nolen and Lucas 2009).

We recorded vocalizations using a Sennheiser ME-66 directional shotgun microphone and a Fostex Portable Digital recorder during the dry season (mid June to mid July 2009). All recordings were made in 44.1kHz and 24-bit waveform file format. During this time, I recorded different types of vocalizations (songs, calls, alarms, and fast calls (potentially mobbing calls) of *T. saturninus*, *M. axillaris*, and *E. haematonota*. *E. haematonota* has high frequency, low amplitude calls and were rare enough that

obtaining sufficient recordings under natural conditions was not feasible. It is unlikely that such calls were used by other species and were thus were not included in the trials where I tested calls.

The volume of recordings can vary greatly depending upon the conditions under which the recording was made. Using a sound meter, playback volume of vocalizations was set at 50-58 dB at 15 m based on measurements made using a sound meter to measure the loudness of natural vocalizations (in decibels) by birds. Control stimuli were made using digital white noise recordings using Raven software to filter the controls to the frequency range, and length of the vocalization in question used to test cues. All recordings were filtered to remove background noise.

### **Playback Trials**

Traditionally, heterospecific cues have been thought of and tested in the context of interspecific competition in which species' responses to heterospecific song have been used as a measure of interspecific aggression that infers competitive processes (Robinson and Terborgh 1995, Doutrelante et al. 2000, and Jankowski et al. 2010). The responses of heterospecifics to cues within mixed-species flocks, however, have completely different interpretations depending on the degree of interdependence among such species. Species with different ecologies form groups in which species confer and receive benefits, resulting from food facilitation or vigilance against predators. In these contexts species may respond to heterospecific cues in order to gain benefits by staying with other flock members.

I conducted a series of playback trials of all vocalizations to flocks. Because all three of the core species used in the playback trials were always present in the flocks themselves, I could not measure the response to the heterospecific cues without also

quantifying the response of the conspecifics. For this reason, I also considered the order in which each species responded to the playbacks in which heterospecific responses were recorded. If a heterospecific responded immediately to the cue, then this would suggest that it was responding to the stimulus itself. If, on the other hand, the heterospecific approached the speaker only after the conspecific began approaching the speaker, then it would suggest that heterospecifics were not responding to vocal cues, but were responding to other information provided by the conspecific such as their movements. In either case, it would be suggestive that species that are permanently associated are cueing in on heterospecific cues. If no response is observed to either heterospecific vocalizations or the changes in movement patterns (diving for cover, approaching the speaker), then this would suggest a lack of heterospecific information use.

Each set of playback trials consisted of measuring species' responses to one type of vocalization (i.e. songs or calls or fast calls/mobbing). For example, in the 1<sup>st</sup> set of playback trials I measured the simultaneous response of the three species to isolated songs of each of the three species. I used recordings from each of eight to ten individuals only once per species and thus tested eight to ten responses per species to playbacks in each set of trials (song, call, mobbing, etc.). Thus I conducted 28-40 trials for each of 7-10 vocalizations for each of three species and one control from 15 July to 29 of August 2009 and x to x October 2010 (Table 3-1). To ensure that trials were conducted with different flocks, I only conducted trials that were at least 300 m apart, a figure based on the home range sizes of these flocks (unpubl. data; see also Munn and

Terborgh 1979 and Jullien and Thiollay 1998. I revisited the same areas on different days to test different vocalizations.

### **Playback Trial Protocol for Song, Call and Mobbing Trials**

During each trial, a flock was confirmed to have all three species at which point a primary observer would remain within 10m of the flock to keep track of its position. A second observer would take a position 25 m from the flock. A speaker would be placed on the ground approximately 5 m from the second observer. A trial would consist of a 5-min pre-stimulus and a 5-min post-stimulus period. During the pre-stimulus period the secondary observer would census by visual or auditory detection the distance and direction of movement of each of the three core species in relation to the speaker. If the flock moved greater than 40m from the speaker during the pre-trial, the speaker was moved closer and the trial began again. During the post-stimulus period, the playback was conducted for the 1<sup>st</sup> 3min of a 5-min trial in which the position, distance, and movements of the three core species were recorded during the entire 5-min post-stimulus period. The closest distance that each species approached the speaker was a measure of response for each of the three species core species (agonistic in the case of the conspecific).

Previous studies have consistently suggested that *Thamnomanes* are the main alarm- calling birds in Amazonian understory flocks (Munn and Terborgh 1979, Munn 1986, Jullien and Thiollay 1998). Because other species are known to occasionally sound alarm calls I quantified which species sounded alarm calls during my censuses of flocks; during full flock censuses where 12 flocks were followed over 5-10 hours, I observed and recorded the number of times alarms were given by each of the three species.

## Data Analysis

I used a logistic regression to determine whether stimuli influenced heterospecific response as a function of the species vocalizing, the type of vocalization, or the species responding. I regarded any net movement towards the speaker as a positive response. Because in some cases birds moved away from the speaker, these would be assigned negative values. Movements away from the speaker were few and showed no consistent pattern, which suggests random movement. I saw no evidence that any of these species systematically avoided the vocalizations used in the trials (e. g., Robinson and Terborgh 1990, Jankowski et al. 2010). Therefore, these values were converted to zeros. I first used a logistic regression factoring in the effect of stimuli on conspecifics-if conspecifics themselves didn't respond to at least one stimulus such as song, one could argue that the stimuli used are not conveying the proper signal. In a separate logistic regression, the heterospecific responses to each species were compared to the controls to determine whether species were moving towards the stimulus provided. Where heterospecific responses were detected, I subsequently used a Chi-Square test to determine the order in which species responded to the stimulus. Thus where responses were observed I determined the first species to respond using a Chi-Square test. All data analyses were performed using the lme4 package in R version 2.1.4.1.

## Results

Species stimuli used in the trials demonstrated a significant effect in causing approaches by conspecifics in the first model (Table 3-2, *T. saturninus*  $P=3.88^{-08}$ , *M. axillaris*  $P=6.39^{-05}$ , and *E. haematonota*  $P=.041$ , Figure 3-1). The second model, from which I removed the response of conspecifics, showed that the only playback trials that invoked heterospecific attraction were those using *T. saturninus* (Table 3-3,  $P=2.18^{-06}$ ,

Figure 3-3). These effects did not vary with vocalization type, although both song and mobbing vocalizations appeared to have a stronger effect on heterospecifics than calls (Figure 3-1 a,c versus 3-1 b). The large number of zeros in the data limited the number of degrees of freedom in the logistic regression. I was therefore not able to explore interactions between the species vocalizing and the type of vocalization used in the analysis; however an examination of the data suggests that songs and fast calls/mobbing calls produced by *T. saturninus* (Figure 3-1 b-c, and Figure 3-3 b-c) accounted for more heterospecific responses than calls (Figure 3-2 b-c). In contrast, vocalizations of *M. axillaris* and *E. haematanota* appeared not to have any effect on heterospecifics (*M. axillaris*  $P=.4763$ , and *E. haematanota*  $P=1.0722$ , Figure 3-3). Even though there were strong responses to the vocalizations of *T. saturninus*, in all cases, the heterospecific did not respond until after the conspecific had already begun to approach, suggesting that the heterospecifics were not necessarily responding to the vocalizations, but may simply have been following *T. saturninus* as it responded to a conspecific playback ( $X^2=16.54$ ,  $df=2$ ,  $p=.00025$ ). In terms of alarm frequencies, *T. saturninus* gave alarms 66 times in 100 hours whereas *M. axillaris* and *E. haematanota* were never heard to give alarms.

## Discussion

The results of this study show no evidence of symmetrical information use, even in a system in which only one species gives alarm calls. Heterospecifics only responded to vocal cues provided by the antshrike (Figure 3-3), which is also the species that provides alarm calls, and only responded after the antshrike itself approached the speaker. The antshrike was rarely observed to respond to any heterospecific calls or follow any of the heterospecifics when they were attracted to their own vocalizations

(Figure 3-1 a, Figure 3-2 a, and Figure 3-3a), including trials that attempted to induce mobbing or agonistic responses using calls of the other two species. This lack of following on the part of the antshrike suggests that it does not derive any benefit from the species with which it associates almost continuously or that it does not use information provided by the other flocking species. These results are contrary to previous studies showing that co-occurring flocking species find mutual benefits through heterospecific alarm calling (Goodale and Kotagama 2008). Sridhar et al. (2012) for example suggested that positive associations of phenotypic traits such as body size in bird flocks may result because species may benefit from each other's specialization on different resources . The evidence from these experiments suggest that core of these multi-species flocks (which can be impressively stable in space and time: Martinez and Gomez 2013) are more likely to represent unidirectional information exploitation of alarm-calling species such as antshrikes by species that have more myopic searching tactics and are therefore more likely to be vulnerable to predation (Figure 3-4).

Previous studies of mixed-species bird flocks have inferred mutual benefits of flocking either through enhanced foraging or anti-predator benefits, in which case bidirectional information use might have been predicted. In some flocks, for example, several alarm-calling species occur together regularly and respond to each other's alarms, which implies mutual benefit (Goodale and Kotagama 2009). The flocks in this study however, are limited to certain habitats throughout Amazonia. In the more well reported flock system from this region one permanent flock member specializes on alarm calling and depends largely on other species to flush insects, whereas the species that flush insects depend predominantly on the alarms of the former species

(Munn and Terborgh 1979, Munn 1986). In that system, we could predict that there would be bidirectional responses to vocalizations because these species may be interdependent through mutual information exploitation. In that system, the species that flush insects should respond to vocalizations of the alarm calling birds to stay close to their source of information about predation risk and the alarm calling bird should follow heterospecifics in response to their conspecific vocal cues. The fact that I did not see this further reinforces the interpretation that the species of antshrike in this study is not benefitting from the presence of the heterospecifics. The lack of any other species of alarm-calling birds (unlike the flocks described by Munn 1986 and Jullien and Thiollay 1998), further suggests that there are no benefits from collective detection of predators as has been documented in other flocks (Goodale and Kotagama 2008). The complete lack of evidence for bidirectional interactions in the flocks studied in this paper suggests they may be very differently organized than flocks studied elsewhere. .

Quantifying variation in ecological traits may provide insight into why information use is unidirectional and thus why exploitation for different types of information that leads to mutualistic interactions among species is unlikely (Hoeksema and Schwartz 2002). Indeed based on vocal signaling inequities, both tropical and temperate (short-lived) flock associations may often be characterized as parasitic or commensalistic (Hino 1998, Contreras and Sieving 2011). Permanent members of these flocks have distinctly different foraging ecologies that include different foraging tactics, different microhabitat preferences or both, which means that copying such as that observed in chickadee flocks (Waite and Grubb 1988) is very unlikely. Foraging observations of *T.saturninus* indicate that it gets a majority of its food items from leaves and suggests

that it accrues little if any benefits from associating with *M. axillaris* and *E. haematonota*. In other words, *T. saturninus* does not forage in a manner that allows it to take advantage of prey items flushed by other permanent flock members. In contrast, its congener *T. schistogynus*, which was not present in these flocks, has been shown to benefit from foraging on the insects flushed by heterospecifics or even by kleptoparasitism—direct stealing of prey from heterospecifics (Munn 1979, Munn and Terborgh 1985, Munn 1986, and Jullien and Thiollay 1998). Similar experiments on the responses to heterospecific cues by *T. schistogynus* may show more bidirectional responses. Variation in the foraging behavior of similar congeners may 1) underscore differing tendencies to respond to information exploitation by heterospecifics through the evolution of kleptoparasitism and 2) the conditions under which species exploitation becomes mutually beneficial.

Irrespective of alarm calling or food benefits there is the possibility that flocks provide benefits through the predator dilution effect (Alexander 1974). The characteristics of the flock and its potential ambush predators, however suggest the opposite. Indeed, *T. saturninus* could possibly incur costs from species that decide to associate with it. I usually sighted located flocks by observing the conspicuous movements of *M. axillaris* and *E. haematonota* (pers. obs.); individual *T. saturninus* were actually very hard to observe; they search leaves at a distance (up to 2m from a perch) and therefore changed perches much less often than the myopically searching antwrens, which moved continuously as they searched (unpublished data). Finding *T. saturninus* as it changes perches would be much more difficult if these other species did not associate with it. From the point of view of visually oriented ambush predators such

as hawks and falcons, it is not unreasonable to suggest that *T. saturninus* may in fact induce a cost of increased conspicuousness in the presence of these two other species, which would suggest a form of parasitism rather than simple commensalism.

A great deal of the literature on information use in mixed-species groups has focused on the evolutionary consequences of alarm calling and the extent to which associated species accrue benefits from information that is acquired through eavesdropping (Rainey et al. 2004, Dall et al. 2005, Magrath et al. 2009, Sridhar et al. 2009, Oommen and Shanker 2009, Sharpe et al. 2011, Hetrick and Sieving 2012). In the system described here, unidirectional reliance on an alarm caller may cause heterospecifics to pay attention to the behaviors of the alarm calling species. Other systems may contain species that provide better information, either in quantity or quality, which may attract a larger number of species. For example, in Sri Lanka, mixed-species flocks contain on average 11 species of over 40 individuals, and have a number of species that provide alarm calls (Goodale and Kotagama 2004, Goodale and Kotagama 2005). Within these flocks certain species give alarm calls more frequently, (e.g., Orange-billed Babblers *Turdoides rufescens*) whereas other species, (e.g., Greater Racket-tailed Drongos *Dicrurus paradiseus*) may provide more reliable threat information (Goodale and Kotagama 2005). Larger groups may in turn provide conditions under which other species with similar traits provide slightly different types of information and thus can become trade partners where each benefits (Hoeksema and Schwartz 2002). Larger flocks could also provide the conditions to attract species with traits that make them vulnerable to deception and therefore provide the conditions for the evolution of false alarm calling, and kleptoparasitism (Brockmann and Barnard

1979). Until now we have only dealt with a few species that benefit from exploitation but we have not dealt with the fact that multiple species can simultaneously benefit from the resource provided by alarm callers. How this affects the coexistence of intraguild competition for information provided by a single species is an unexplored topic (Stanton 2003). Identifying how species depend on and respond to cues as a function of ecological traits would be a useful step in understanding the evolution of information exchange and its consequences for species interactions that underlie the organization of mixed species groups.

Table 3-1. Number of trials used in experiment. THSN=*T. saturninus*, MYAX=*M. axillaris*, EPHA=*E. haematonota*

Experiment	Stimulus				Total Trials
	THSN	MYAX	EPHA	Control	
Song	10	10	10	10	40
Call	10	10	-	10	30
Mobb	7	7	7	7	28
Alarm	8	-	-	8	16

Table 3-2. Results of mixed effects model (where flock was a random effect), testing for movement toward stimulus including the effects of conspecifics.

Fixed Effects	Estimate	Std.Error	z value	Pr(> z )
(Intercept)	-3.9318	0.6136	-6.408	1.48e-10 ***
Treatment EPHA	1.2232	0.5985	2.044	0.040981 *
Treatment MYAX	2.1322	0.5333	3.998	6.39e-05 ***
Treatment THSN	2.9276	0.5326	5.496	3.88e-08 ***
Target MYAX	1.3173	0.3783	3.482	0.000498 ***
Target THSN	0.6706	0.3843	1.745	0.080937 .
Cue MOBB	0.6436	0.3927	1.639	0.101244
Cue SONG	0.6683	0.3818	1.751	0.080028 .

Table 3-3. Results of mixed effects model (where flock was a random effect), testing for movement toward stimulus after removing the effects of conspecifics.

Fixed effects	Estimate	Std. Error	z value	Pr(> z )
(Intercept)	-2.727	0.4766	-5.721	1.06e-08 ***
Treatment EPHA	1.236	0.6536	1.891	0.0586 .
Treatment MYAX	0.4789	0.6673	0.718	0.473
Treatment THSN	2.4464	0.5471	4.471	7.77e-06 ***

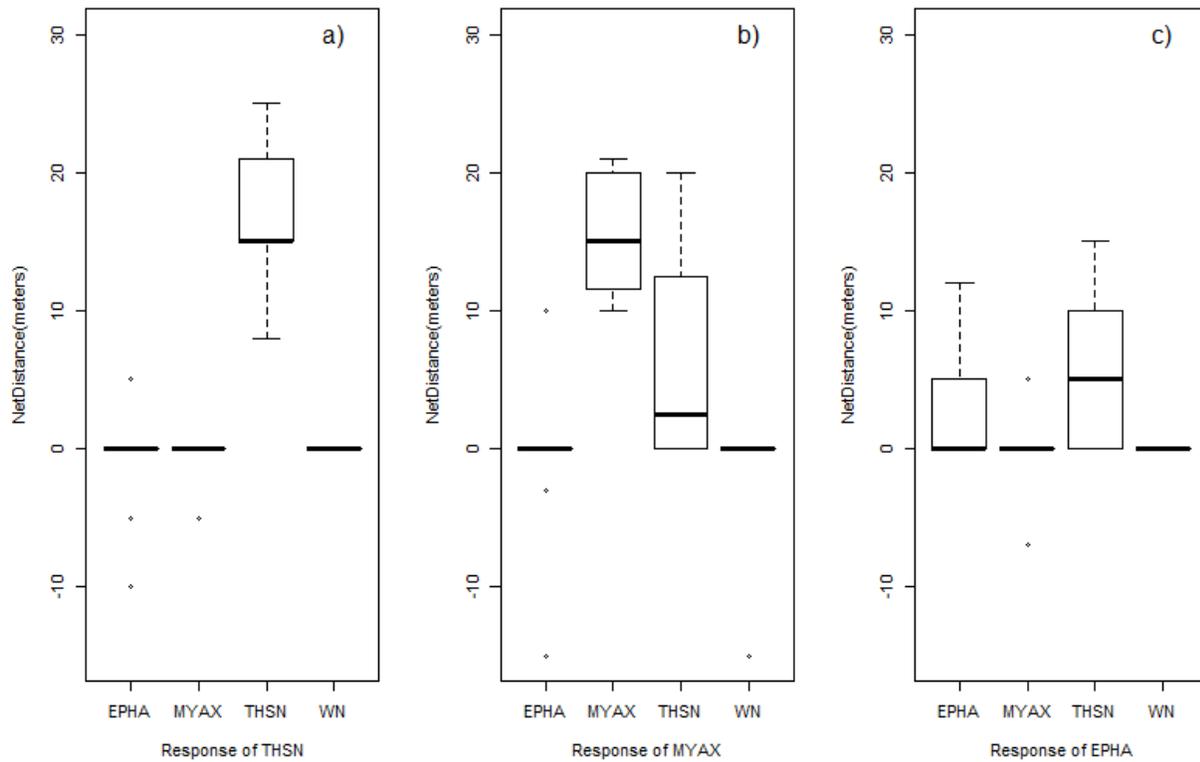


Figure 3-1. Boxplots showing net movement of a) *T. saturninus* b) *M. axillaris* and c) *E. haematonota* towards the speaker in response to 4 different song stimuli during playback trials, where EPHA=*E. haematonota*, MYAX=*M. axillaris*, THSN=*T. saturninus*, and WN=White Noise(Control).

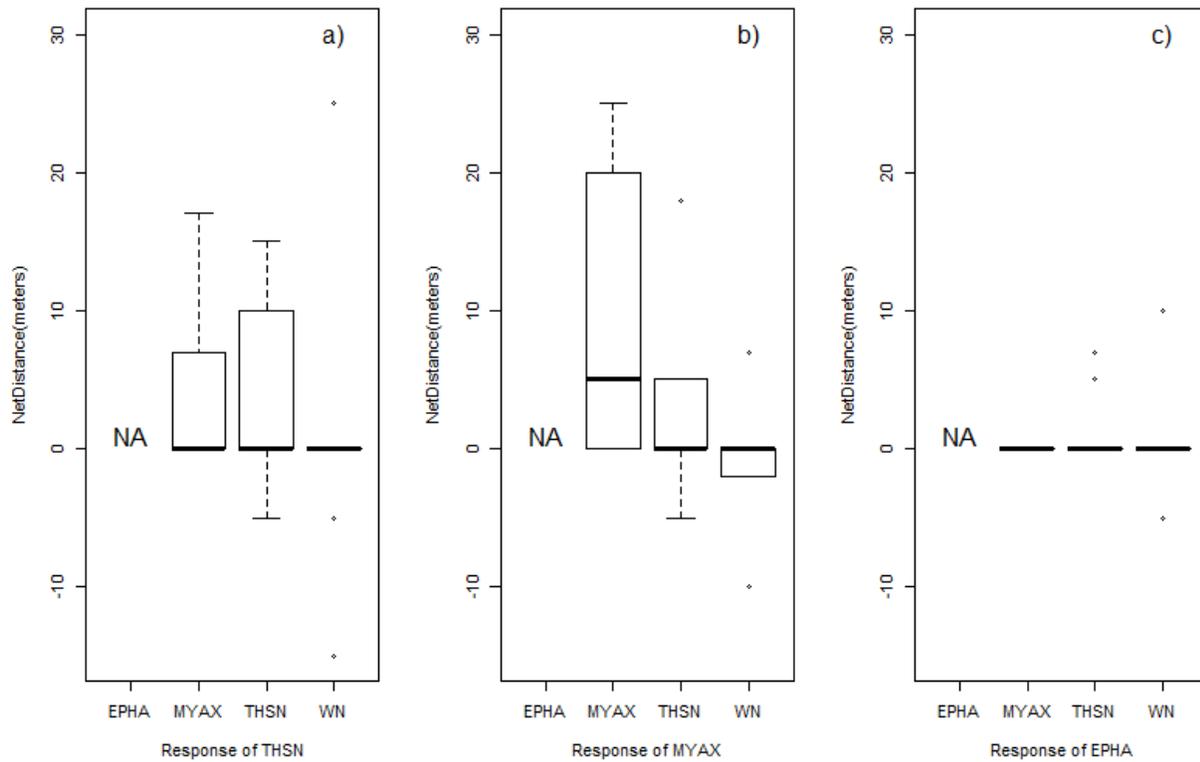


Figure 3-2. Boxplots showing net movement of a) *T. saturninus* b) *M. axillaris* and c) *E. haematonota* towards the speaker in response to 2 different call stimuli during playback trials, where EPHA=*E. haematonota*, MYAX=*M. axillaris*, THSN=*T. saturninus*, and WN=White Noise(Control).

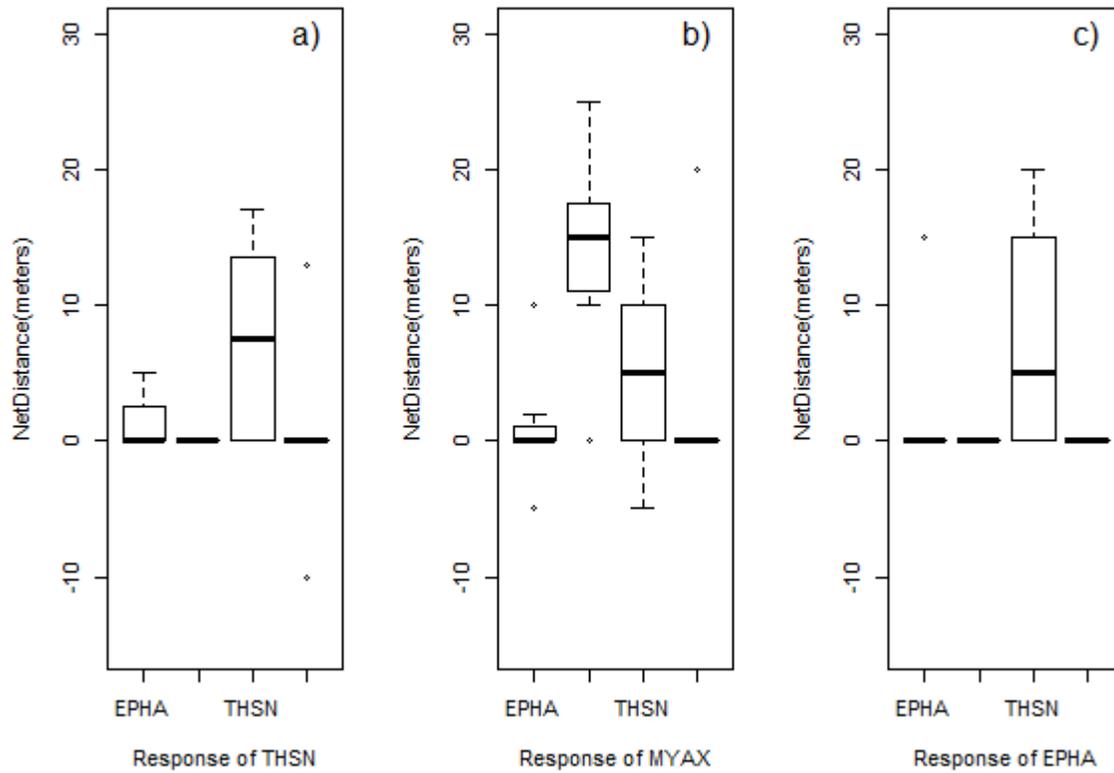


Figure 3-3. Boxplots showing net movement of a) *T. saturninus* b) *M. axillaris* and c) *E. haematonota* towards the speaker in response to 4 different fast call/mob stimuli during playback trials, where EPHA=*E. haematonota*, MYAX=*M. axillaris*, THSN=*T. saturninus*, and WN=White Noise(Control).

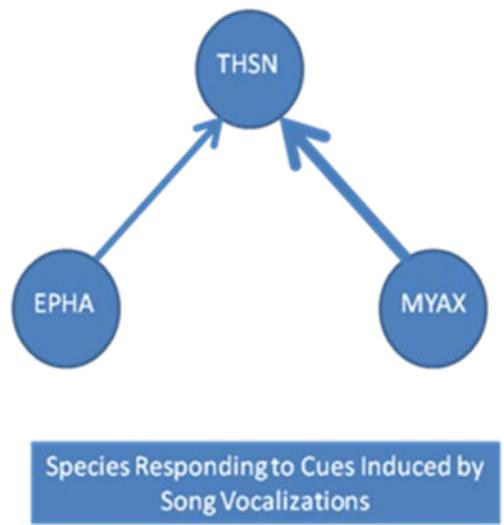


Figure 3-4. Flow diagram showing the probability of response of each of three flock members to different stimulus presented using song vocalizations. Arrows of increasing thickness represent increased probability of response based on probabilities estimated through logit transformation using estimates of the logistic regression model. EPHA=*E. haematonota*, MYAX=*M. axillaris*, and THSN=*T. saturninus*.

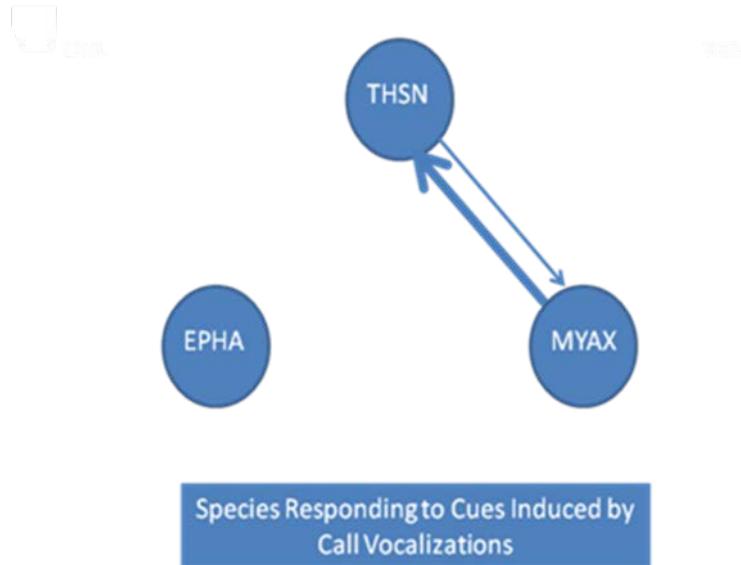


Figure 3-5. Flow diagram showing the probability of response of each of three flock members to different stimulus presented using call vocalizations. Arrows of increasing thickness represent increased probability of response based on probabilities estimated through logit transformation using estimates of the logistic regression model. EPHA=*E. haematonota*, MYAX=*M. axillaris*, and THSN=*T. saturninus*.

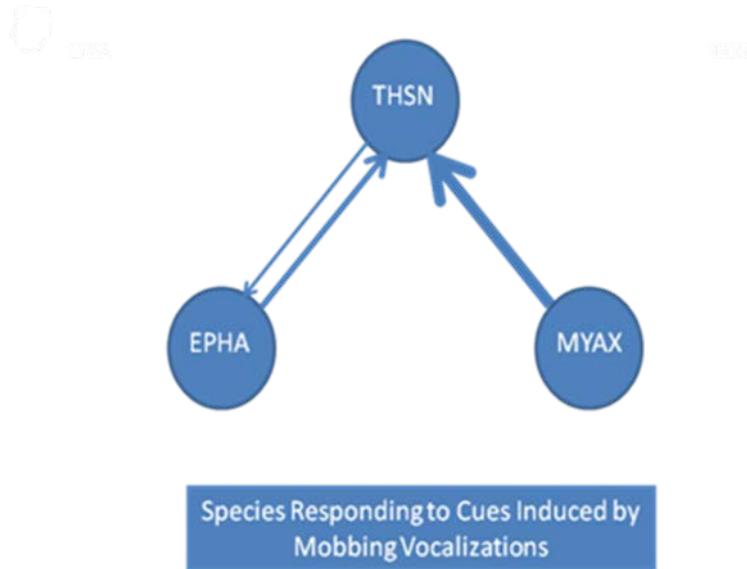


Figure 3-6. Flow diagram showing the probability of response of each of three flock members to different stimulus presented using mobbing vocalizations. Arrows of increasing thickness represent increased probability of response based on probabilities estimated through logit transformation using estimates of the logistic regression model. EPHA=*E. haematonota*, MYAX=*M. axillaris*, and THSN=*T. saturninus*.

## CHAPTER 4 FORAGING GUILD INFLUENCES DEPENDENCE ON HETEROSPECIFIC ALARM CALLS IN AMAZONIAN BIRD FLOCKS

### **Introduction**

Information use by animals reduces uncertainty and minimizes risks. A growing body of literature stresses the pervasiveness of information use and its consequences for animals and its potential as a unifying concept in ecology and evolution (Schmidt et al. 2010). Information can be broadly defined as being either private where it is possessed by an organism and inaccessible to others, or public which can be obtained through interactions with other organisms (Wagner and Danchin 2010). Although all animals use private information to reduce uncertainty, the use of social information both through cues and signals has received particular attention because of its consequences for conspecifics and heterospecifics from both an evolutionary and ecological perspective (Dall et al. 2005, Seppanen et al. 2007 and Schmidt et al. 2010). Much less is known, however, about the implications of social information use by heterospecifics in influencing the organization of animal communities (Goodale et al 2011).

Assessing the types of information transfer that occur among organisms has been a primary approach for attempting to understand the mechanisms underlying multi-species animal group formation. Eavesdropping on alarm calls of other species is a primary example of the use of public information in multi-species groups, and has been the focus of numerous studies across a range of taxa (Boinski and Garber 2000, Kirchoff and Hammersmidt 2006, Sridhar et al. 2009, and Sharpe 2010). There have been many approaches to studying the consequences of alarm calling and how it

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Reprinted with permission from Martinez AE, Zenil RT. 2012. Foraging guild influences dependence on heterospecific alarm calls in Amazonian bird flocks. *Behavioral Ecology* 23:544-550.

reduces predation risk. From an evolutionary perspective, alarm calls have been shown to have adaptive value by including a large amount of information, encoding both the types and the degree of threats (Templeton 2005, Courter and Ritchison 2010, Sieving et al. 2010). On the other hand, the use of false alarms has demonstrated an evolved role of providing false information to deceive eavesdropping individuals and thus to manipulate eavesdropping heterospecifics for the benefit of conspecifics that provide the alarms (Munn 1986 and Ridley and Child 2009). Other studies have shown the interspecific dependence of species on each other's alarms and have inferred that mutualistic interactions underlie heterospecific group formation (Macgrath et al. 2007, and Goodale and Kotagama 2008). Thus it seems reasonably clear that information transfer is an underlying advantage of forming groups.

In birds, minimizing predation risk through eavesdropping has been hypothesized to be a primary advantage of mixed-species flock formation (Sridhar et al. 2009). To date, attention has focused on variation in information provided by the alarms of the signaler. Flocks, however, contain species with different foraging ecologies, which might make them more or less vulnerable to predators. We know little, however, about whether species with different foraging behaviors respond differently to alarm calls.

High species diversity within Neotropical bird flocks is thought to be made possible by the diverse array of foraging specializations among flocking birds: insectivorous birds specialize on live leaves, dead leaves, twigs, branches, and tree trunks and some catch insects in the air (Munn and Terborgh 1985). These different foraging ecologies, by influencing the field of vision experienced by a bird, may play a role in determining the extent to which different species depend upon heterospecific

information as a resource in mixed-species flocks. Understanding species' variation in responses to threat information therefore may, in part, dictate the rules that determine the assembly of species within flocks and determine the nature of interspecific interactions within flocks.

Species that forage by myopically searching substrates should depend upon alarm calls more than species that search for prey at a distance and would therefore be more likely to detect predators on their own. These latter species may have more opportunities to evaluate heterospecific signals because they have private information on predation risk based on their own monitoring of the environment. Because the multi-species flocks of the Amazon contain species with a wide array of foraging tactics, they provide an opportunity to evaluate how species ecologies influence reliance on heterospecific threat information. We ask -How does variation in foraging guild influence species responses to heterospecific threat information? Because species that forage in dead leaves myopically probe their head into dead leaf clusters, we predicted they would be at the greatest risk of predation and most dependent upon public information in the form of alarm calls. Species that are live-leaf insectivores search leaves myopically but appear less vulnerable to predators than dead-leaf insectivores because their vision is less obstructed by their foraging behavior. We predicted that these species would show a lower level of response to simulated alarm calls; in other words, they would resume foraging sooner than dead leaf counterparts. Species that catch prey in the air (flycatching) search for prey at greater distances because they scan beyond the immediate vegetation close to the perch and therefore have a greater opportunity to use private information about the true level of threat posed during alarm

calls. By using playbacks of alarm calls when there are no real predators attacking, we are measuring the dependence upon alarm callers and the potential dependence of different species on heterospecific alarm calls.

## Methods

### Study Site

This project was conducted in the vicinity of the Madre Selva Biological Station, along the Rio Orosa, a blackwater tributary of the Amazon east of Iquitos, in the region of Loreto, Peru (Latitude 3,37'2"S, Longitude 72,14'8"W). Playback experiments were conducted within tierra firme forests adjacent to the station and seasonally inundated forest approximately four km upriver. Within each forest, mixed-species flocks are abundant and although only a few species are shared between them, both forest types contain species with similar foraging ecologies. Each flock type consists of one species that is responsible for the majority of alarm calls. In the upland tierra firme forests, the alarm calling species is *Thamnomanes saturninus*, the Saturnine Antshrike.

Conversely, the main alarm calling species in the inundated forests is its congener, *Thamnomanes schistogynus*, the Bluish-slate Antshrike (see Figures 4-1 a and 4-1 b for alarm calls of *T. saturninus* and *T. schistogynus*, respectively). In many areas, two species of *Thamnomanes* occur in the same flocks (Munn and Terborgh 1979, and Jullien and Thiollay 1999), but in the Madre Selva area, they rarely occur together; instead, each species forms the nucleus of its own flock. (Author, unpubl. Data)

From each forest type we selected a flocking species representing each of three distinct foraging guilds: a live-leaf gleaner, a dead-leaf gleaner and a flycatching species. In the inundated forest type we selected the gray antwren, *Myrmotherula menetriesii* (a live-leaf gleaner), the moustached wren *Thryothorus genibarbis* (a dead-

leaf gleaner), and gray-headed tanager *Eucometis penicillata* (a flycatching tanager). In the tierra firme forest, we selected the white-flanked antwren, *Myrmotherula axillaris* (a live-leaf gleaner), the stipple-throated antwren *Epinecrophylla haematonota* (a dead-leaf gleaner), and the Cinnamon-rumped flycatcher *Terenotriccus erythrura* (a flycatcher).

## Recordings

We recorded alarm calls using a Sennheiser ME-66 directional shotgun microphone and a TASCAM DR-07 Portable Digital recorder during the dry season (mid June to mid-July) 2009 and 2010. All recordings were made under 44.1kHz and 24-bit waveform file format. Alarm calls were recorded under two types of conditions: 1) after throwing artificial hawk models at alarm calling birds and 2) under natural conditions by following flocks and recording alarm calls generated by birds responding to perceived threats. In the former case, a hawk was made out of balsa wood and covered with pheasant feathers and thrown from approximately 10m-20m away from alarm calling birds. A second person would record any vocalizations generated while simultaneously holding a sound meter to record the dB level of the recording. In the latter case, flocks were followed within 15-20m with a microphone constantly recording between ~2-5 hours. Alarms were prompted in response to actual predators such as hawks and also to larger birds such as woodpeckers and pigeons that fly into or through the flock. We used length of each alarm and peak frequency to determine whether alarm calls generated under the two protocols shared the same characteristics (Table 4-1). In the case of *T. schistogynus* the only alarm that was generated using a model hawk fell within the range of values observed for natural calls (Table 4-1). We found no significant differences between calls generated by the two protocols in any of the characteristics measured (call length: T-test .273, df=3.686, p=.7995; peak frequency: T-

test.281,df=4.645, p=.791), which allowed us to use all playbacks for subsequent experiments. Alarm calls were filtered to remove background signals attributed to other bird calls. Previous work has only described short and long alarm calls by *T. schistogynus* (Munn 1986). However, there is likely to be referential information (type of threat) provided by alarm calls of both species as well. For *T. saturninus*, the alarm calls naturally vary from 2-6 repetitions of the same note. *T. schistogynus* calls vary both in length and in the types of notes they use. Because short term calls were much more frequently generated, both under natural and induced conditions, we selected them for use in the experiment during which we maintained a sample rate of 44.1kHz and 24-bit waveform file format.

The volume of recordings can vary greatly depending upon the conditions under which the recording was made. Using a sound meter, playback volume of alarms was established at 55 dB at 15 m based on measurements made using a sound meter to measure the loudness of natural alarms (in decibels) by birds when a hawk model was used to generate alarms. Control stimuli were made using digital white noise recordings using Raven software to filter the controls to the frequency range, and length of alarm calls of the respective species used in each forest flock.

### **Playback Trials**

Alarm calls were used to test the response of individuals of each of the target species using alarm calls of sentinels from their respective flock type. We used alarm calls from each of eight individuals only once per species. We intended to test eight individual responses per species (based on variances in preliminary data) to playbacks of alarms and controls. Thus in each forest type we conducted 48 trials: 8 controls and 8 alarms for each of three species from 15 July to 29 of August 2010. Because species

in mixed-species flocks often share the territory we tested individuals of different species that were approximately 300 meters apart, to assure that tests of individual birds were from different territories based on territory sizes of flocks from past studies (Munn and Terborgh 1979, Jullien and Thiollay 1999). We revisited the same areas on different days to test different species. Two-observer teams alternated between forest types in order to complete enough trials. In each area we conducted just one trial per day. We measured the response by having a primary observer locate an individual of the target species and observing foraging activity for ~20 seconds pre-stimulus. A second person would playback the assigned stimuli by placing on the ground a pignose amplifier in the direction of the target species at a distance of ~15 meters from the bird. Sentinel birds range widely in their perch heights in the understory and occasionally can be found on the ground. While it is unlikely that alarm calls are generated frequently from the ground, the most important feature is where the receiver is in relation to the alarm signal. As listening birds can be located and do respond in virtually any direction (above, below and to the side) from alarm calling birds, we feel that placing the speaker on the ground should not greatly influence responses of individual birds. Playbacks were conducted using an Edirol R-07 waveform recorder. The first observer would continue to observe the response of the individual post-stimulus until the bird was lost from view. Birds typically respond to alarms by scanning up, and either freezing or diving into thicker cover. We measured the length of the response from the start of evasive action (either freezing or diving) until the bird resumed foraging activity. In several cases when birds dived into thicker cover they were lost from view in which

case we were unable to use the trial because we could not see when they resumed foraging. We re-tested these birds two or more days later.

## **Data Analysis**

We compared the responses of species among foraging guilds for each forest type. In order to detect differences among foraging guilds, we chose to model the latency to resume foraging following an alarm stimulus. We considered that this random variable could be modeled through an exponential distribution since it is well known in the literature its ability to represent waiting times until the occurrence of some event (Karlin and Taylor 1979, Williams et al. 2002). This assumption was tested using a Kolmogorov-Smirnov test (Corder and Foreman 2009) for each foraging guild in each forest type. Kolmogorov Smirnov tests for each group did not reject the hypothesis of an exponential distribution, except for the flycatching guild in the inundated forest. We proceeded using this model for resumption of foraging since it assigns high probability to short latency responses and low probability to long responses, which can be observed in our samples. The parameter of an exponential distribution  $\theta$  is understood as mean time that a bird waits until resuming foraging activity. We were interested in making inferences about the time to resume foraging so we calculated the likelihood function of the parameter  $\theta$  using the sample of the latency responses per foraging group and per forest. In order to detect differences in latency response according to foraging group we performed a likelihood ratio test (LRT). The null hypothesis of this type of test states that the latency response of all foraging guilds is the same. Our main goal was to reject the latter hypothesis since this represents significant evidence of differences in latency response by foraging group. Subsequently for each of the two forest types, we estimated the mean latency responses for three

different groups ( $\theta$ ) and calculated the confidence intervals for each mean assuming the exponential distribution for latency responses. Maximum likelihood estimates (MLE) for the mean latency response and confidence intervals around the MLE allowed us to detect relevant differences of response to alarm calls among species within different foraging guilds for both upland and inundated forests. All data analyses was done with R package 2.12.1

## Results

We combined trials among observers but analyze forest types separately in order to generalize how birds with different foraging ecologies responded to alarm calls. Differences were statistically significant for lengths of response to alarm calls by foraging type for each forest and showed little or no effect of controls on influencing bird responses (Figure 4-2). The exponential assumption was analyzed using the Komolgorov-Smirnov tests and results are shown in Table 4-2. In all cases but one we are not able to reject the assumption of an exponential distribution for latency responses (Table 4-2, Figure 4-3 a-f). In the only case (flycatching species in inundated forests) where we rejected this assumption we were able to detect that a significant departure from the exponential is given by the large number of zeros in the data (no response) and the sample size, which could indicate a zero-inflated exponential distribution (Figure 4-3 f). However, in order to compare with other foraging guilds it's reasonable to maintain the exponential assumption: in spite of being a poor fit, it would nonetheless approximate the data relatively better than other distributions. The LRTs indicated differential effects of foraging guild depending on forest type (Table 4-3). In the case of the upland forest, both the live-leaf and dead-leaf species showed similar latency responses (Table 4-3,  $X^2=.605$ ,  $P=.799$ , Figure 4-4 a) and when combined these two

groups they show significantly different behavior compared to the latency response of the flycatching species, *T. erythrurus* (Table 4-3,  $X^2=.605$ ,  $P=.0006$ , Figure 4-4a). In the analysis of species from the inundated forest, the LRTs for each of the groups showed significant differences in their latency responses (Table 4-3, live-leaf gleaner versus dead-leaf gleaner  $X^2=23.9$ ,  $P=1.0*^{-06}$  and for distributions of all three groups  $X^2=68.45$ ,  $P=1.0*^{-15}$ , Figure 4-4 b and 4-4 c). The relative likelihoods showed that for the inundated forest each group responded differently to alarms with flycatching species responding the least and live-leafers showing the strongest response (Table 4-4, Figures 4-2 ,4-4 b and 4- 4 c).

### **Discussion**

Our results suggest that foraging guild influences both the dependence of different species on heterospecific alarm calls and the ability of species to evaluate threat information (Tables 4-4, Figures 4-2 and 4-4). As we predicted, species that search for prey at a distance from a perch responded weakest and recovered fastest from alarm calls suggesting that their foraging strategy makes them less dependent upon heterospecific alarm calls. In this system, species that searched myopically were more dependent on the alarm calls; they usually stopped foraging. Thus while flycatching species have the lowest response in both forest types, consistent with our prediction, there is no difference in the response of life leaf and dead leaf gleaning species in the upland forest and a stronger response of live leaf gleaning species compared to dead-leaf gleaning species in the inundated forest, contrary to our prediction. Therefore, these species may depend more completely upon public threat information of the sort that is available in flocks where vigilant species frequently give alarm calls of the kind used in the experiment. We nonetheless recognize that a

limitation of our study is the use of only two species per foraging guild, and that future studies will need to incorporate more species per foraging guild.

Nonetheless, there were differences in responses of dead-leaf searching species by forest type: Dead-leafers responded less strongly to alarm calls than those that searched in live leaves in the inundated forest, which suggests that other factors may determine their dependence upon heterospecific alarm calls. Dead leaves sometimes occur in dense clusters in vine tangles or in fallen branches, areas where *T. genibarbis* often forages, and thus may provide abundant cover from predators. Dense clusters of vine tangles with dead leaves in fact are more common in the inundated forest than the upland forest (pers obs.) When foraging in these contexts, dead-leafers may not need to rely as much on heterospecific alarms calls. Of the trials in these species that resulted in no response in each forest type, four of the five occurred when the species was in dense vegetation and therefore safe from attack (Author pers. obs.). Vegetation density has often been proposed as a primary determinant of vulnerability and to affect which species do and do not join flocks (Jullien and Thiollay 1998, Thiollay 1999). Our results suggest that foraging guild may further influence the degree to which species are found in vegetation of varying density and therefore exposed to aerial predators.

Flycatching birds may be the least likely to join flocks because of anti-predator benefits, but may benefit from enhanced foraging opportunities. Indeed, one of the alarm-calling species, *T. schistogynus*, which seems to form the core of the floodplain flocks, appears to benefit primarily from the prey flushed by the other members of the flock (Munn 1986). Srinivasan et al. (2010) suggested that flycatching birds should be highly associated with flocks because they are often group leaders that maintain

cohesion and or play the role of vigilant species. While flycatching antshrikes in the genus *Thamnomanes* are thought to be the flock leaders in Amazonian forests, those species represent only a small percentage of the flycatching species present in these forests (Terborgh et al. 1990). The vast majority of flycatching species do not participate regularly in mixed-species flocks, suggesting that they derive few benefits (Munn and Terborgh 1979, Author, unpublished data). Thus, the only flycatching species that may benefit consistently from flock formation may be those that regularly catch prey flushed by other flock members.

In our study, we standardized the experiments by using short alarm calls and thus do not address potential variation in threat information. There is considerable evidence from previous studies that both degree and types of threat significantly influence the behavior of species receiving the information (Rainey 2004, Templeton 2005, Soard and Ritchison 2009 and Sieving et al. 2010). Determining how graded and referential information interact with foraging guild would help us understand the mechanisms that promote the evolution of dependence on heterospecific signals. The short alarm calls used in our experiments are urgent signals that don't always accurately reflect threat (distant raptors or large, but harmless species such as woodpeckers that may have been mistaken for threatening species). Indeed, alarm calls that provide a higher sense of urgency have generated responses in flycatching species (Author, unpubl. data), and are generated when raptors, or raptor-sized birds fly directly through the flock. In both flock types, however, short alarm calls are far more frequent suggesting that responding to these calls is potentially costly in terms of lost foraging opportunity when alarm callers mistakenly perceive threats (woodpeckers or

non-raptors flying through flocks). Our results suggest that the degree of dependence on heterospecific information should make some species more easily manipulated than others and therefore might have led to the evolution of kleptoparasitism, which has previously been documented in this system (Munn 1986).

Much attention has recently focused on the linkage between information transfer and its implications for animal communities (Goodale et al. 2011). Schmidt et al. (2010) suggested that information use may play a role as an axis in evaluating ecological niches. We suggest that variation in species' dependence on heterospecific information could be incorporated as a trait to assess assembly rules in mixed-species flocks. Species joining mixed-species flocks are known to vary greatly in their flocking propensities, and this has often been correlated with vegetation density (Jullien and Thiollay 1998) or with home range size (Munn and Terborgh 1979, Munn 1985, Jullien and Thiollay 1998). However, if species within flocks have foraging ecologies that influence their response to alarms and thus reliance on heterospecific threat information, then this may also explain variation in flocking propensity among species. Magrath et al. (2009) demonstrated that ecologically distinct species (flocking versus a non-flocking species) showed variation in response to heterospecific alarms as a function of perceptions of signal reliability. Species-specific variation in anti-predator vigilance has been linked to other traits such as body height and size in African grazers (Fitzgibbon 1990, and Illius and Fitzgibbon 1994) and auditory bullae and bipedal development in rodents (Brown et al. 1988). These traits potentially provide a mechanism to interpret interspecific dependence and a partial basis for understanding the formation of mixed species groups in the context of predation risk. Additional

experiments testing whether variation in different traits influences whether species use heterospecific information as a resource would be a useful step in incorporating information use in community ecology and evolution.

Table 4-1. Characteristics of alarm calls for both natural and model prompted alarm calls. Alarm Length is in seconds, peak frequency is in kHz. Mean=mean length of alarm calls, SD=+/-1 Standard Deviation, n=sample size, Y=Alarm was prompted through model presentation, N=Alarm was recorded without model presentation.

Species	Model Prompted	Sample Size	Alarm Length Mean	Alarm Length SD	Peak Frequency Mean	Peak Frequency SD
<i>T. saturninus</i>	Y	3	0.74	0.09	4019.53	99.48
<i>T. saturninus</i>	N	5	0.71	0.09	3962.10	507.16
<i>T. schistogynus</i>	Y	1	1.371	-	3273	-
<i>T. schistogynus</i>	N	7	1.84	0.72	3420.69	321.19

Table 4-2. Results of Kolmogorov-Smirnov Tests to determine whether the distribution of data from each guild x forest type is derived from the exponential distribution. For forest type U= Upland forest, and I=Inundated forest. For Guild LL=Live-leaf gleaning species, DD=Dead-leaf gleaning species, and F=Flycatching Species. D=test statistic providing the ratio difference between the data and exponential function.

Forest Type		Guild	D	P value
U	LL	LL	0.4548	0.04957
I	LL	LL	0.3524	0.2151
U	DL	DL	0.375	0.2106
I	DL	DL	0.25	0.6994
U	F	F	0.6667	0.1389
I	F	F	0.75	0.002468

Table 4-3. Results of Likelihood Ratio Test with null hypothesis that foraging guild does not influence latency responses. All null hypotheses are rejected indicating significant different behavior of each foraging group. The only exception occurs in upland forest where we were not able to detect differences in responses between live-leaf and dead-leaf species.

Foraging Guild Comparisons	Forest Type	Chi-Square Test	df	P-value
Live Leaf vs. Dead Leaf	Upland Forest	0.065	1	0.799
Live and Dead Leaf versus Flycatching	Upland Forest	0.065	1	0.0006
Live Leaf vs. Dead Leaf	Inundated Forest	23.9	2	$1.01 \times 10^{-06}$
Live Leaf vs. Dead Leaf vs. Flycatching	Inundated Forest	68.45	2	$1.36 \times 10^{-15}$

Table 4-4. Maximum Likelihood Estimation (MLE) for the mean time of latency responses per foraging guild in each forest type and 95% confidence intervals.

Species	Foraging Guild	Forest Type	MLE estimate for Mean Response Time	95% Confidence Intervals
<i>Myrmotherula axillaris</i>	LL	Upland Forest	42.87	22.9-94.9
<i>Epinecrophylla haematonota</i>	DL	Upland Forest	37.7	20.1-83.4
<i>Terenotriccus erythrurus</i>	F	Upland Forest	2.0	.764-8.19
<i>Myrmotherula menetriesii</i>	LL	Inundated	68.9	36.7-152
<i>Thryothorus genibarbis</i>	DL	Inundated	4.37	2.33-9.6
<i>Eucometis penicillata</i>	F	Inundated	.875	0.467-1.93

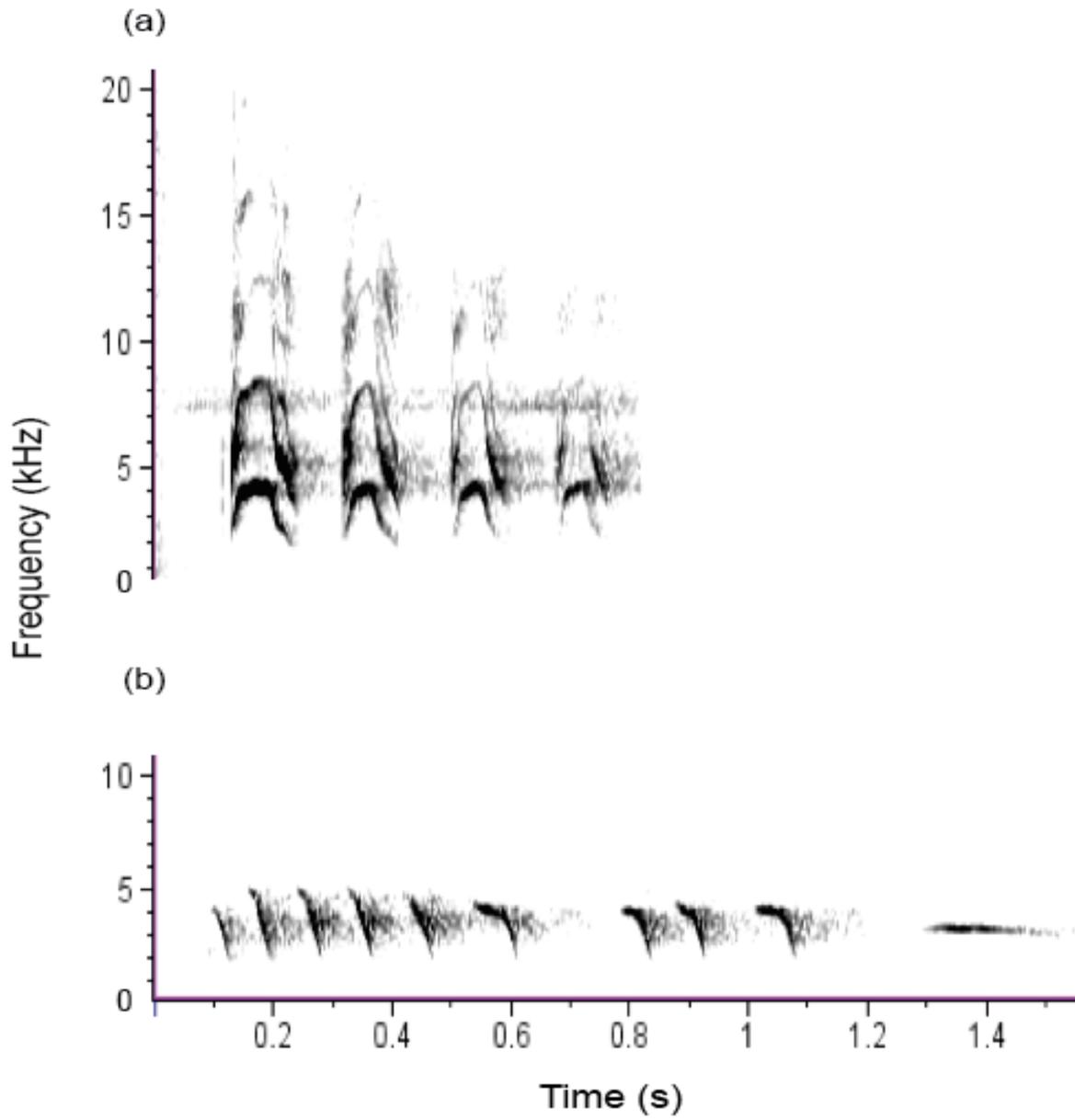


Figure 4-1. Sonogram of alarm call of a) *Thamnomanes saturninus* and b) *Thamnomanes schistogynus*.

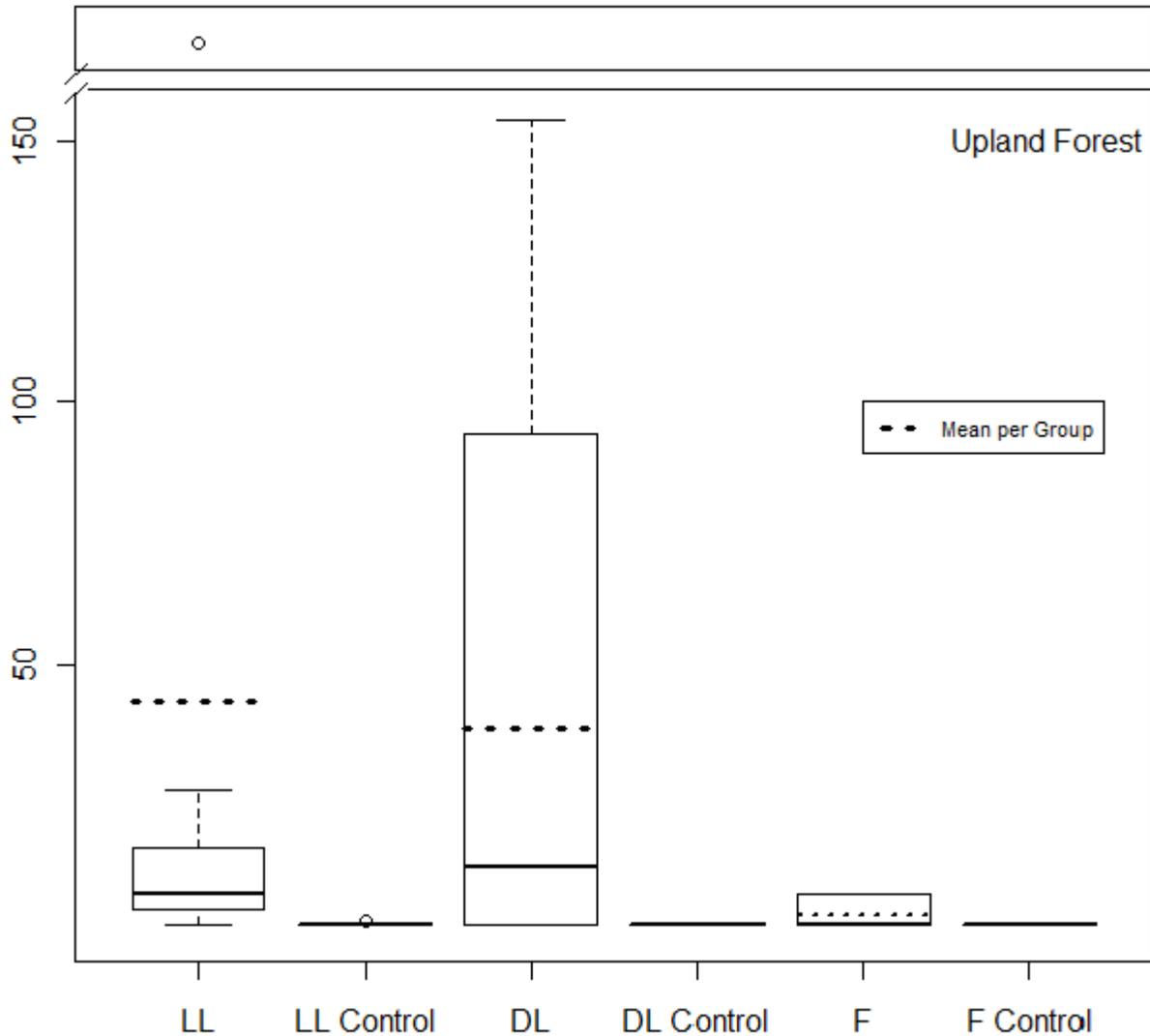


Figure 4-2. Box and whisker plots of latency to resume foraging after hearing alarm stimulus (in seconds) grouped by foraging strategy. Dashed lines shown mean response in seconds by averaging all trials by foraging guild. A “response” indicates that birds take some sort of evasive action upon hearing an alarm stimulus. LL=Live-leaf Foraging Guild, DL=Dead-leaf Foraging Guild, F=Flycatching Guild. C=Control Trials Upland Forest: Live-leaf n=8, Dead-leaf n=8, Flycatching n=3

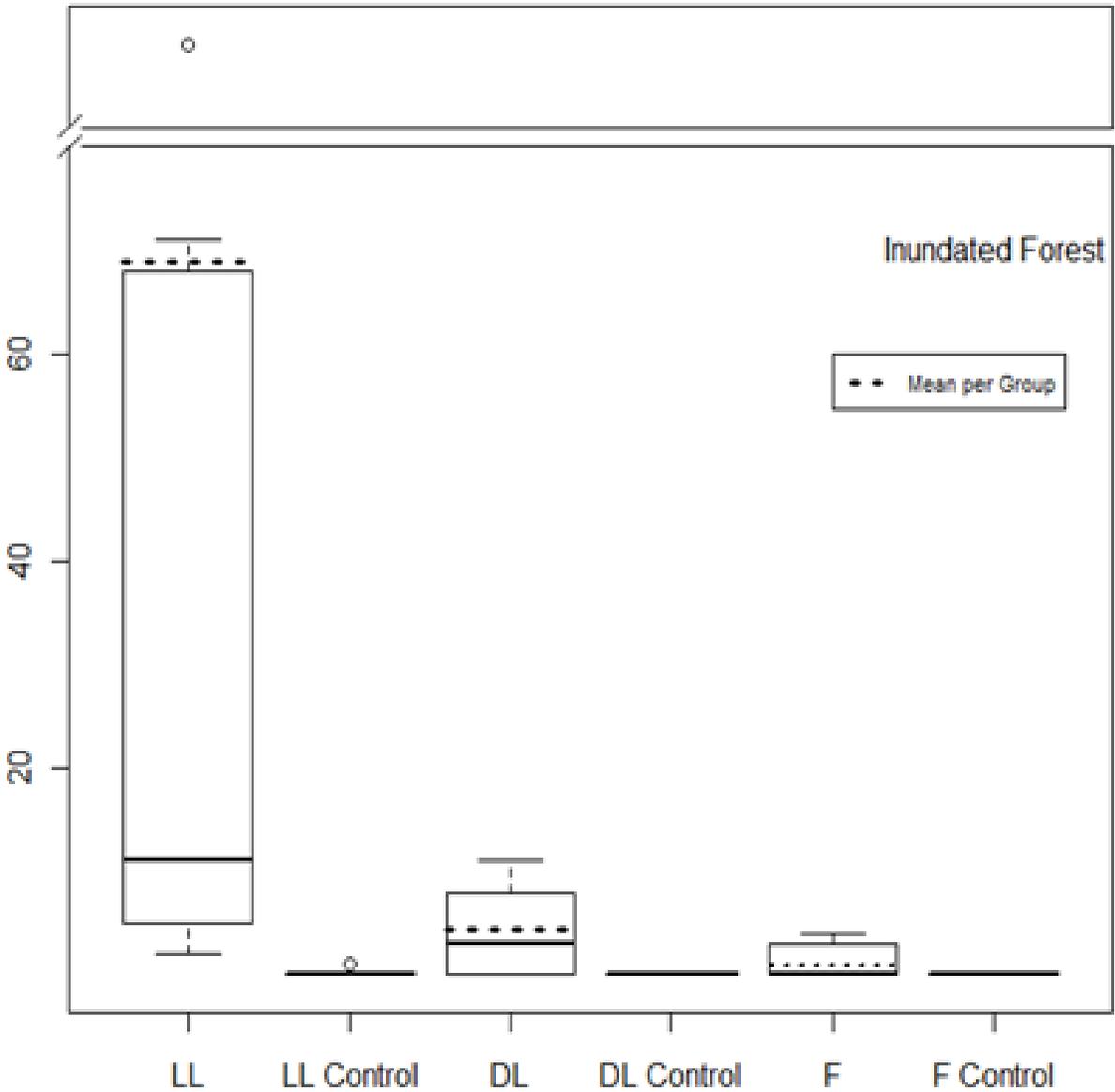


Figure 4-3. Box and whisker plots of latency to resume foraging after hearing alarm stimulus (in seconds) grouped by foraging strategy. Dashed lines shown mean response in seconds by averaging all trials by foraging guild. A “response” indicates that birds take some sort of evasive action upon hearing an alarm stimulus. LL=Live-leaf Foraging Guild, DL=Dead-leaf Foraging Guild, F=Flycatching Guild. C=Control Trials; Inundated Forest: Live-leaf n=8, Dead-leaf n=8, Flycatching n=8.

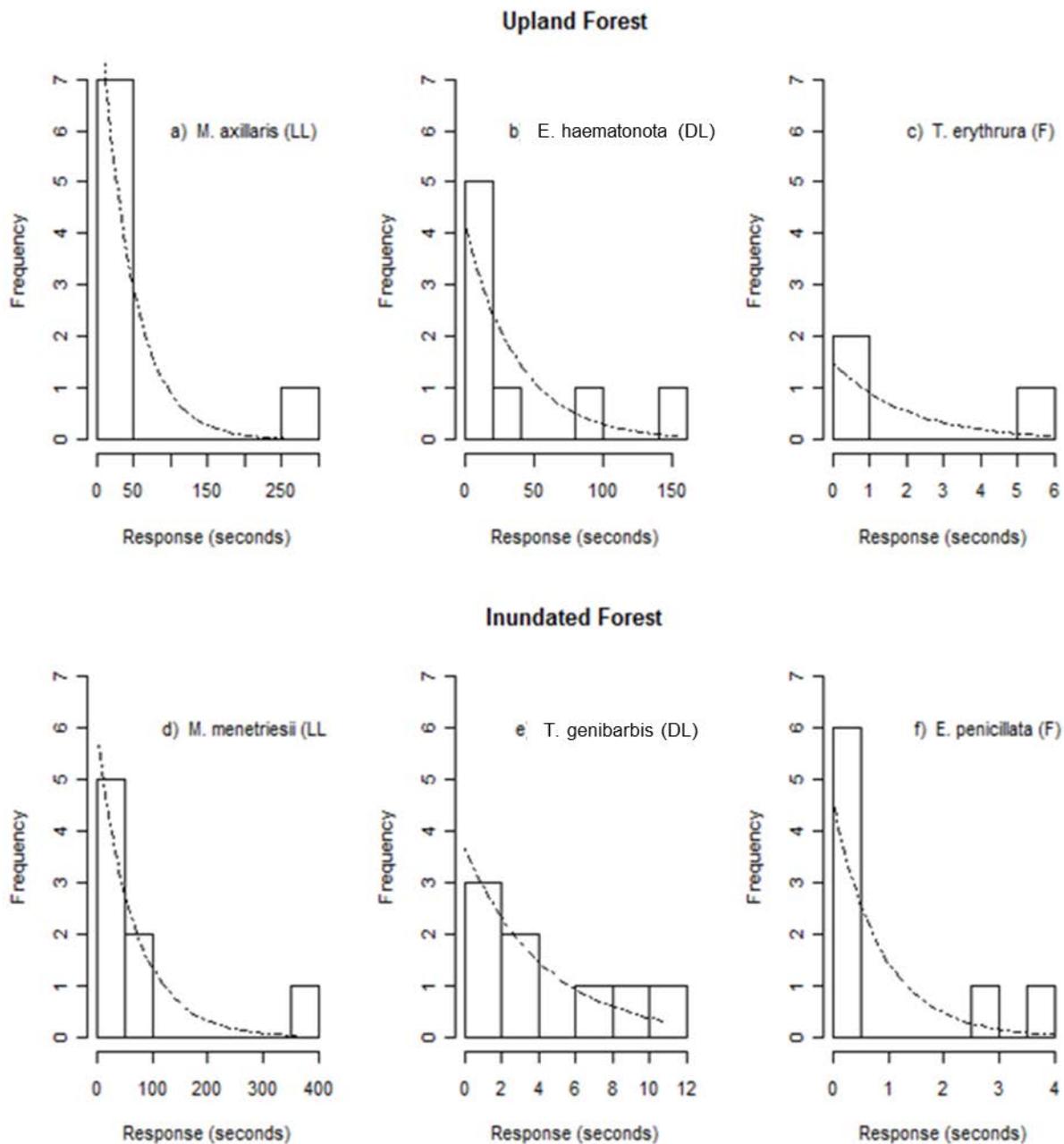


Figure 4-4. Histograms of latency response by species with superimposed estimated exponential distribution. LL=Live-leaf Guild, DL=Dead-leaf Guild, F=Flycatching Guild Upland forest = a) *M. axillaris* b) *E. haematonota*, c) *T. erythrurus*, Inundated forest = d) *M. menetriesii*, e) *T. genibarbis*, f) *E. penicillata*

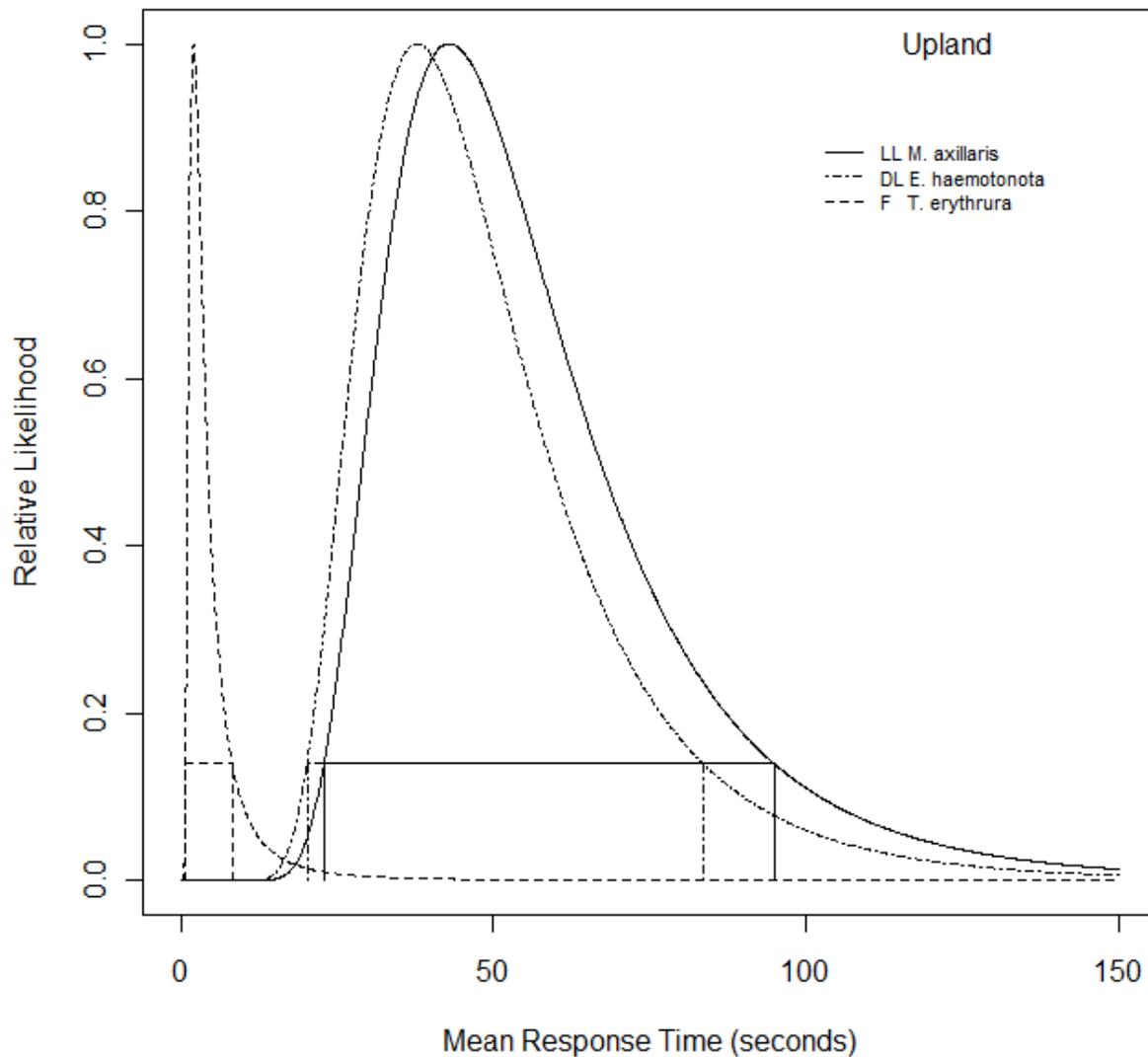


Figure 4-5. Relative likelihood functions for the mean response time to resume foraging by foraging strategy. The horizontal lines show the 95% confidence intervals for each likelihood. LL=Live-leaf, DL=Dead-leaf, and F=Flycatching. Upland Forest: LL (n=8), DL (n=8), F (n=3); A) Compares all three groups in upland forest.

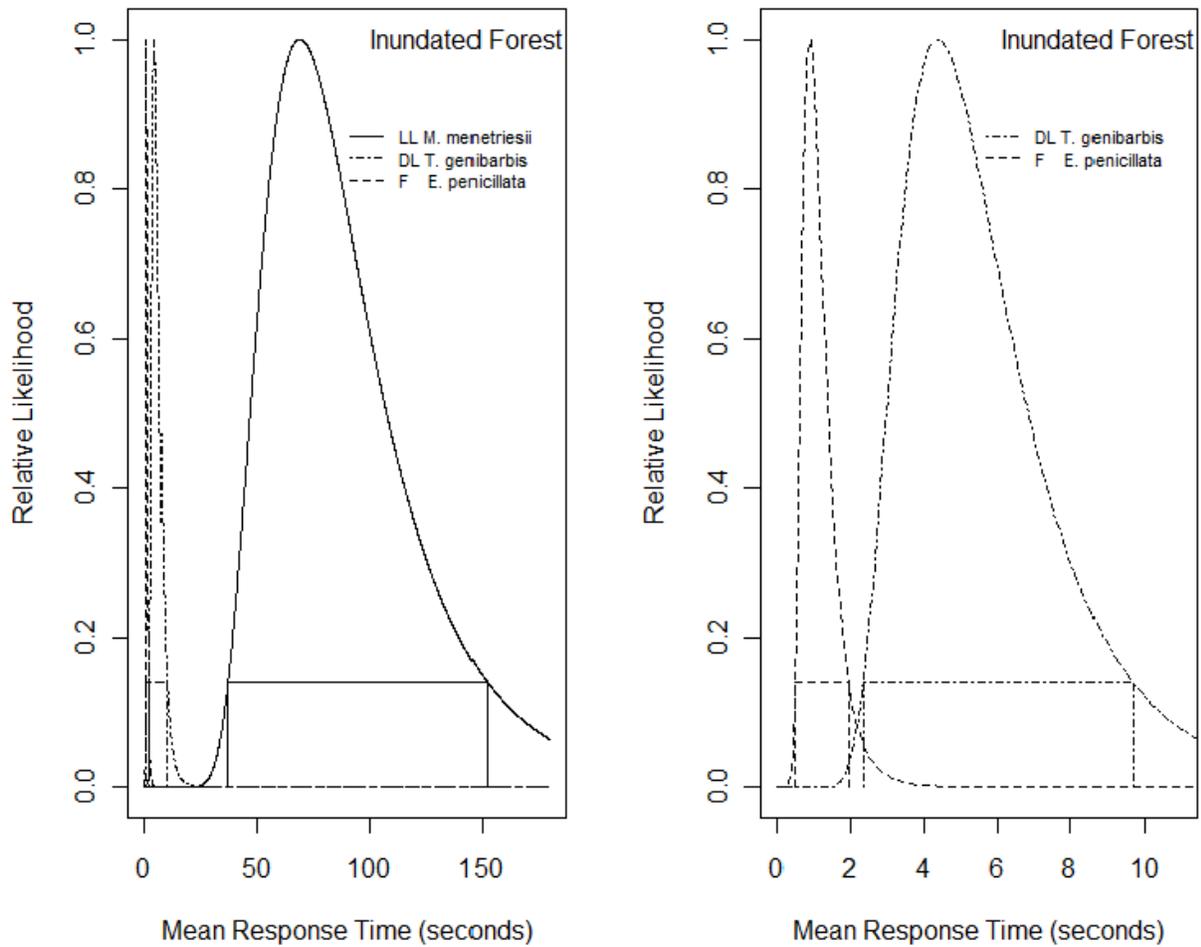


Figure 4-6. Relative likelihood functions for the mean response time to resume foraging by foraging strategy. The horizontal lines show the 95% confidence intervals for each likelihood. Inundated Forest: LL n=8, DL n=8, F n=8. Left Hand Panel) Compares all three groups in Inundated Forest and Right Hand Panel) Magnifies the estimates in inundated forest between the dead-leaving species and flycatching species.

CHAPTER 5  
BEHAVIORAL AND MORPHOLOGICAL TRAITS THAT INFLUENCE FLOCK  
PARTICIPATION AND PERCEIVED PREDATION RISK IN AMAZONIAN  
UNDERSTORY MIXED-SPECIES FLOCKS

**Introduction**

Access to information can affect an animal's fitness (Dall et al. 2005, Blanchet et al. 2010). Perhaps one of the most important types of information concerns predation risk (Laundre et al. 2010), which is a selective pressure that shapes decisions made by potential prey to avoid predators (Lima and Dill 1990, Lima 1998). The perception of predation risk can lead to behavioral, physiological and/or demographic responses from threatened species (e.g. Forsman et al. 2007, Zanette et al. 2011). The spatial distribution of animals may be affected by their perception of predation risk; this distribution is sometimes called the landscape of fear (Laundre et al. 2001 and Sridhar et al. 2007). Throughout a shared environment, conspecific or heterospecific animals that also share similar risks can provide information to each other (Seppanen et al. 2007 and Goodale et al. 2010), and this information transfer and its interpretation can affect community membership and assembly (Goodale et al. 2012).

How does information transfer related to predation risk influence species interactions and ultimately community assembly in heterospecific groups of animals (Goodale et al. 2010 and Sridhar et al. 2012)? Mixed-species bird flocks, in which species respond to heterospecific alarm calls, provide some of the best examples of interspecific social information transfer. In these flocks, species potentially benefit from the alarm calls of other species, which suggests mutualistic interactions resulting from heterospecific information transfer (Goodale and Kotagama 2008, Magrath et al. 2007, and Magrath et al. 2009). Evidence from many different regions of the Neotropics

indicates that a large number of species that flock may respond to the alarm calls of the birds that lead these flocks (the “sentinels”: Munn 1986). Thus, different species may join flocks to minimize predation risk, and ultimately increase survival rates, through the use of heterospecific information (Thiollay 1998, Thiollay 1999, Sridhar et al. 2009 and Sridhar et al. 2012).

Among forest bird species, there is a continuum of “flocking propensity,” which ranges from species that spend their entire lives with a single flock to species that never join flocks. This variation in flocking propensity occurs even if all species have access to flocks and the information provided by flock members, such as alarm calls (Munn 1980, Jullien and Thiollay 1999). Thus, the extent to which species respond to heterospecific threat information might provide insight into the degree to which different species share the same level of perceived predation risk. Perceived predation risk, may have far reaching consequences for individual reproductive success (Zanette et al. 2011).

Experimental tests of responses to heterospecific threat information by different species that vary in flocking propensity and other functional traits may shed light on how the degree of dependency on social information available in flocks influences community assembly of flocking birds. In this study we used an experimental approach to address the following questions: What specific functional traits of forest bird species influence perceived predation risk? Do only flocking species share these traits? What specific functional traits of forest bird species determine patterns of sociality and are they correlated with perceived predation risk? If forest species differ in their responses to alarm calls, and thus perceived predation risk, we predict that the response to alarm

calls are positively correlated with flocking participation. Alternatively, if perceived predation risk is pervasive among understory species, and thus all species in the understory respond to the alarm calls, we predict there should be no relation between flocking propensity and responses to sentinel alarm calls.

We also hypothesize that flocking behavior is associated with species' use of alarm calls and that body size, foraging strategy, and vegetation density influence both flocking propensity and perceived predation risk. Specifically, we predict that smaller species which inhabit less dense cover and those that search nearby substrates for food are more vulnerable to predators and hence more likely to share perceived predation risk. If increased flocking propensity is primarily a response to perceived predation risk, then smaller birds that forage myopically in open areas should have higher flocking propensities than larger birds that search for prey at a distance or birds that search in dense cover.

We tested the response of a variety of species of different flocking propensities to the alarm calls of the most prominent sentinel bird of flocks at Nouragues Field Station in French Guiana, and we also evaluated whether morphological, and behavioral relationships explain any observed differences in their responses to alarms or flocking propensity. Responses to alarm calling, have been widely used to measure perceived predation risk (Templeton 2005, Soard and Ritchison 2009, Sieving et al. 2010). Previous studies at the Nouragues field station mapped the territories of all of the flocks present in the 120 ha main grid of the station, and these flocks appear to be stable in composition and space over ecological time periods of almost two decades (Jullien and Thiollay 1994; Martinez and Gomez 2013). Additionally there is detailed information on

species abundances and flocking propensities at this site (Thiollay 1994; Jullien and Thiollay 1998).

## **Methods and Procedures**

### **Study Organisms**

Because mixed-species flocks in neotropical forests form stable associations (Munn 1980, Greenberg and Gradwohl 1986, Jullien and Thiollay 1998), they are ideal systems for testing mechanisms underlying community assembly (Graves and Gotelli 1990). These flocks consist of permanent groups of 5-10 species, each represented by a pair that share and defend a common territory. Additionally, up to 50 other bird species may regularly join these flocks throughout some part of their daily foraging routine within a single community (Munn 1980, Jullien and Thiollay 1998). Two “sentinel” species in the genus *Thamnomanes* typically lead understory mixed-species flocks in Amazonia and in the Guianas (Munn and Terborgh 1979, Wiley 1980, Jullien and Thiollay 1998). The sentinels constantly vocalize and appear to sound “alarm calls” in the presence of predators. They also lead the flock as it moves. The rest of the flock consists of multiple species in genera such as *Myrmotherula* and *Automolus* that serve as “beaters”, species that search for insects, often while probing their entire head into dense clusters of leaves. The beaters appear to benefit from the sentinels’ vigilance toward predators, whereas the sentinels benefit from the insects flushed by the beaters (Munn 1986). Under certain conditions, the sentinels behave more like kleptoparasites, stealing food from the beaters rather than just exploiting the insects that are flushed (Munn 1986).

## **Field Site**

Nouragues Field Station (hereafter Nouragues) is an especially amenable field site for this study because of the baseline ecological data previously collected on the bird communities at the site (4°05' N - 52°41'W). It is located in the north east of French Guyana, where there has been little recent impact of human disturbance on the native forests.

## **Data Collection**

### **Collection of alarm calls**

From October 6 to 22 we followed flocks from dawn to dusk, recording constantly with a Sennheiser ME66 Shotgun microphone and a TASCAM DR-07 digital recorder alarm calls given by *T. caesius* (see Figure 5-1). Because we were able to discern in several cases when hawks or hawk-like birds flew through the flocks, we could identify alarm calls that we then used as our criteria for selecting similar alarm calls from other flocks. In this way we were able to select alarm signals from six different *T. caesius* for use as independent replicates in our playback experiments. These recordings were filtered and standardized to the same amplitude using Raven 1.3 sound software. These replicate calls were similar in length and number of notes. We also developed control playback signals, using white noise similar in length and matching the frequency range and amplitude of the alarm playbacks.

### **Field experiments**

From 24 October to 30 November we tested whether individuals of 58 species responded to alarms of *T. caesius* by walking the Nouragues. When a species was encountered, one observer would spot an individual beforehand and would signal a second observer to broadcast the stimulus recording, from a speaker held waist-high

and 10 to 20m away from the target bird. The response of the bird was documented in a handheld voice recorder by the first observer. The height of the bird and distance from the stimulus were measured with a range finder. In addition the primary observer would also visually estimate the vegetation density in a 1-meter sphere around the bird in four categories: 0-25, 26-50, 51-75, and 76-100 percent volume (Remsen and Robinson 1990). Playback trials were conducted between 0645 and 1600 hours when light permitted visual observations. We tested individuals of 58 species in random order; once a playback trial was conducted, we did not test any other individual from any other species within 100 m on the same day. In addition no two individuals from the same species were tested within 300 meters for playback trials throughout the study. We attempted to get up to six different alarm responses and six different control responses per species. Following this same methodology, we performed at least one control per species using the white noise sound created using the alarm call parameters.

### **Response to alarm calls and flocking propensity**

Species respond to alarm calls by either diving or freezing (Munn 1986, Lima et al., Seppanen et al. 2007). Although the magnitude of the response can be measured by the latency time for a bird to resume normal activity after hearing an alarm, this is logistically very difficult to measure for many different species (Martinez and Zenil 2012). Thus, we measured responses to alarms as a binomial outcome for each trial. Individual birds that exhibited one or both of these behaviors displayed a positive response to an alarm trial whereas birds that neither dived or froze displayed a negative response. By following each individual bird to conduct an experimental trial we recorded whether or not the bird was in a flock. Thus we could tally the proportion of individuals for each species that flocked (i.e. flocking propensity).

## **Species Traits**

We assembled data on body mass from previous work carried out at the same field site (Thiollay 1994, Jullien and Thiollay 1998). Foraging strategies were assigned from accounts in the literature (Thiollay 1994), and foraging height of each individual of each species was measured during the experiments. In addition, the distance that a foraging bird maintains between itself and the alarm caller may influence the degree to which it relies on the information provided by the alarm caller. Therefore, we also tested whether distance to the alarm source influenced a species' response to alarm calls. To control for possible effects of playbacks on our experiments, we tested the null hypothesis that the frequency of positive responses to white noise did not differ from the frequency of positive responses to alarm calls using the binomial test, based on the binomial sampling distribution of alarm calls.

We used likelihood-ratio tests to evaluate 1) the effects of foraging strategy, mass, foraging height and foraging density, on flocking propensity and 2) individually the effects of foraging strategy, mass, foraging height and vegetation density and alarm source on the response of individuals to alarms. In each case by comparing a null model under a logistic regression to models generated incorporating the traits above as terms in the model. The response variable in each case was binary: flock, no flock and response and no response. Mass, height and distance were continuous variables and foraging strategy and vegetation density were categorical variables. Individuals of a species may have varied responses depending on a number of conditions so we tested responses across individuals (i.e., multiple trials) to provide for a more comprehensive assessment of the conditions under which species perceive threat. We conducted tests

of models using single terms and if more than one term was significant we included model tests using interaction terms. We then selected the lowest AIC value.

Our analyses might be biased because of the covariance in traits due to the phylogenetic relationships among species (Felsenstein 1985). However, only two sister species occur within the sample of species used in these analyses and therefore phylogenetic autocorrelation is not likely to play a significant role in influencing patterns seen due to the traits we evaluate.

## **Results**

Given that the proportion of positive responses generated from control playbacks was exceedingly small compared with the proportion generated through alarm playbacks ( $p < .00001$ ), we conclude that the artifact of playback trials did not influence the responses of birds to our alarm playbacks.

### **Evaluation of Morphological and Behavioral Influences on Flocking Participation**

We report model results, along with AIC values for the Null Model and each single term model in Table 5-1. Because multiple terms were significant we also included the model with interaction terms and which also had the lowest AIC value (Table 5-1). Thus the model with the interaction terms increased explanatory power compared with the null and thus is the one we use to interpret the influence of behavioral and morphological effects on flocking propensity.

In evaluating traits that influence flocking propensity, foraging height, body mass foraging strategy and Density increased the explanatory value of the logistic model compared to the null (Table 5-1,  $X^2$  test, Foraging Strategy  $P < 4.7^{-15}$ , Mass  $P < .00016$ , and Foraging Height  $P < 4.41^{-05}$ , Density  $P < .022$ ). Bark-gleaning and leaf gleaning birds showed a higher propensity to flock than ground foraging, ant-following and sallying

birds (Figure 5-2). With respect to mass, propensity appears to decrease with body size, although small birds show a high degree of variation with respect to flocking propensity (Figure 5-3). Foraging Height was highly variable but seems to be driven by a large concentration of species that forage low to the forest floor. In general species higher than 5 meters appear to exhibit higher flocking propensities (Figure 5-4).

### **Evaluating Responses to Alarm Calls**

Foraging strategy significantly increased the explanatory value of the model compared to the null, whereas the other models did not (Table 5-2). The results strikingly mirror the influence of foraging strategy on flocking propensity: Bark gleaners and leaf gleaners had the highest response, whereas flycatchers, ground foragers and army ant followers had much lower proportions of responses (Figure 5-5). Species with high flocking propensities always responded to alarms, whereas species with low flocking propensities included both species that responded to alarms and species that did not. Sallying and ground-foraging species responded less to alarm calls than bark-gleaning and leaf-gleaning species (Figure 5-5).

### **Discussion**

Our results indicate that foraging strategy influences both the propensity of species to flock and their response to alarm calls given by flock sentinels (Tables 5-1 and 5-2, Figs. 5-2 and 5-5). These results are consistent with the prediction that birds that search myopically on leaf surfaces are more likely to perceive higher predation risk than birds that search at a distance (Martinez and Zenil 2012). Birds that search myopically (on green leaves or clusters of dead leaves) are less likely to be aware of ambush predators and thus would incur costs due to investment in vigilance if they were not to rely on alarm calls from other species. Birds feeding on trunks, (woodcreepers

and woodpeckers) showed high responses to alarm calls, which may reflect the fact that as birds climb up tree trunks they are blind to 180 degrees of their environment. Although trunks can serve as a foraging substrate as well as obstructions to predators, woodcreepers and woodpeckers may be more reliant on other birds for vigilance when in flocks (Lima 1992). Their reliance on vigilance from other species would explain both their high degree of social tendency and their high level of response to alarm calls (Figure 5-2 and Figure 5-5). Conversely birds that flycatch and therefore catch prey at a distance, can double up on the cost of searching for predators while searching for food and would be expected to provide a higher proportion of their own vigilance (Munn 1986).

Previous analyses suggest flycatching birds found in flocks should take advantage of prey items flushed from other birds (Srinivan 2010, Sridhar et al. 2012), but these studies do not consider whether or not flycatching species may also be those that provide alarm calls. Indeed those flycatching species found in Amazonian understory flocks are also the alarm-calling “sentinels” (Munn 1986).

The high variation in flock propensity for gleaning birds suggests that flocking is not the only way that species can minimize risk. Amongst non-social birds, some live in microhabitats that likely minimize risk (Lima and Dill 1990), whereas others have other traits that enable them to deal with higher predation risk. High flocking-propensity birds were typically found between 5-15 meters off the forest floor and many low-flocking propensity birds were found less than 5 meters (Figure 5-3). High vegetation density was typically the most parsimonious explanation for why low foraging heights are safer from ambush predators. Vegetation density did appear to influence p flocking

propensity but not predation risk (Tables 5-1 and 5-2) partially contrary to our prediction. Thus the large amount of low propensity flocking birds at low heights may be more indicative of constraints on flight and movement behavior.

Species variation in antipredator escape behavior and proximity to microhabitats, such as distance to cover may influence their perception of vulnerability to predators (Lima and Valone 1991). Evidence from other systems suggests that functional traits or habitat structure also can influence species sense of vulnerability to predation. For example, variation in perceived predation risk from lions has been demonstrated among browsers and grazers and among prey of different body size (Valiex et al. 2009, Periquet et al. 2012). From a structural perspective, predation risk appears higher in old growth forests where sensory cues provided by coarse woody debris aid the hunting success of American martens (Andruskiw et al. 2008). Detecting variation in perceived risk across habitat on a coarser scale, however, may be easier to test. Our study attempted to evaluate variation in predation risk *within* a habitat. While we attempted to evaluate vegetation density as a proxy for vulnerability, it is possible that our methods were not fine scaled enough to measure differences meaningful to bird's perception, and thus we may need to reevaluate our measure of vegetation density.

Our results suggest that perceived vulnerability is independent of the range of body sizes (6 to 199 grams) used in our study (Table 5-2), even though flocking propensity was negatively correlated with body mass (Table 5-2, Figure 5-4). We assumed that body mass would play a large role in determining vulnerability because similar-sized prey are more likely to share predators; indeed, similarities in body size have been hypothesized to be a trait that explains positive associations among flock

members (Sridhar et al. 2012). Our results suggest that while body size does not influence perceived predation risk, it may influence the ability of species to stay with a flock based on metabolic requirements. However, the conclusion that body size does not influence predation risk assumes that the alarm calls used accurately convey threats to birds of varying body size (Lima and Dill 1990). There is evidence to suggest that specific aerial predators may target only certain size birds. We do not know the extent to which our alarm calls represent graded or referential information (Sieving et al. 2010, Hetrick and Sieving 2011) and this assumption needs to be tested. These results also indicate a large amount of individual variation within some species' responses suggesting that predation risk, which is variable among habitats, is also context dependent *within* a habitat.

Distance from alarm source did not affect species responses which suggests that birds that remain within 18-20 meters of an alarm-calling bird might still benefit from anti-predator vigilance provided by that bird. Benefit from information transfer in starlings has shown to vary as a function of distance between the sender and receiver of such information (Fernandez-Juricic and Kacelnik 2004). Assuming that risk from aerial ambush predators is the primary driver for species to flock in forested environments, it would be interesting to test whether the degree of flocking cohesion is determined by the effective distance at which species can respond to heterospecific alarm calls.

The results we report here suggest that 1) foraging strategies influence perception of predation risk and the social tendency to flock and that 2) species that live in predation risk environments, especially gleaning birds, do not invariably evolve a

tendency to join flocks. Thus species that share perceived predation risk may employ different evolutionary strategies for coping with this perceived risk. Future work should investigate the additional traits that might explain alternative strategies for dealing with perceived risk and the reliance on social information that influences the organization of mixed species animal groups.

Table 5-1. Results of likelihood ratio tests evaluating flocking propensity as a function of foraging strategy, body size, foraging height and density using a generalized linear model with normalized distribution. Foraging height and foraging density were averaged across all individuals for each species. Number of species used=3.

Term	AIC	DF	Deviance	Residual DF	Resid.Dev	Pr(>Chi)
1 NULL	422.77			304	420.77	
2 Foraging Strategy	357.52	4	73.239	300	347.53	4.70E-15
3 Mass	404.6	1	20.154	303	400.61	7.15E-06
4 Density	424.5	1	0.29729	303	420.47	0.5856
5 Height	397.3	1	27.427	303	393.34	1.63E-07
6 Model w/ Interactions	333.12			304	420.77	
FStrategy		4	73.239	300	347.53	4.70E-15
Mass		1	14.173	299	333.36	0.0001667
Density		1	5.24	298	328.12	0.0220769
Height		1	16.685	297	311.43	4.41E-05
Density:Height		1	2.006	296	309.43	0.15672
FStrategy:Density		4	4.614	292	304.81	0.329258
Mass:Height		1	2.98	291	301.83	0.0842739
FStrategy:Mass		4	16.29	287	285.54	0.0026533
FStrategy:Height		4	3.786	283	281.75	0.4357256
Mass:Density		1	0	282	281.75	0.9883516
FStrategy:Density:Height		1	1.764	281	279.99	0.1841034
FStrategy:Mass:Height		4	4.835	277	275.16	0.3046236
Mass:Density:Height		1	0.002	276	275.15	0.9621321
FStrategy:Mass:Density		0	0	276	275.15	

Table 5-2. Results of likelihood ratio tests evaluating flocking propensity as a function of foraging strategy, body size, foraging height and density and distance using a generalized linear model with a binomial distribution. Number of individuals used=148.

Model	AIC	DF	Deviance	Residual DF	Resid.Dev	Pr(>Chi)
1 Null Model	216.8692			154	214.87	
2 Foraging Strategy	191.3642	5	35.5	149	179.36	1.19-06***
3 Body Mass	217.4152	1	1.454	153	213.41	0.2279
4 Foraging Density	216.0849	1	2.7842	153	212.09	0.0952
5 Foraging Height	216.2632	1	2.606	153	212.26	0.1065
6 Distance from Alarm Source	218.5636	1	0.30554	153	214.56	0.5804

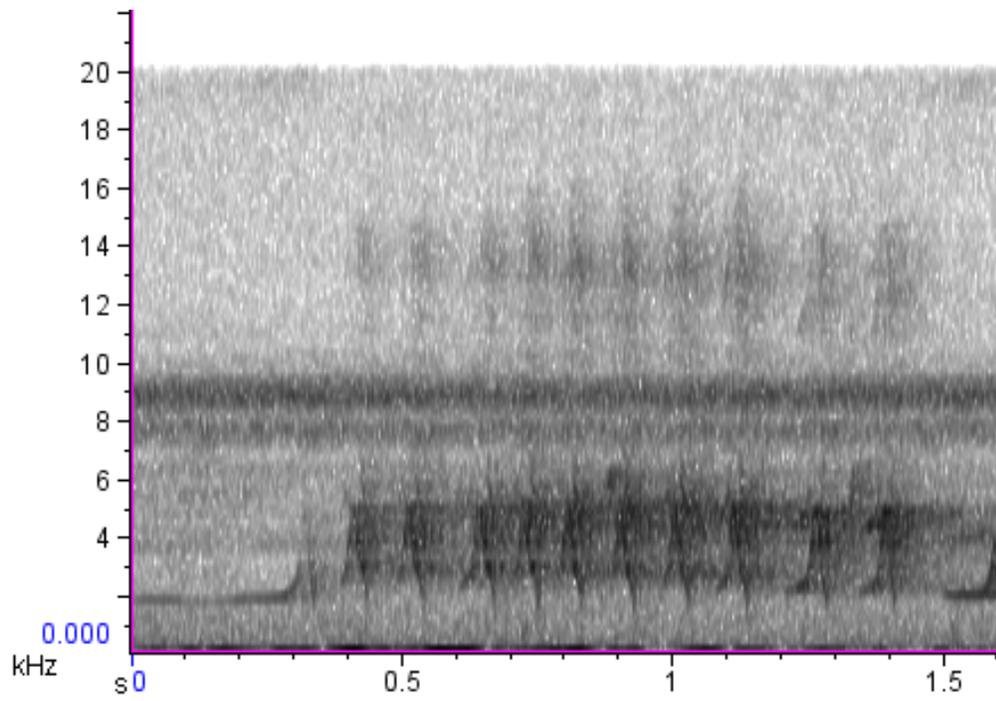


Figure 5-1. Sonogram of an alarm call of *Thamnomanes caesius*, the alarm calling bird of mixed-species flocks, used in the experiments.

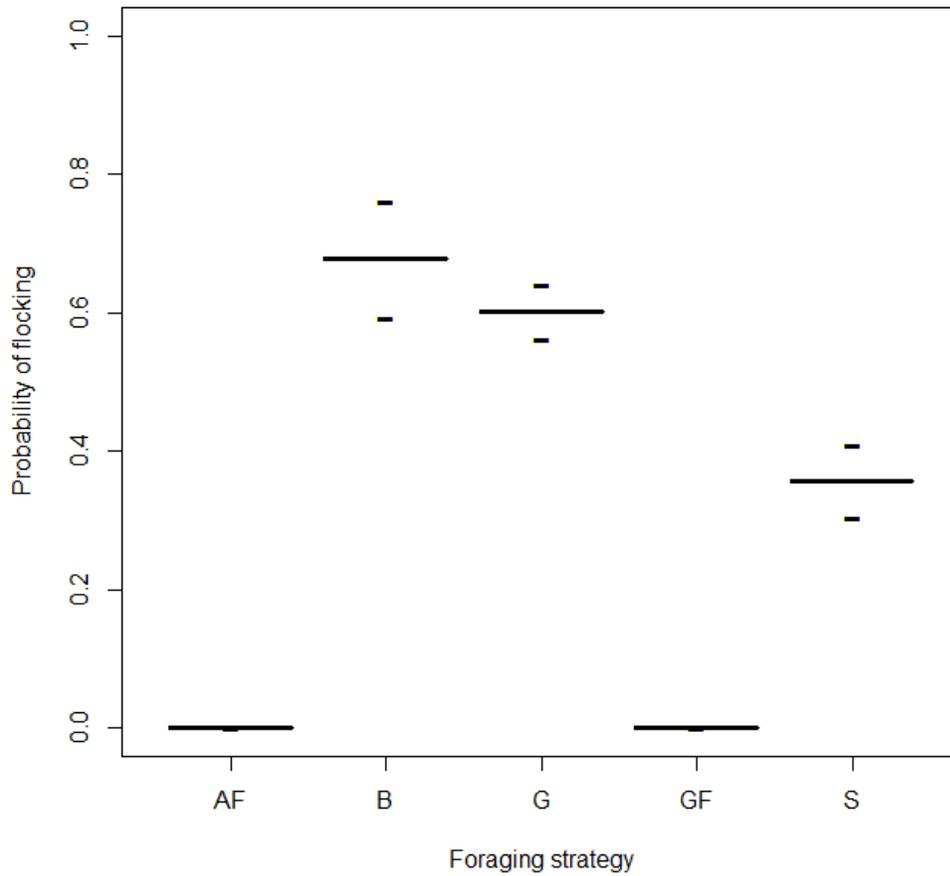


Figure 5-2. Values of propensity as a function of foraging strategy. AF=Army ant follower, B=Bark feeding, G=Gleaning, GF=Ground Forager and S=Flycatching species. . Values are the total proportion of individuals that participate in flocks as a function of mass  $n=304$  individuals. Bars show 95% confidence intervals generated by the logistic model.

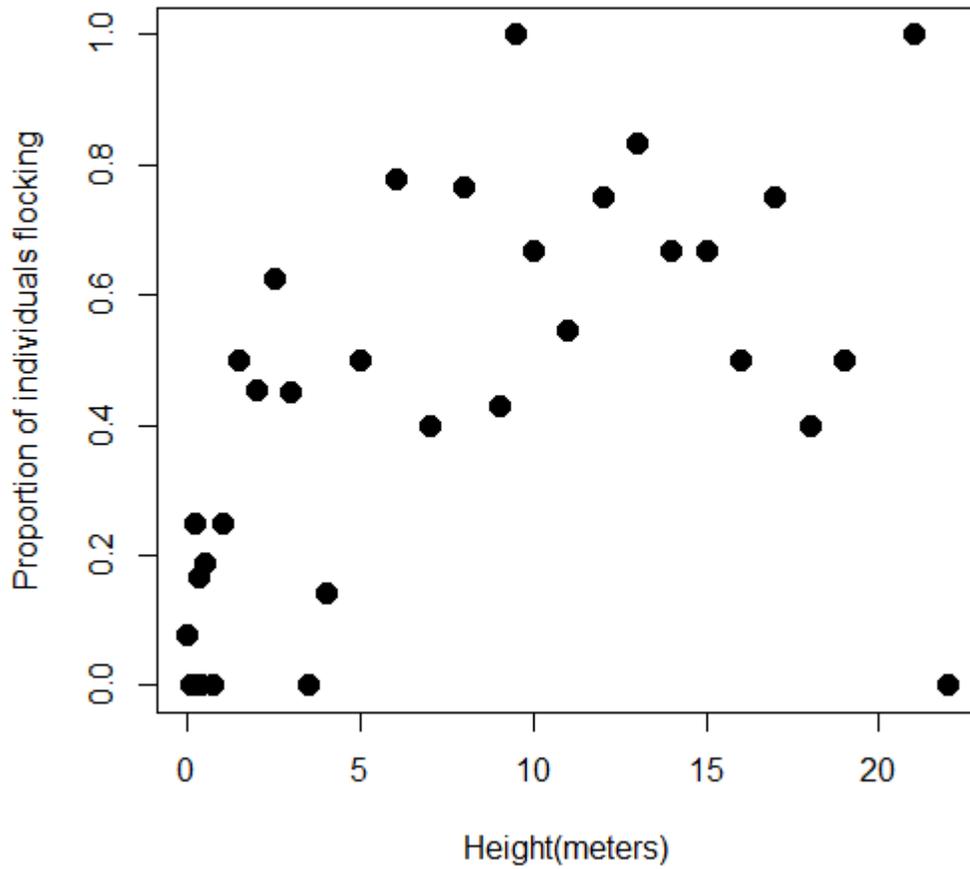


Figure 5-3. Flocking propensity as a function of mean height per species. Values are the total proportion of individuals that participate in flocks as a function of mass n=304 individuals

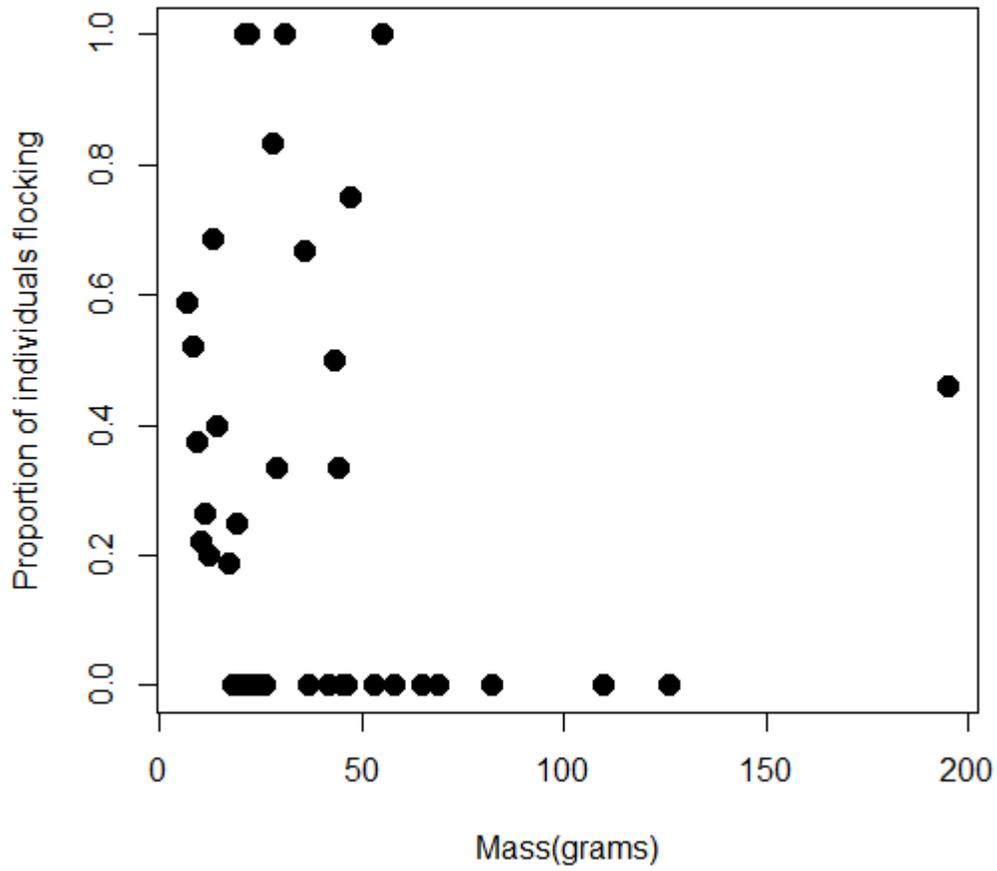


Figure 5-4. Propensity as a function of body mass. Values are the total proportion of individuals that participate in flocks as a function of mass n=304 individuals

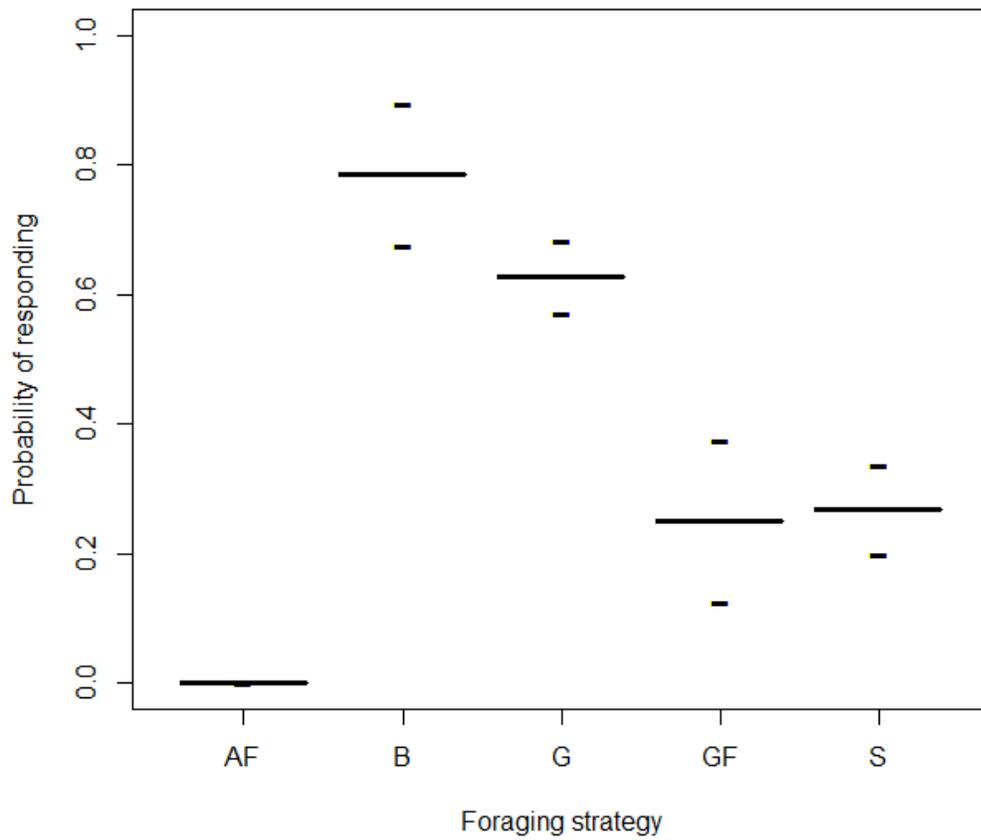


Figure 5-5. Proportion of positive responses of species to alarm calls as a function of their foraging strategy. AF=Army ant follower n=6, B=Bark feeding n=14, G=Gleaning n=75, GF=Ground Forager n=12 and S=Flycatching species n=41. Bars show 95% confidence intervals generated by the logistic model.

## CHAPTER 6 CONCLUSION

Mixed species groups have been a primary focus for understanding how social information influences the cohesion and organization of species assemblages. In many systems of mixed-species groups, it has been hypothesized that information flow is based on threat information about predators. In such systems, either one or two species provide alarm calls that attract other eavesdropping species. My work quantifies the extent to which alternative types of information in addition to alarm calls may influence the cohesion and organization of Amazonian mixed species flocks. By conducting reciprocal playbacks I demonstrate that this system in particular is indeed unidirectional where multiple species eavesdrop on an alarm calling species suggesting that these previously documented permanent and stable groups may reflect a commensalistic or parasitic relationship between alarm calling species (producers of information) and eavesdropping (receivers of information). Because this system, consistent with patterns from mixed species bird flocks in other systems, appears to be oriented around alarms that provide information about predators, I experimentally show that specific traits may influence dependency on such information and thus the types of species that participate in mixed species flocks. My results demonstrate that foraging strategy influences the strength of response to heterospecific alarm calls. In other birds that myopically search close by substrates are much more dependent on alarm calls than species that search for prey at farther distances. In addition, by evaluating across a suite of species the traits that correlate with participation in flocks and how those traits influence responses to heterospecific alarm calls, I demonstrate that foraging strategy indeed explains variation in both tendency to participate in flocks and response to alarm calls. Thus

variation in traits may explain dependency on social information provided by other species and thus may explain much of the variation underlying assembly rules in mixed species animal groups. Incorporating experimental approaches that evaluate how species depend on social information in other biological communities will further our understanding of how specific traits of species influence the organization of mixed species animal groups and thus some of the emergent properties underlying this widespread biological phenomena.

APPENDIX  
SPECIES LIST AND FLOCK OCCURRENCES FOR EACH TIME PERIOD

Table A-1. Species list and the proportion of flocks in which each species was found in sampling Nouragues station flocks in 1994 and 2012. Taxonomy follows Clements, J.F., T.S. Schulenberg, M.J. Iliff, B.L. Sullivan, C.L. Wood and D. Robinson. 2011. The Clements checklist of birds of the world: Version 6.6.

Species	1994	2012
<i>Epinecrophylla gutturalis</i>	100	100
<i>Glyphorynchus spirurus</i>	100	100
<i>Myrmotherula axillaris</i>	100	100
<i>Thamnomanes ardesiacus</i>	100	100
<i>Thamnomanes caesius</i>	100	100
<i>Xiphorhynchus pardalotus</i>	100	100
<i>Myiobius barbatus</i>	80	91
<i>Myrmotherula longipennis</i>	100	91
<i>Myrmotherula menetriesii</i>	100	91
<i>Philydor erythrocerum</i>	100	91
<i>Automolus infuscatus</i>	60	82
<i>Cercomacra cinerascens</i>	0	82
<i>Ramphocaenus melanurus</i>	20	82
<i>Mionectes macconelli</i>	28	73
<i>Xenops minutus</i>	67	73
<i>Cymbilaimus lineatus</i>	26	64
<i>Hylophilus ochraceiceps</i>	53	64
<i>Herpsilochmus sticturus</i>	0	55
<i>Lanio fulvus</i>	46	45
<i>Monasa atra</i>	33	45
<i>Piculus flavigula</i>	53	45
<i>Hylophilus muscicapinus</i>	0	36
<i>Thamnophilus punctatus</i>	0	36
<i>Celeus grammicus</i>	0	27
<i>Hemitriccus minor</i>	0	27
<i>Hypocnemis cantator</i>	0	27
<i>Microrhophias quixensis</i>	20	27
<i>Piprites chloris</i>	0	27
<i>Platyrhynchus saturatus</i>	7	27
<i>Rhynchociclus olivaceus</i>	33	27
<i>Pheugopedius coraya</i>	20	27
<i>Veniliornis cassinii</i>	0	27
<i>Campephilus rubricollis</i>	0	18

Table A-1. Continued

Species	1994	2012
<i>Coereba flaveola</i>	0	18
<i>Cyanerpes caeruleus</i>	0	18
<i>Deconychura longicauda</i>	53	18
<i>Microbates collaris</i>	20	18
<i>Myrmotherula guttata</i>	53	18
<i>Tachyphonus luctuosus</i>	0	18
<i>Tachyphonus surinamus</i>	26	18
<i>Thamnophilus amazonicus</i>	20	18
<i>Trogon rufus</i>	26	18
<i>Campylorhamphus trochilirostris</i>	0	9
<i>Celeus elegans</i>	0	9
<i>Dacnis cayana</i>	0	9
<i>Dendrocolaptes certhia</i>	0	9
<i>Euphonia cayennensis</i>	0	9
<i>Galbula albifrons</i>	0	9
<i>Galbula dea</i>	0	9
<i>Herpsilochmus stictocephalus</i>	0	9
<i>Hylexetastes perrotii</i>	7	9
<i>Leptopogon amaurocephalus</i>	0	9
<i>Myrmotherula brachyura</i>	13	9
<i>Myiopagis caniceps</i>	0	9
<i>Pachyramphus minor</i>	0	9
<i>Percnostola rufifrons</i>	13	9
<i>Picumnus exilis</i>	13	9
<i>Rhytipterna simplex</i>	0	9
<i>Saltator grossus</i>	13	9
<i>Selenidera culik</i>	0	9
<i>Tangara gyrola</i>	0	9
<i>Tachyphonus phoenicius</i>	0	9
<i>Terenotriccus erythrurus</i>	0	9
<i>Terenura spodioptila</i>	0	9
<i>Turdus albicollis</i>	0	9
<i>Xiphorhynchus guttatus</i>	0	9
<i>Tolmomyias assimilis</i>	7	9
<i>Attila spadiceus</i>	7	0
<i>Automolus rubiginosus</i>	14	0
<i>Campylorhamphus procurvoides</i>	40	0
<i>Cyphorinus arada</i>	20	0
<i>Dendrexetastes rufigula</i>	7	0
<i>Momotus momota</i>	20	0

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## BIOGRAPHICAL SKETCH

Ari Martinez obtained both his Bachelor of Arts in biological sciences and Master of Arts in aquatic biology and populations from the University of California at Santa Barbara. After doing a number of seasonal field jobs in different parts of the Sierra Nevada and travelling throughout the Caribbean, central America, and the Middle east, he served in the Peace Corps first in Nicaragua then in Bolivia. In Bolivia, he started to learn neotropical birds while coordinating a project to train local guides. He eventually stayed on to conduct local conservation projects on birds for the local Birdlife partner in Bolivia, Armonia. He then worked for the Instituto Boliviano de Investigacion Forestal as an Avian Ecologist where he surveyed tropical bird communities on logged forest plots in the tropical lowlands of eastern Bolivia.