

# Functional Traits, Flocking Propensity, and Perceived Predation Risk in an Amazonian Understory Bird Community

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**ABSTRACT:** Within a community, different species might share similar predation risks, and, thus, the ability of species to signal and interpret heterospecific threat information may determine species' associations. We combined observational, experimental, and phylogenetic approaches to determine the extent to which evolutionary history and functional traits determined flocking propensity and perceived predation risk (response to heterospecific alarm calls) in a lowland Amazonian bird community. We predicted that small birds that feed myopically and out in the open would have higher flocking propensities and account for a higher proportion of positive responses to alarms. Using generalized linear models and the incorporation of phylogeny on data from 56 species, our results suggest that phylogenetic relationships alongside body size, foraging height, vegetation density, and response to alarm calls influence flocking propensity. Conversely, phylogenetic relationships did not influence response to heterospecific alarm calls. Among functional traits, however, foraging strategy, foraging density, and flocking propensity partially explained responses to alarm calls. Our results suggest that flocking propensity and perceived predation risk are positively related and that functional ecological traits and evolutionary history may explain certain species' associations.

**Keywords:** predation risk, information transfer, mixed-species bird flocks, community assembly, alarm calls.

## Introduction

Predation risk (Laundré et al. 2010) 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 prey species (e.g., Forsman et al. 2007; Zanette et al. 2011). Such responses may come at the expense of foraging opportunities and generate a foraging–predation risk trade-off (where species must decrease foraging opportunities in order to detect and avoid predators) with consequences at the level of individual fitness, populations, and communities (Cress-

well 2008). Throughout a shared environment, community members that also share similar risks often gain information from each other about such risks (Seppänen et al. 2007; Sridhar et al. 2009). Thus, information transfer and its interpretation can affect community membership and assembly (Goodale et al. 2010).

Mixed-species bird flocks, in which species respond to heterospecific alarm calls (Sridhar et al. 2009), provide some of the best examples of interspecific information transfer related to predation risk. In particular, species that forage in areas that make them conspicuous to predators often compensate by associating in heterospecific groups (Boinski and Garber 2000; Goodale et al. 2010; Sridhar et al. 2012; Journey et al. 2013). In these flocks, species potentially benefit from alarm calls of other species (Magrath et al. 2007, 2009, 2014; Goodale and Kotagama 2008). Studies from different forest regions indicate that different bird species may form flocks around “sentinel” species (Munn 1986; Sridhar et al. 2009) and consistently respond to their alarm calls. Evidence to date suggests that different species may join flocks to minimize predation risk and/or increase survival rates (Dolby and Grubb 1998; Jullien and Thiollay 1998; Thiollay 1999b; Jullien and Clobert 2000; Sridhar et al. 2009). Whereas community assembly is normally viewed as the result of a process occurring through evolutionary time (Diamond 1975), community assembly in flocks is also a product of ecological processes that occur on a daily basis (Sridhar et al. 2012).

Forest bird species exhibit a wide range of flocking propensities, from species that spend their entire lives within a single flock to species that never join flocks. Flocking and nonflocking species overlap in space and time, suggesting that many nonsocial species have access to and may benefit from information from social species such as alarm calls (Munn and Terborgh 1979; Jullien and Thiollay 1998; Lea et al. 2008; Magrath et al. 2014). Flocking species exhibit a wide variety of ecological traits and forage in distinct microenvironments. Determining the nature and intensity of responses to the same heterospecific threat calls in these environments may increase understanding of the mecha-

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nisms that generate variation in perceived predation risk and, hence, flock participation. One way to assess the dependency of different members of a community on heterospecifics for predator information is to evaluate the relationship between different traits (e.g., body size, foraging height, foraging strategy, and the nature of the microenvironment within which a bird forages) and species' response to heterospecific alarm calls. Because mixed-species flocks in Neotropical forests form stable associations (Munn and Terborgh 1979; Gradwohl and Greenberg 1980; Greenberg and Gradwohl 1986; Graves and Gotelli 1993; Jullien and Thiollay 1998; Martinez and Gomez 2013), they are ideal systems for evaluating how perceived predation risk is related to flock participation and ultimately the community assembly of flocks (Graves and Gotelli 1993).

In this study we tested the influence of behavioral and morphological traits on both flocking propensity and the level of response to the alarm calls of the primary alarm-calling bird of flocks at Nouragues Field Station (hereafter Nouragues) in French Guiana. Nouragues is well suited for this study because of baseline ecological data previously collected on bird communities at the site (Thiollay 1994; Jullien and Thiollay 1998). Previous work demonstrated that a species' foraging strategy influences response to heterospecific alarm calls, but this study was limited to testing only a few species and only one behavioral trait (Martinez and Zenil 2012). We hypothesize that flocking propensity is associated with species' use of alarm calls and that body size, foraging strategy, foraging height, and vegetation density influence both flocking propensity and dependence on alarm calls. Specifically, we predict that smaller species that inhabit less dense cover and those that search nearby substrates for food (such as leaves for insects) are more vulnerable to predators. Hence we suggest that these species are more likely to join multispecies groups and ultimately more likely to respond to alarm calls. If increased flocking propensity is primarily a response to perceived predation risk, then smaller birds that forage nearby substrates in open areas should have higher flocking propensities than larger birds that search for prey at a distance. To test these ideas, we evaluated the influence of different ecological traits on propensity and response to alarm calling by analyzing (1) observational data (collected from the literature and supplemented with our own field data), (2) alarm call playback experiments, and (3) estimated the correlation of flocking propensity and response to alarm calls among species due to evolutionary relationships.

## Methods and Procedures

### *Study Organisms*

Amazonian mixed-species flocks consist of permanent groups of 5 to 10 species, each represented by a pair that

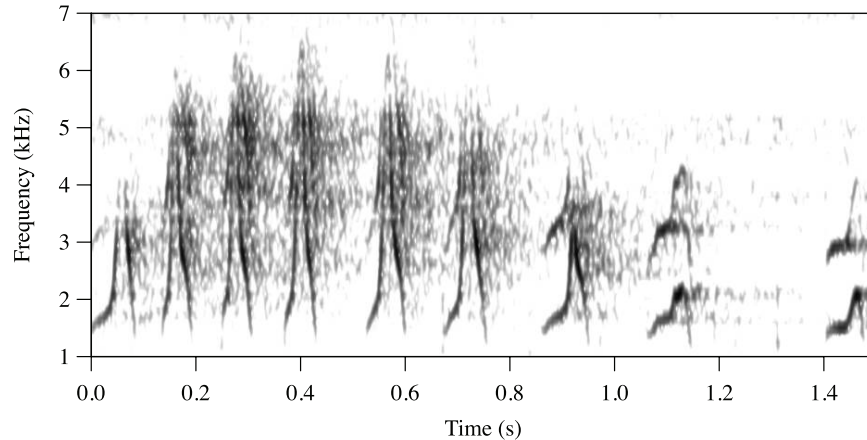
shares and defends a common territory. Additionally, up to 50 other bird species may regularly join these flocks throughout some part of their daily foraging routine within a single community (Munn and Terborgh 1979; Jullien and Thiollay 1998). Two "sentinel" species in the genus *Thamnomanes* typically lead understory mixed-species flocks in Amazonian rainforests (Munn and Terborgh 1979; Wiley 1980; Jullien and Thiollay 1998). The sentinels constantly vocalize, emitting alarm calls in the presence of predators, and are hypothesized flock leaders. The rest of the flock consists of multiple species in genera such as *Myrmotherula* and *Automolus* that search for insects using differing foraging strategies. These other species appear to benefit from the sentinels' vigilance toward predators, whereas the sentinels benefit from the insects flushed from these other birds (Munn 1986; Satischandra et al. 2007). Under certain conditions, the sentinels behave more like kleptoparasites, stealing food from other flock members in addition to exploiting the insects that are flushed (Munn 1986; Sridhar et al. 2009).

### *Field Site*

Nouragues is located in northeast French Guyana (4°05'N, 52°41'W) and is situated at the base of a large inselberg (isolated rock hill) in lowland wet tropical rainforest (Poncy et al. 1998). The forest is characterized as undisturbed old-growth forest and receives ~3,000 mm/yr rainfall, with a wet season from December to July, and receives <100 mm/mo precipitation during the dry season (Maréchaux et al. 2015).

### *Data Collection*

*Collection of Alarm Calls.* From October 6 to October 22, 2011, we followed flocks from dawn to dusk, constantly recording with a Sennheiser ME66 Shotgun microphone and a TASCAM DR-07 digital recorder to capture periodic alarm calls given by *Thamnomanes caesioides* (fig. 1), the primary alarm caller among flocking birds. Because we were able to discern in several cases when raptors flew through the flocks, we identified alarm calls that we then used as criteria for selecting similar alarm calls from other flocks. By so doing, we were able to select alarm signals from six different *T. caesioides* for use as independent replicates in our playback experiments. These recordings were filtered using Raven 1.3 sound software. Using a sound meter (measurements were A weighted), we set the peak amplitude to 56 dB at 15 m, which was the amplitude of a natural alarm measured at a distance of ~15 m from the source when following flocks. These replicate calls were similar in length and number of notes, and subsequent analyses revealed no differences in responses explained by different exemplars (Fisher exact test,



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

$P = .934$ ). 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 October 24 to November 30, 2011, we tested whether individuals of 56 species responded to alarms of *T. caesius* by walking forests trails around the Nouragues field station. When a species was encountered, one observer would spot the individual beforehand and would signal to a second observer to broadcast the stimulus recording from a speaker held waist high and 10–20 m away from the target bird. The response of the bird was documented in a handheld voice recorder by the first observer. Playback trials were conducted between 0645 and 1600 hours when light permitted visual observations. We tested individuals of 56 species as they were encountered; once a playback trial was conducted, we did not test any 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 m for playback trials throughout the study. We attempted to collect up to six different alarm responses and six different control responses per species. Following this same method, we attempted to perform at least one control per species using the white noise sound created using the alarm call parameters. Alarms and controls were randomized in the order they were presented for individual trials within each species.

*Flocking Propensity and Response to Alarm Calls.* Species respond to alarm calls by either diving into vegetation or freezing (Munn 1986; Lima 1998; Seppänen et al. 2007). 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 nor froze displayed

a negative response. By following each individual bird to conduct an experimental trial, we recorded whether the bird was in a flock (within 15 m of another foraging species over a 15-minute period; Jullien and Thiollay 1998). Thus, we could tally the proportion of individuals for each species that flocked (i.e., flocking propensity). To increase sample sizes for each species when estimating flocking propensity, we pooled our data with the data of Jullien and Thiollay (1998), who used the same methodology as ours at the same site where we conducted our study (table 1). We previously have shown that the location and species composition of flocks has remained remarkably similar over the approximate 20-year gap between these two studies (Martinez and Gomez 2013), which is very likely indicative of a stable forest environment.

*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 and unpublished data (Schulenberg 1983; Myers 1990; Thiollay 1994), and we included five categories in the analysis: (1) sally (catching insects in the air), (2) glean (taking prey from a substrate while perched), (3) bark gleaning (taking prey from a bark substrate while perched), (4) army ant following (catching insects flushed by army ants), and (5) ground foragers (catching insects in the leaf litter and vegetation on the forest floor). We also included foraging height of each individual of each species 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. The latter two measurements were measured with a laser range finder. Last, we also

**Table 1:** Sample sizes for propensity and alarm responses from this study (data collected from 2011), from Jullien and Thiollay (1998), and from the two studies combined

Species	2011				1998		Combined	
	Alarm trials	Control trials	Propensity	<i>n</i>	Propensity	<i>n</i>	Propensity	<i>n</i>
<i>Automolus infuscatus</i>	2	4	83.3	6	100	45	98	51
<i>Bucco capensis</i>	1	0	0	1	0	3	0	4
<i>Celeus undatus</i>	2	0	0	2	NA	NA	0	2
<i>Cercomacra cinerascens</i>	1	1	0	2	10	58	10	60
<i>Corapipo gutturalis</i>	1	2	0	3	0	5	0	8
<i>Corythopis torquatus</i>	2	1	33.3	3	7	28	9.7	31
<i>Cymbilaimus lineatus</i>	2	1	33.3	3	15	20	17.4	23
<i>Cyphorhinus arada</i>	2	1	0	3	10	30	9.1	33
<i>Formicarius colma</i>	2	2	0	4	0	18	0	22
<i>Galbula albirostris</i>	4	4	0	8	0	16	0	24
<i>Glyphorhynchus spirurus</i>	6	6	41.7	12	48	141	47.7	153
<i>Gymnopathys rufigula</i>	3	3	0	6	9	31	8.1	37
<i>Hemitriccus josephinae</i>	1	0	1	1	NA	NA	0	1
<i>Hemitriccus zosterops</i>	1	1	50	2	NA	NA	50	2
<i>Hylopezus macularius</i>	3	3	0	6	0	9	0	15
<i>Hylophilus ochraceiceps</i>	5	5	80	10	94	16	88.5	26
<i>Hylophylax naevius</i>	4	3	0	7	19	26	15.2	33
<i>Hypocnemis cantator</i>	6	6	16.7	12	14	36	14.6	48
<i>Lipaugus vociferans</i>	3	3	0	6	9	21	7.4	27
<i>Malacoptila fusca</i>	1	1	0	2	14	14	12.5	16
<i>Microcerculus bambla</i>	4	5	22.2	9	19	21	20	30
<i>Microrhophias quixensis</i>	2	1	33.3	3	14	14	17.6	17
<i>Momotus momota</i>	2	1	0	3	10	31	8.8	34
<i>Monasa atra</i>	1	1	0	2	21	29	19.4	31
<i>Myiobius barbatus</i>	4	5	66.7	9	63	35	63.6	44
<i>Myrmeciza ferruginea</i>	5	6	0	11	0	21	0	32
<i>Myrmornis torquata</i>	2	2	0	4	5	38	4.8	42
<i>Myrmotherula axillaris</i>	6	6	100	12	94	53	95.4	65
<i>Myrmotherula guttata</i>	6	6	50	12	27	26	34.2	38
<i>Myrmotherula gutturalis</i>	6	6	100	12	100	55	100	67
<i>Myrmotherula longipennis</i>	6	6	100	12	100	61	100	73
<i>Myrmotherula menetriesii</i>	6	6	91.7	12	100	50	98.4	62
<i>Percnostola leucostigma</i>	1	2	0	3	0	15	0	18
<i>Percnostola rufifrons</i>	2	2	0	4	22	32	19.4	36
<i>Philydor erythrocerum</i>	6	6	100	12	100	58	100	70
<i>Philydor pyrrhodes</i>	1	0	100	1	9	11	16.7	12
<i>Phoenicircus carnifex</i>	1	0	100	1	6	16	11.8	17
<i>Piculus flavigula</i>	2	2	75	4	64	11	66.7	15
<i>Pithys albifrons</i>	2	3	0	5	9	62	9	67
<i>Platyrrhinus coronatus</i>	5	5	0	10	13	31	9.8	41
<i>Platyrrhinus saturatus</i>	1	0	100	1	9	11	16.7	12
<i>Ramphocaenus melanurus</i>	1	0	100	1	25	12	30.8	13
<i>Rhynchocyclus olivaceus</i>	1	2	100	3	29	17	40	20
<i>Rupicola rupicola</i>	1	0	100	1	7	42	9.3	43
<i>Saltator grossus</i>	2	2	50	4	13	22	19.2	26
<i>Sclerurus rufigularis</i>	1	2	33	3	NA	NA	33.3	3
<i>Tachyphonus surinamus</i>	1	3	25	4	21	28	21.9	32
<i>Thamnomanes ardesiacus</i>	6	6	91.7	12	100	64	98.7	76
<i>Thamnophilus amazonicus</i>	1	1	0	2	20	10	16.7	12
<i>Thamnophilus murinus</i>	2	1	0	3	10	20	8.7	23
<i>Pheugopedius coraya</i>	2	3	40	5	16	37	19	42
<i>Turdus albicollis</i>	2	1	33.3	3	9	52	10.9	55
<i>Willisornis poecilinotus</i>	2	2	0	4	9	54	8.6	58
<i>Xiphorhynchus pardalotus</i>	6	6	100	12	100	73	100	85

Note: NA = not available.

used a subjective visual evaluation of vegetation density in a sphere of 0.5-m radius around the bird in four categories based on the amount of light that passes through the sphere: 0%–25%, 26%–50%, 51%–75%, and 76%–100% volume (Remsen and Robinson 1990). Two observers assessed the density independently, and the final estimate was derived from these two independent evaluations.

### Data Analyses

The objective of the data analysis is to test the hypotheses that both flocking propensity and alarm response (as a proxy for predation risk) can be explained by morphological and behavioral traits exhibited by each species, by evolutionary time separating species, and by the strength of natural selection on the response variables. We used as response variables both flocking propensity and alarm response. Flocking propensity was measured as the proportion of times that individuals of a particular species were found in a flock, and the alarm response was measured as the proportion of time individuals from a given species reacted with an evasive behavior on hearing playback of an alarm call.

### Model Fitting

For each response variable, we fitted a family of generalized linear models (McCullagh and Nelder 1989) consisting of various combinations of the independent variables: body mass, foraging height, foraging density, foraging strategy, and a null model. For the alarm response models, we also used distance from alarm source as an independent variable. We also included the response to alarm calls as one of the predictors in the models for propensity and vice versa.

The guiding principle of our model fitting and model choice methodology was to be able to carry out mirrored analyses with and without considering phylogenetic dependencies. The rationale to do so was to seek a better understanding of the influence of the ecological factors on the response variables while testing the assumption that species are independent replicates of the sampling process. Such an assumption often does not hold, because closely related species are likely to be more similar than distantly related ones (Felsenstein 1985). However, there are some cases in which traits evolve fast enough for the evolutionary dependency to dissipate and the assumption of independence among species would hold. In practice, we first used conventional multimodel selection procedures (see below) using generalized linear models for flocking propensity and alarm response and then repeated the same process using generalized linear models that incorporated phylogenetic signal. We considered traits to be either binomially distrib-

uted as a result of a series of Bernoulli trials or continuously distributed as the arcsin square root transformation of the proportion of individuals responding to an alarm call or found foraging with a flock (appendix, available online).

*Models of Trait Evolution.* The nature of the trait data (binomial or continuous) specified the type of model of trait evolution. When we considered the traits to be binomially distributed, the model of trait evolution assumed that the difference between species was proportional to the length of the branches separating them, multiplied by a constant rate of change  $\alpha_{01}$  between 0 and 1 (Ives and Garland 2010). When  $\alpha_{01}$  is large, the trait is assumed to have strong phylogenetic signal. Alternatively, if  $\alpha_{01} \leq -4$ , then the trait is assumed to be independent of the phylogenetic relationships between species (Ives and Garland 2010). The branch lengths were derived from a maximum likelihood tree for the species in our data set downloaded from the database <http://birdtree.org/> (Jetz et al. 2012).

When we considered the response variables to be normally distributed, we used two well-known phylogenetic models of trait evolution: the Brownian motion (BM) model and the Ornstein-Uhlenbeck (OU) model (Hansen 1997; Butler and King 2004; Hunt et al. 2008; Dennis and Ponciano 2014). In these analyses, we followed the statistical recommendations of Ho and Ané (2014) to fit and interpret these models. In these two evolutionary models, the trait (in evolutionary timescale) undergoes random drift with variance accumulation rate  $\sigma^2$ . Under the OU model, however, the trait is also attracted to a selection optimum with a given selection strength  $\alpha_{ss}$ . In both the BM and OU models, strong phylogenetic signal is assumed when  $\sigma^2$  is small, suggesting that the tree topology explains most of the variance in the trait. In the OU model, the strength of selection toward the optimum increases with increasing  $\alpha_{ss}$ .

Briefly, the interpretation of the results given by these models is as follows: if the best model of either flocking propensity or the alarm response turns out to be a model including phylogenetic effects besides one or more ecological factors, that means that the trait in question is largely explained as an ancestral character. Furthermore, if among phylogenetic models the OU process is preferred to the BM model, that means that the variability of the trait in question is better understood not only as an ancestral character but also as one that is under significant selection strength.

*Generalized Linear Models.* The models used to test our hypotheses can be divided in two sets. In the first set, we assumed that response variables were binomially distributed. In the second set, the models for propensity and alarm response were expressed as fractions.

We implemented the binomial approach in two different ways. First, we used a standard logistic regression in which

the values of the dependent variables were set to 1 if a species was found with a flock or responded to an alarm call and 0 otherwise. In this approach, intraspecific variation in the tendency to flock and to respond to alarm call was incorporated by weighting the 56 observations by the number of trials per species. The phylogenetic model in this case was constructed by using the model proposed by Ives and Garland (2010; see appendix for details), with the caveat that it cannot be weighted by the sample size.

The second implementation of the binomial model consisted of a binomial regression in which the number of successes was taken as the number of individuals that were found flocking or responded to an alarm call out of the total number of individuals of that species that were assayed. The observations are automatically weighted because the entire set of observations is used. The latter setup of the data set cannot be used directly in the Ives and Garland (2010) phylogenetic model. In this case, an alternative is to add as many tips to the phylogenetic tree as individuals assayed. According to the suggestions of Ho and Ané (2014), we first computed the intraspecific variance of the trait and used this to construct a star phylogeny per species with number of tips equal to the number of individuals observed during our study. The branch lengths of this star tree were set to be the magnitude of the intraspecific variation (Ho and Ané 2014). We then added the star phylogenies of each species to the original tree. To keep all tips contemporaneous (see Ives and Garland 2010), we subtracted the length of each star tree from the length of the branch leading to that species. With this new tree and following Ho and Ané (2014), we performed Ives and Garland's (2010) phylogenetic logistic regression to incorporate intraspecific variation and sample size variation.

The second set of models assumed that the dependent variable was normally distributed. We fitted a linear model without phylogeny and a linear model assuming that traits evolved according to BM and OU models of evolution. Such an approach greatly facilitated the incorporation of observations weighted according to sample size and eased numerical convergence problems of all the phylogenetic regressions. We refer the reader to the appendix for a discussion of the statistical benefits and caveats of each approach and the mathematical details of the models' specification.

### *Model Selection*

To select among models we used the Schwarz information criterion, also known as the Bayesian information criterion (BIC; Schwarz 1978). This criterion, derived within the framework of evidential statistics (Royall 2004; Taper and Lele 2004), penalizes likelihood improvements due to an increase in the number of parameters in the model. We assume strong support for a single model if the difference be-

tween the model with the smallest BIC and any other model ( $\Delta_i \text{BIC}$ ) is greater in absolute value than 2 (Taper and Ponciano 2016). In order to provide standard model diagnostic statistics, we computed for each model McFadden's pseudo- $R^2$  in the case of the binomial generalized linear models and the standard  $R^2$  when assuming that the response variable was normally distributed. All of the analyses were performed in R v 3.0.2 (R Development Core Team) and the packages *phylolm* (Ho and Ané 2014), *nlme* (Pinheiro et al. 2013), and *ape* (Paradis et al. 2004).

We stress that the nature of the data (mostly observational as opposed to experimental and in a controlled environment) called for including several statistical and biological considerations in the analysis for both response variables. The analyses involved the use of nontrivial mathematical approaches, which are explained in detail in the appendix. All the R code used in the analyses is found in "Analyses" (available online as a zip file).

As a control for our playback experiments, we monitored the response to white noise and compared it to the bird's response to alarm calls. We compared results using a binomial sampling test. In this test, the null hypothesis was that the frequency of positive responses to white noise did not differ from the frequency of positive responses to alarm calls. The alternative hypothesis was that the frequency of positive responses to white noise differs from the frequency of positive alarm responses.

Within the limits imposed by our sample sizes, we tested all the possible main effects models. The independent variables we used for both responses were body mass, foraging height, foraging density, and foraging strategy. Given that sample size per species (number of individual birds per species) could not be explicitly controlled in the playback experiments, in the analyses the observations per species were weighted by sample sizes per species. Thus, species (observations) with fewer sample sizes contribute less to the process of estimation and testing (Myers 1990).

Different logical arguments can be made in favor of including, for instance, the response to alarm calls as a predictor in the model of propensity and vice versa. Hence, our models included both variants as one of the model candidates to explain the data. After presenting the results of both variants, we discuss their relative merits.

## **Results**

### *Controlling for the Effect of Playbacks*

Given that the proportion of positive responses generated from control playbacks was exceedingly small compared with the proportion generated through alarm playbacks (proportion of positive responses of alarms = 0.51 vs. controls = 0.08 with  $n = 153$  and  $n = 151$ , respectively;  $P < .001$ ), we

**Table 2:** Summary of best models for interpreting the effects of different functional traits on propensity

Model	$\alpha$	Intercept	Mass	Height	Density	Alarm response	Fstrategy					$R^2$	
							AF	B	G	GF	S		
<i>Linear</i>													
Null		.73											114.7
<b>Mass + density + height + alarm response</b>		<b>.93</b>	<b>-.006</b>	<b>.06</b>	<b>-.6</b>	<b>.35</b>							96.75
<i>Linear with phylogeny BM</i>													
Null		1.39											120.8
Mass + density + height		.85	-.004	.07									103.3
<i>Linear with phylogeny OU</i>													
Null	.07	.75											113.9
<b>Mass + density + height + alarm response</b>	<b>.07</b>	<b>.88</b>	<b>-.006</b>	<b>.06</b>	<b>-.53</b>	<b>.32</b>							<b>96.6</b>
<i>Binomial</i>													
Null		-.3											1,627.9
Mass + density + height + alarm response			-.03	.22	-2.39	1.3	.47	1.26	.56	-.42	.72		956.3

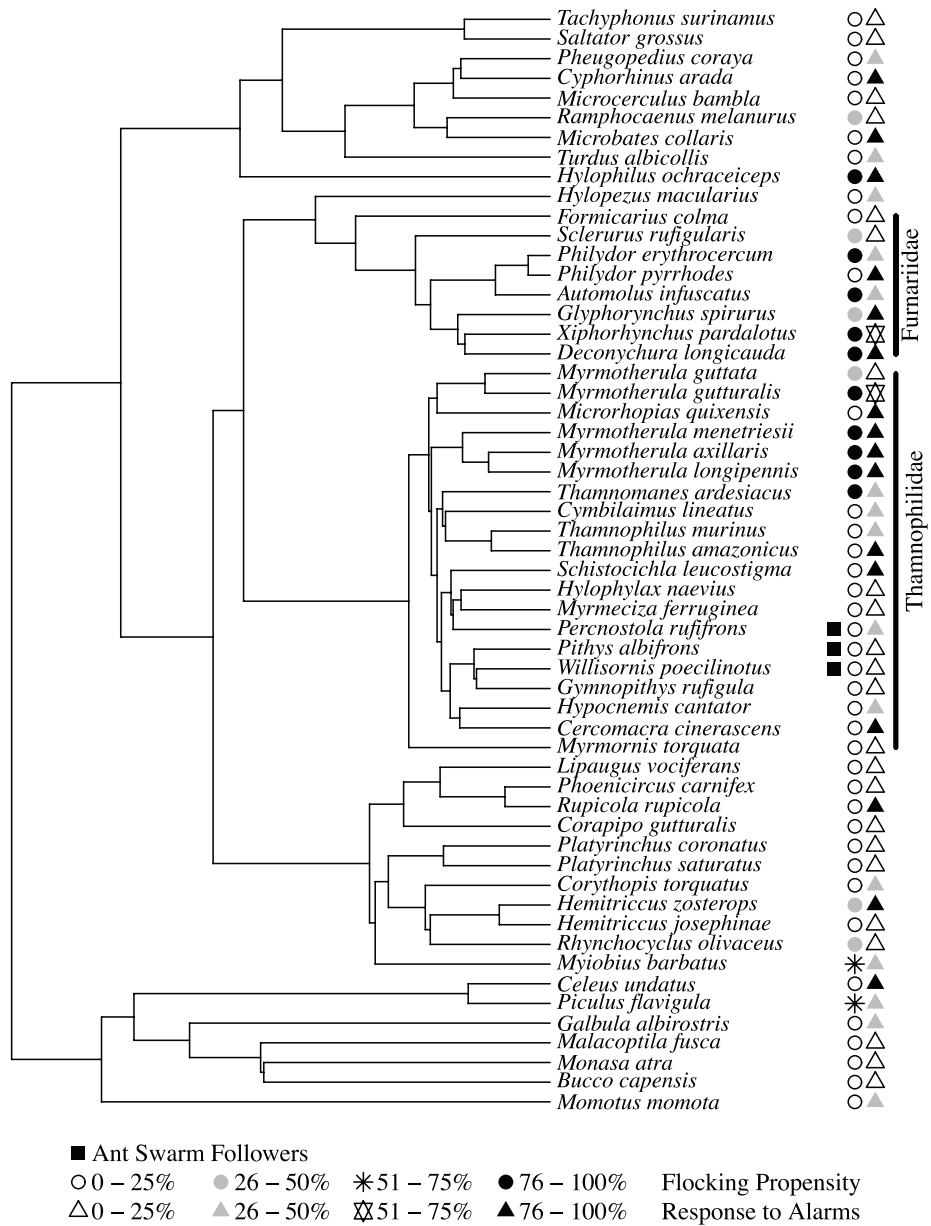
Note: Each case represents the lowest Bayesian information criterion (BIC) value for each of the family of generalized linear models (normal or binomial) with and without phylogeny (see tables S1, S2, available online as a zip file) for results of all the models tested with different combinations of main term effects. Italics indicate the class of model being tested. Bold indicates the best models to explain the data.  $\alpha$  = strength of selection for an ancestral state under the existence of strong phylogenetic signal. The functional traits are mass, height, density = density of vegetation where bird forages, and Fstrategy = foraging strategy (AF = army ant followers, B = bark gleaners, GF = ground foragers, and S = sallying).  $R^2$  = regression coefficient under the family of linear models and McFadden's pseudo- $R^2$  under the family of binomial models. BM = Brownian motion; OU = Ornstein-Uhlenbeck.

Table 3: Summary of best models for interpreting the effects of different functional traits on probability of responding to alarm calls

Model	$\alpha$	Intercept	Propensity	Density	Distance	Fstrategy						BIC	$R^2$	
						AF	B	G	GF	S				
<i>Linear</i>														
Null		.78										112.25		
<b>Fstrategy + density + propensity</b>			<b>.59</b>	<b>.39</b>								<b>99.54</b>	<b>.48</b>	
<i>Linear with phylogeny BM</i>														
Null		.62										126.9		
Density		-.1		.8								125.2	.1	
<i>Linear with phylogeny OU</i>														
Null	1.92	.78										116.28		
Fstrategy + density + propensity	1.92		.59	.39			.39	.11	-.21	-.3		103.57	.48	
<i>Binomial</i>														
Null		-.01										146.7		
Density + propensity			1.35	2.03			-1.37	-2.37	-3.37	-3.57		126.46	.31	

Note: Each case represents the lowest Bayesian information criterion (BIC) value for each of the family of generalized linear models (normal or binomial) with and without phylogeny (see tables S3, S4, available online in a zip file) for results of all the models tested with different combinations of main term effects. Italics indicate the class of model being tested. Bold indicates the best model to explain the data.  $\alpha$  = strength of selection for an ancestral state under the existence of strong phylogenetic signal. The functional traits are mass, height, density = density of vegetation where bird forages, and Fstrategy = foraging strategy (AF = army ant followers, B = bark gleaners, GF = ground foragers, and S = sallying).  $R^2$  = regression coefficient under the family of linear models and McFadden's pseudo- $R^2$  under the family of binomial models. BM = Brownian motion; OU = Ornstein-Uhlenbeck.





**Figure 2:** Propensity (tendency of species to flock) and response to alarm calls mapped onto a phylogeny of resident forest bird species presented in this study. Black circle = 76%–100% tendency to flock, gray circle = 51%–75%, white circle = 26%–50%, white triangle = 0%–25%. Black squares denote equal-obligate army ant followers, which, although rarely if ever found with understory flocks, are always found in flocks of birds that follow army ant swarms.

concluded that the artifact of playback trials did not influence the responses of birds to our alarm playbacks.

*Model Selection and Inference*

Most of the models evaluated using phylogenetic logistic regression did not converge or had convergence problems.

Thus, we report only the linear regressions with and without phylogeny and the binomial model without phylogeny. Using linear regressions of the arcsin square root–transformed response variables with and without phylogeny, we found that (1) the best predictor model for propensity included phylogenetic effects (tables 2, S1 [tables S1–S4 available online as a zip file]), as well as body size, density, foraging

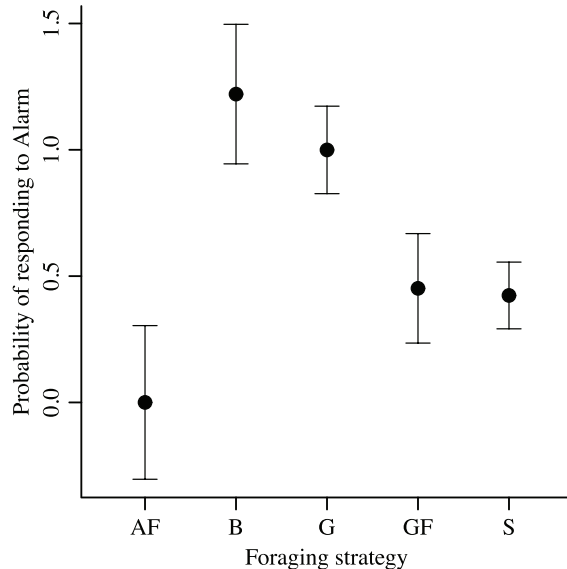
height, and response to alarm calls, and (2) the best predictor model for alarm response was a model that included foraging strategy, foraging density, and flocking propensity without phylogenetic signal (tables 3, S2).

*Evaluation of Morphological and Behavioral Traits on Flocking Propensity.* Body mass and foraging density were negatively related, whereas height and probability of alarm response showed a positive relationship to flocking propensity (table 2;  $R^2 = 0.45$ ). Because when we accounted for phylogeny the OU model of trait evolution was preferred over the BM model, we interpret this to mean that flocking propensity is under significant stabilizing selection over an evolutionary timescale. Species with the highest flocking propensities are noticeably concentrated in two bird families, Thamnophilidae and Furnariidae (fig. 2), which explains the influence of phylogenetic signal in explaining flocking propensity. Data underlying figure 2 are deposited in the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.18v4b> (Martinez et al. 2016).

The  $\Delta$ BIC between the best model (linear OU model) and the linear BM model is 6.68, which is indicative of strong evidence in favor of the OU model. We found that  $\Delta$ BIC = 0.11 between the best model and the linear model without phylogeny. Conversely, the binomial model had by far the highest BIC and the least explanatory power of all of the models ( $\Delta$ BIC = 839.54).

*Evaluation of Morphological and Behavioral Traits on Response to Alarm Calls.* Foraging strategy, vegetation density, and flocking propensity were all factors influencing the response of species to alarm calls (table 3;  $R^2 = 0.48$ ; table S2). Vegetation density and flocking propensity were positively related to the probability of responding to alarm calls. Bark-gleaning and gleaning birds had the highest probability to respond to alarm calls, whereas ant-following, ground-foraging, and sallying species had low probabilities of responding to alarm calls (table 2; fig. 3). Data underlying figure 3 are deposited in the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.18v4b> (Martinez et al. 2016).

Birds foraging at slightly higher vegetation densities and birds with higher flocking propensities tend to respond more to alarm calls (table 2). Incorporating the influence of phylogenetic relationships on the probability of alarm response did not improve the fit of the model using foraging strategy (table 2). Three other models had  $\Delta$ BIC < 2 when compared to the best model, and all were linear models without considering the effect of phylogeny. These models included some combination of foraging strategy, flocking propensity, and density at which the bird forages (tables S2, S4). The best binomial model had a high difference in BIC ( $\Delta$ BIC = 26.91); however, it was congruent with the best linear model.



**Figure 3:** Proportion of positive responses of species to alarm calls (values on the Y-axis are arcsin square root transformed) as a function of their foraging strategy. AF = army ant follower,  $n = 6$ ; B = bark gleaning,  $n = 14$ ; G = gleaning,  $n = 75$ ; GF = ground forager,  $n = 12$ ; and S = sallying,  $n = 41$ . Bars show 95% confidence intervals generated by the logistic model.

## Discussion

The results we report here suggest that (1) flocking participation in the forest understory at this site is influenced by ecological traits as well as by species' evolutionary history, whereas (2) ecological traits alone influence species' response to alarm calls. Ultimately, probability of responding to alarms (predation risk) appears to be positively related to flocking propensity (table 2). However, species that are considered vulnerable to predators (e.g., gleaning birds) do not invariably evolve a tendency to join flocks (see response to alarm calls, fig. 2). The fact that many species that do not join flocks actually positively respond to alarm calls produced by the flock sentinel suggests that species that share the same risks do not necessarily employ similar strategies for reducing such risk.

The fact that linear models both with and without phylogeny have similar weight in explaining flocking propensity (table 2) suggests that this trait has weak phylogenetic signal. Given the nature of BIC, in which models with higher parameters are heavily penalized, we suggest that phylogenetic signal, although weak, is still significant. The phylogenetic model has two additional parameters compared to the nonphylogenetic model and still has a lower BIC. To have a lower BIC, the likelihood of the phylogenetic model has to be much higher than the nonphylogenetic one supporting the significant phylogenetic signal. The phylogenetic sig-

nal reveals that virtually all of the closely related species that join flocks are in fact leaf-gleaning or bark-gleaning birds that respond almost invariably to heterospecific alarm calls (see *Thamnophilidae* and *Furnariidae*, fig. 2).

Our results (see tables 2, S1) suggest that smaller-sized birds have variable flocking propensities but that larger-sized birds consistently have low flocking propensities (Thiollay and Jullien 1998). Indeed, body size has previously been shown to explain some variation in species assembly in some flocks (Sridhar et al. 2012). Similarly, there is some tendency for species with higher flocking propensities to associate with midstory forest strata, where vegetation is relatively less dense and which is assumed to be a riskier area in which to forage due to ambush predators (Thiollay and Jullien 1998; Thiollay 2003). Our finding of some phylogenetic signal influencing flocking is a result that has been previously reported (Gomez et al. 2010). In an evaluation of the evolutionary history of flocking species that follow army ants, Brumfield et al. (2007) showed that once a clade evolves the tendency to flock, there is a very low probability that closely related relatives will evolve a nonflocking condition. These authors concluded that flocking propensity could only increase over evolutionary time. These previous findings, and the fact that the OU model of trait evolution in our analyses was the best model, suggest some evidence for stabilizing selection on the ancestral character state for flocking propensity (table 2).

Foraging strategy along with foraging density and flocking propensity appear to partly explain variation in responses to alarm calls (table 3; fig. 3), and those traits without phylogeny (fig. 2) comprised the best model from the set of models we tested (tables 3, S2). Our results are consistent with the prediction that insectivorous birds that feed by gleaning (that search on green leaves or clusters of dead leaf surfaces) are more likely to perceive higher predation risk than birds that search at a distance (Thiollay 2003; Martinez and Zenil 2012). Antbirds and ovenbirds (specifically *Furnariids*) found in these flocks are primarily live-leaf gleaners, bark gleaners, or dead-leaf gleaners that may rely on vigilance from other species, and this may explain the high level of response to alarm calls. Conversely, birds that catch insects on the wing can simultaneously search for predators and food, which means that they are not reliant on the alarm calls of the sentinels (Munn 1986). In addition, species responded more to alarm calls in areas open enough to move around and forage but just dense enough to obscure ambush predators (Thiollay 1999a).

Alarm calls are known to carry information about types of predators and the degree of threat; we do not know, however, the extent to which our alarm calls encode these types of information (Courter and Ritchison 2010; Sieving et al. 2010; Hetrick and Sieving 2012), and this assumption needs to be tested. The alarm calls we used may rep-

resent only one subset, and different responses might be elicited by different alarm calls. For example, the conclusion that body size does not influence predation risk assumes that the alarm calls we used accurately conveyed threats to birds of varying body size (Lima and Dill 1990). There is evidence to suggest that alarm calls may encode information about different threats (Templeton et al. 2005; Roth 2006), so alarm calls that encode information about certain predators may elicit responses by birds of specific body sizes.

A related limitation of our study is that we test the alarm calls of a single species of alarm-calling bird. Even though this species is one of the most prominent alarm-calling birds in Amazonian forests, other species do give alarm calls, and these species may use them in different contexts to elicit different responses from heterospecifics, something we have not considered here. Indeed, understanding the context of relevant and reliable information used by any given species may require the integration of alarm calls from multiple species (Magrath et al. 2014). Future studies should evaluate variation in responses from different alarm-calling species to describe more completely the community eavesdropping network (Magrath et al. 2014).

Our study represents a first step toward a comprehensive evaluation of traits that influence the degree to which species use heterospecific information. Although we provide some experimental evidence for a relationship between perceived predation risk and flocking propensity, this assumes that we correctly interpret response to alarm calls as a proxy for perceived predation risk. We caution that other factors, such as physiological sensitivity to signals, behavioral plasticity, and personality syndromes, may also explain the patterns we see and require further testing. An evaluation of traits that influence reliance on heterospecific information will advance understanding of the evolution of interspecific communication networks and their role in the assembly of communities over both evolutionary and ecological time.

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Understory flock birds of northern Amazonia. *Left*, chestnut-rumped woodcreeper (*Xiphorhynchus pardalotus*); *upper right*, cinereous antshrike (*Thamnomanes caesius*); *lower right*, brown-bellied antwren (*Epinecrophyllos gutturalis*). Painting by Micah Riegnier.