**Title**

Alarm Calling to an Aerial Predator: Ecological and Evolutionary Drivers in a Neotropical Bird Community

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# Alarm calling to an aerial predator: ecological and evolutionary drivers in a neotropical bird community

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of the requirements for the degree of

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in

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by

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# Abstract

## Alarm calling to an aerial predator: ecological and evolutionary drivers in a neotropical bird community

Predation risk exerts strong selective pressure on animals, and many species have evolved alarm calls to warn about threats in the environment. While avian alarm calling is well known in mixed-species flocks, few studies have directly tested how variation in intrinsic and extrinsic factors drives alarm behavior. We quantified several extrinsic ecological parameters and intrinsic factors such as degree of sociality, body size, and foraging strategy while controlling for phylogenetic signal. We exposed 69 species that vary in these qualities to a model predator (hawk fly-by) in the Peruvian Amazon. We found a clear positive relationship between social complexity and alarm calling—solitary birds alarmed least frequently, while mixed-species flocks alarmed most. Contrary to expectations, the ecological context (e.g., vegetation density and bird height) in the immediate environment had little influence on alarm behavior. Instead, phylogenetic linear mixed models revealed a strong phylogenetic signal in alarm calling propensity at the clade level. We also assessed the roles of species-specific foraging maneuvers and foraging substrates and their relative influence on alarm calling. The tendency to produce alarm calls appears to be rooted in evolutionary history, shaped by species-specific ecological traits and ancestral relationships more than by moment-to-moment environmental variation. Our findings provide new insight into the evolutionary and ecological drivers of anti-predator communication in avian communities.

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## Introduction

Animals produce a variety of signals and cues that provide potential information about the surrounding environment to receivers (Bradbury and Vehrencamp 2011). Such information is critical for individual survival, and may help individuals identify safe foraging areas (Luttbeg et al. 2020), gain information about potential threats (Templeton et al. 2005), identify territorial boundaries (Benedict et al. 2012), and assist in finding and assessing mates (Bee 2008). Some signals can encode information about rapid changes in the surrounding environment (Savage et al., 2021). For example, alarm calls may be associated with the presence of predators or the relative predation risk in the environment (Barati and McDonald 2017; Blumstein & Armitage 1997), and both conspecific and heterospecific receivers (Schmidt et al. 2008) may extract information from these calls as a tactic to increase their own survivorship (Magrath et al. 2014). Both the structure and the widespread use and similar patterns among communication signals used by animals strongly suggest that these traits are conserved by natural selection, indicating that evolutionary history may explain their variation.

Alarm calls are specialized vocal signals that convey information about potential threats in the environment (Soltis et al. 2014). These calls are widespread, particularly across mammals and birds, and a large body of work has documented the different types of alarm calls used in different predator contexts (Gill and Bierema 2013). For example, Manser et al. (2002) demonstrated that meerkats (*Suricata suricata*) produce distinct call types depending on the predator: low grunts for terrestrial threats, high-pitched rapid calls for aerial predators, and broadband calls that span much of their vocal range in response to snakes. A similar pattern has been observed in northern mockingbirds (*Mimus polyglottos*), which modify their vocalizations according to the threat type (Savage et al. 2021). In birds, alarm communication has been studied in the referential contexts of mobbing (Carlson et al. 2020; Griesser and Suzuki 2016), aerial predation, (Jung et al. 2020; Goodale and Kotagama 2006; Soard and Ritchison 2009; Martinez and Zenil 2012; Krama et al. 2023) as well as terrestrial threats (Ha et al. 2020; Cunningham and Magrath 2017; Igic and Magrath 2014; Binazzi et al. 2011). These widespread patterns of specified referential signals suggest that the structure of alarm calls has been shaped by natural selection to optimize communication effectiveness under different ecological conditions. However, for many species, it is still unknown whether alarm calling in response to predators forms any part of their communication behavior. Therefore, understanding the context across species and when they are more likely to produce alarm signals remains poorly understood (Carlon et al. 2020; Sieving et al. 2010).

An animal's alarm calling behavior may change depending on the social context of their environment; a phenomenon known as the audience effect (Gyger 1990, Fuong et al. 2015). While some signals are thought to be directional towards an intended receiver (Witkin 1977), alarm calls are widely recognized to have multiple possible receivers (Carro and Fernández 2021; Lowney, Flower, and Thomson 2020; Dutour, Léna, and Lengagne 2017; Baigrie, Thompson, and Flower 2014). In one example, Patricelli et al. (2007) determined that red-winged blackbirds (*Agelaius phoeniceus*) selectively direct their vocalizations depending on the context, with mating calls being highly directional, discouraging eavesdropping, and alarm calls being omnidirectional to alert surrounding conspecifics, encouraging eavesdropping. Additionally, information content may vary due to community composition, and variation in contexts of conspecifics and heterospecifics has demonstrated that alarm callers may use deception or true alarm calls based on different motivations such as competition or mutualism (Flower 2011, Flower et al. 2014, Krama et al 2023). For example, some species exhibit kleptoparasitism, using false alarm calls to manipulate the behavior of other individuals for a selfish benefit (Flower 2011; Ridley, Child, and Bell 2007) Thus, while it is understood that there is a benefit to reciprocal communication to kin directly (Trivers 1971), there remains more to be learned about the behavioral motivations that underlie the signaller/receiver relationship within communities and amongst heterospecific species. Therefore, it is likely that the composition (e.g., mate presence, kin/non-kin) and relative proximity of receivers to signalers have an influence on communication and social structures.

Traditionally, the use of alarm calls across species that exhibit the behavior has been documented in mixed-species groups of animals (Goodale et al. 2020, Seyfarth and Cheney 2003, Hetrick and Sieving 2012), but less so in other social contexts.  In mammals, Meise et al. (2020) suggest that an animal's ability to transfer referential information signals about predator threats is a key component in the formation of mixed-species groups of ungulates in the African savanna. Thus, while alarm calling has been well documented in some species and social groups (Goodale et al. 2020; Martínez et al. 2017; Freeberg and Harvey 2008; Hollén and Radford 2009; Caro 2005), there remains a considerable gap in our understanding of patterns of alarm calling across broader animal communities. Similarly, while mixed-species groups have been the focus of extensive study, other social structures—such as competitive aggregations (e.g., lekking manakins and obligate ant-followers), breeding pairs, and single-species flocks—which may serve as a proxy for audience effects, have received comparatively little attention. In these less-studied social contexts, research has largely concentrated on vigilance behavior (Fuller et al. 2013; Mainwaring and Griffith 2013; Jaatinen, Öst, and Lehikoinen 2011; Yasukawa and Cockburn 2009), with alarm calling itself often overlooked. Moreover, many existing studies focus on alarm calling as a direct response to predators, without accounting for other potential ecological or evolutionary factors (Kikuchi et al. 2023; Lima 2009) that might influence the propensity to alarm call. This leaves open critical questions about the broader drivers of alarm calling behavior, including intrinsic traits like phylogenetic history (McCracken and Sheldon 1997) or specific traits like foraging strategy. Additionally, alarm calling behavior may also depend on the ecological contexts that may drive risk in anti-predator strategies (Lima and Dill 1990). For example, proximity to vegetation or approaching predators may determine the extent to which an individual will communicate in response to predator threats (Powell 1989, Thiollay 1999). It has also been been hypothesized that animals that are preyed upon by ambush predators such as forest raptors are likely less vulnerable in dense vegetation (refuge), or in extremely open habitats (early detection) than in intermediate categories of vegetation that are typical of the understory and midstory of forests (Thiollay 1999), thus alarm calling may more generally be related to being in a safe position (Collier et al. 2010).

I investigated patterns in alarm calling as a function of ecological context, shared ancestry, and functional traits such as sociality, body size, and foraging strategy in a hyperdiverse community of Amazonian rainforest birds. Amazonian forest avian communities are an ideal study system for testing the different drivers of alarm calling for a variety of reasons because they contain many species that have different social organizations (Marra and Remsen 1997), feeding strategies, and morphologies (Remsen and Robinson 1990), and they come from multiple evolutionary lineages (Coddington et al. 2023; Pigot, Trisos, and Tobias 2016). I hypothesized that phylogenetic signal (Freckleton, Harvey, and Pagel 2002; Pagel 1999) — the tendency for closely related species to retain similar traits (Losos 2008) due to shared ancestry — is a primary driver of alarm-calling behavior (e.g., foraging strategy) (Martínez and Zenil 2012). Additionally, I hypothesized that immediate ecological factors, such as vegetation density and foraging height may also influence alarm propensity .

The appearance of aerial predators, because of their speed, create an often instantaneous increase in predation risk and many species emit alarm calls in response. By simulating the appearance of an aerial predator, I can study the drivers of the propensity to call.  I expect, given many previous studies (Coddington et al. 2023; Ridley, Flower, and Thomson 2013; Mundry et al. 2012; Williams and Lindell 2019; Suhonen 1993), that a bird's immediate surroundings explain some variation in the propensity to call (e.g., vegetation density, foraging height, and predator proximity). For example, I hypothesized that vegetation density provides safety, and also reduces relative vigilance capacity, and therefore, alarm propensity would decrease as vegetation density increased. A similar trend would be shown in bird height: birds on the ground are likely more difficult for an aerial predator to detect and have more relative safety. Therefore, they would have a lower alarm likelihood, whereas a bird perched in the lower midstory would be at greater risk and therefore more likely to produce an alarm. Finally, predator proximity is a likely predictor for alarm production (Mundry et al. 2012). If the predator is too close, the prey target will likely save itself and fly away for safety, and not alarm. But if the predator is farther away, the alarm producer may be in a relatively safer context, and may be more likely to produce an alarm.

By examining the relationships of sociality between various bird species and their propensity to produce alarm calls, I may gain further insight into the processes that may explain the development of social strategies in birds. There are numerous social strategies employed by birds to navigate their environments and ensure survival. In this context, I outlined six possibilities (see Table 1) along a gradient of social complexity driven by variable audience effects: 1) solitary individuals, 2) socially monogamous pairs, 3) manakin leks, 4) cooperative single-species flocks, 5) ant-following flocks, and 6) mixed-species flocks. Each strategy offers unique advantages and challenges regarding whether to incorporate alarm calls into survival behavior. For example, alarm calling may pose a high risk for a solitary bird, as it could inadvertently reveal its location to a predator. To further explore social complexity, I also considered that variation in alarm calling might be influenced by whether species interactions are primarily mutualistic or competitive.

**Table 1** *A priori* predictions of interspecific alarm calling behavior across different social group contexts. Interaction types are categorized based on expected ecological dynamics, ranging from mutualistic cooperation to competitive exclusion.

| Social Group | Predicted Alarm Response | Predicted Interaction Type |
|---|---|---|
| Solo | None / Low | None |
| Pair | Low | Mutualistic |
| Single-species Flock | Moderate | Mutualistic |
| Mixed-species Flock | High | Mutualistic / Facilitative |
| Ant-following Flock | None / Low | Competitive |
| Manakin Lek | None | Competitive (sexual) |

Another intrinsic evolutionary aspect I explored was the relationship between foraging strategy and substrate—that is, the maneuver a bird uses to obtain food and the type of food or feeding surface it targets. My *a priori* hypothesis was that different foraging strategies would be associated with varying levels of vigilance (Martinez and Zenil 2012), and higher levels of vigilance would have a higher alarm propensity (see Table 2). Here, vigilance is defined as a bird's visual awareness of its surrounding environment (Van Langevelde, Suselbeek, and Brown 2022). Birds in the Amazon use a wide range of foraging strategies, reflected by the high level of niche specialization (Shulenberg et al. 2007; Remsen & Robinson 1990; Terborgh et al. 1990). For instance, woodcreepers probe for insects and other food on the bark of tree trunks. Due to this strategy, they have a relatively low level of vigilance because their focus is limited to what is immediately in front of them by only a few centimeters, and they may rely on their peripheral vision to detect danger. Conversely, species that employ aerial maneuvers (e.g., flycatching) are predicted to have the highest level of vigilance, and I expected these species to be more likely to have aerial alarm calls in their repertoire.

**Table 2.** *A priori* predictions relative to alarm response and relative vigilance associated with different foraging strategies, subdivided into maneuvers (physical movement) and substrates (feeding niche).

| **Foraging Strategy** | **Predicted Alarm Response** | **Relative Vigilance** |
|---|---|---|
| *Maneuver* | | |
| Probe | None / Low | Low |
| Ground | None / Low | Low |
| Pounce | Low / Moderate | Moderate |
| Glean | Moderate / High | Moderate / High |
| Sally | High | High |
| *Substrate* | | |
| Ground | None / Low | Low |
| Bark | Low | Low |
| Fruit | Low | Low |
| Dead Leaf | Moderate | Moderate |
| Green Leaf | Moderate / High | Moderate / High |
| Air | High | High |

## Methods

### *Study Site*

The field component of this study was conducted in the Peruvian Amazon lowland rainforest within the department of Madre de Dios. Sampling took place in two major habitat types: várzea (seasonally flooded forest) and terra firme (non-flooded upland forest). Local habitat classifications included primary forest, secondary forest, edge habitats, and agricultural areas. Data were collected from multiple field sites to evaluate alarm-calling behavior across a broad geographic and ecological gradient. One site was located within Amazon Victory Brazil nut (*Bertholletia excelsa*) concession (-12.205066, -69.054394; elevation ≈ 15 meters above sea level) spanning 1,500 hectares in terra firme forest, where mature nut-bearing trees dominate the canopy, and the rest of the forest is relatively mature secondary growth. A second site was Kawsay Biological Station (-12.526376, -69.018899, elevation ≈ 16 m asl), a 200-hectare conservation area consisting primarily of secondary-growth seasonally inundated forest and accessible via the Madre de Dios River. A third site was located within an agricultural area of the Tambopata National Reserve south of Puerto Loero (-12.670084, -69.158586; elevation ≈ 16 m asl).

### *Experimental Design & Field Methods*

To simulate realistic predator-prey interactions, I used a model hawk to mimic the flight of an aerial predator. The model was painted to resemble a locally abundant and ecologically appropriate native species of raptor–Bicolored Hawk, *Accipiter bicolor*–selected for the unpredictable and opportunistic hunting strategy present in that genus (Bednekoff and Lima 1998). This simulated threat was introduced to a phylogenetically diverse assemblage of species, enabling systematic observation and documentation of their anti-predator responses across ecological, phylogenetic, and social contexts.

I conducted experiments between sunrise and sunset using an area search protocol, wherein the observer freely roamed the study site and identified target species by sight and sound. The target pool of potential species encompassed a broad range of understory passerines and near-passerines occurring below 10 meters in the forest strata. Once detected a target individual, it was followed for a minimum of five minutes to assess behavior before exposing a target bird to the model hawk, and also record any associated species within a 10 meter proximity to determine sociality. Following this baseline observation period, the model hawk was launched to fly ~15-20 meters  (Munn 1985; Soard and Ritchison 2009). For each experimental trial, a tripod-mounted omnidirectional audio recording device (iPhone 12 using the Voice Record Pro 7 app) was positioned prior to the trial to record the sounds and calls from the surrounding area. Additionally, a handheld directional shotgun microphone (Sennheiser ME66 K6) was connected to another recording device (Zoom F3) to directionally capture acoustic responses from the target bird in each experiment. For each trial, I also recorded  several extrinsic ecological variables. I estimated spherical vegetation density using the method used by Remsen and Robinson (1990), categorizing the relative vegetation cover within a one-meter radius surrounding the target individual into five ordinal classes: 0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100%. Other measurements included estimated average understory height within a five-meter radius of the bird to one meter, as well as observer distance, estimates of the closest model hawk proximity to the target bird, the maximum apex height of the hawk flight, the maximum distance of the hawk flight, and the height of the target bird at the time of the experiment. Exact distances for observer difference, flight distance, and target bird height were determined using a laser range finder (TIDEWE 700Y). I estimated the height of the hawk flight to the nearest meter. I calculated the height difference of the hawk to the target bird by subtracting the target bird's height from the hawk's apex: height difference = target bird height - hawk apex height.

### *Statistical Analysis*

To assess predictors of alarm calling across species, I employed a multi-step modeling framework, incorporating phylogenetic information, species-level foraging traits, and ecological data from each experiment. I used generalized linear models (GLMs) to investigate the role of extrinsic ecological traits within two well-sampled species. Then, to identify the drivers of alarm call production across species, I used a two-step procedure using phylogenetic generalized linear mixed models (PGLMMs). First by using a Bayesian model for alarm call probability at the species level, and second using the phylolm package (Ho and Ane 2014) to analyze more specific ecological and evolutionary factors that may influence alarm calling behavior. All analyses were performed in R (v4.3.2, R Core Team 2025)

### *Evaluating Extrinsic Ecological Factors*

I first constructed binomial generalized linear models (GLMs) at the species level, using ecological data from focal trials involving the two best-sampled species: red-crowned ant tanager ( $n = 15$ trials) and dusky-throated antshrike ( $N = 33$ trials).

For both species, I considered the following set of predictors of alarm probability: vegetation density, understory height, target species sex, target bird height, and three variables based on the model-hawk: closest proximity to the target, maximum height (i.e., apex), and height difference relative to the target bird height. I ran univariate models for each predictor, as well as an additive global model that included all predictors. Finally, to ensure that all possibilities were considered, I coded a custom dredge function that iterated over one to three predictors in both additive and two-way interactive combinations, while ensuring model nestedness. Subsequently, I used model averaging to obtain final coefficient estimates (Burnham and Anderson 1998). Weighted coefficient means and standard errors for each predictor were calculated by weighting models by AIC.

### *Evaluating Intrinsic Evolutionary Factors*

I considered a suite of factors as possible interspecific drivers of alarm calling across species. I obtained data on phylogenetic relatedness from a consensus tree calculated from 69 posterior distributions from the Global Bird Phylogeny (Jetz et al. 2012) using the Hackett et al. (2008) phylogenomic backbone. The consensus tree was created with 1,000 trees using the package Phytools (Revell 2024). The tree was rooted on the Rufous Motmot, *Baryphthengus martii*, which represents the earliest diverging lineage for species in the dataset (Gill et al. 2025). I also assembled a trait database of all the 69 target species' social systems (Table 1), as well as their foraging behaviors and substrates (Table 2), using my own field observations and standard references (Cornell University 2020; Schulenberg et al. 2007). I sourced species mean body mass from AVONET (Tobias et al. 2022).

Since many rainforest species are rare (Leitão et al. 2016), I obtained a highly uneven sampling distribution across species (mean = 2.99, SD ± 4.62, min = 1, max = 34). Nevertheless, the 69 species covered a broad range of social strategies, foraging behaviors, and functional traits, spanning 28 families and 7 orders. I used a two-step procedure to evaluate the drivers of alarm calling probability across species: first, I estimated a proportion of alarm-calling behavior that is uniquely due to differences among species, and second, I then explored how variation in traits explains this interspecific variation in alarm calling. For step one, I fitted a binomial PGLMM on all 208 observations of 69 species. The response variable was binary, indicating whether or not a species gave an alarm call during an experiment. Thus, I chose a Bernoulli distribution for the response variable and the logit as the link function. I used an intercept as the only predictor variable, along with species-level variance and a phylogenetically pooled species-level random intercept (Smith et al. 2019). A variance-covariance matrix derived from the consensus tree of the Global Bird Phylogeny was used to inform random effect covariance. I fitted this model using the R package ‘brms’ (Bürkner 2018, Bürkner 2017), using four chains, with 25,000 iterations, 15,000 samples as warm up, and a thin rate of 10. I used standard uninformative priors for the analysis, and conservatively set the acceptance probability to 0.99 and set tree depth to 11 to improve mixing. The model converged satisfactorily with all Gelman-Rubin statistics < 1.1, high effective sample sizes above 4000, and favorable mixing. From this model, I extracted the species-level posterior means of the phylogenetic random intercepts and subsequently used them, along with the posterior mean of the intercept, to predict species-level mean probabilities of producing alarm calls.

For step two, I explored these 69 newly predicted species-level alarm calling probabilities. I used the R package phytools to calculate phylogenetic signal with Pagel's lambda and Blomberg's K and visualize their distribution on the consensus tree (Revell 2009). Next, I used a phylogenetic regression model to identify which predictors explain variation in alarm calling probability across species. I treated the predicted alarm call probability as the response variable, and considered social group, foraging substrate, behavior, and log-transformed species mean body mass (Tobias et al. 2022) as predictor variables. According to my hypothesis about the relation between alarm calls and degree of social complexity, I treated social group categories as a ranked continuous variable according to Table 1. Additionally, to improve interpretability, I joined the competitive groups to their analogous mutualist categories because those groups did not produce alarm calls–specifically, manakin leks were grouped with single-species flocks, and ant-following flocks with mixed-species flocks. Next, to ensure model terms represented valid combinations of foraging behavior and substrate (Table 2), I combined both variables into one and treated this as a categorical variable. Prior to model fitting, I centered and scaled continuous predictor variables and ensured that predictors were independent (all VIF < 10, Vittinghoff et al. 2007). I fitted this phylogenetic regression model in the R package 'phylolm' (Ho and Ane 2014), using the consensus tree as above, allowing for variable branch-length transformations by estimating Pagel's lambda. I examined three different models to test which predictors explained alarm call responses to an aerial predator using the parameters of social group, foraging strategy, and body mass. Model fit was evaluated using ΔAICc. Last, I performed post-hoc pairwise comparisons with the phylogenetic regression model with the lowest ΔAICc (i.e., social group + foraging strategy) for the variable that describes foraging maneuvers and substrates. As post-hoc tests are not readily implemented in phylogenetic regression models fitted in the 'phylolm' package (Ho and Ane 2014), I wrote a custom function that iteratively contrasts levels within categorical predictors, effectively performing a battery of all possible pairwise comparisons among levels (code provided in supplement). I applied this post-hoc procedure on the maneuver/substrate combinations to test my predictions in Table 2.

## Results

Overall, the probability of alarm calling is low across all the species tested, averaging 5.3%. No single ecological predictor (see Table 3) produced statistically significant p-values for an alarm call response after weighted means averaging across all individual species-level models for *T. ardesiacus and H. rubica*, although vegetation density had a marginally significant positive effect for *T. ardesiacus* (p = 0.007).

**Table 3.** Weighted estimates from GLM averaging for the dusky-throated antshrike (*Thamnoames ardesiacus)* and the red-crowned ant tanager (*Habia rubica)*

| Predictors | Weighted estimate | Weighted SE | z score | p value |
|---|---|---|---|---|
| *T. ardesiacus* | | | | |
| Vegetation Density | 0.808 | 0.562 | 1.437 | 0.075 |
| Hawk Apex | -0.409 | 0.374 | -1.095 | 0.137 |
| Hawk Proximity | 0.148 | 0.377 | 0.392 | 0.347 |
| Hawk Height Difference | -0.067 | 0.423 | -0.157 | 0.437 |
| Bird Height | -1.009 | 0.980 | -1.029 | 0.152 |
| Target Sex M | -0.109 | 0.749 | -0.146 | 0.442 |
| Understory Height | 0.024 | 0.589 | 0.040 | 0.484 |
| *H. rubica* | | | | |
| Vegetation Density | -0.076 | 0.727 | -0.104 | 0.459 |
| Hawk Apex | -0.660 | 0.792 | -0.833 | 0.202 |
| Hawk Proximity | -0.355 | 0.512 | -0.694 | 0.244 |
| Hawk Height Difference | -0.442 | 0.973 | -0.454 | 0.325 |
| Bird Height | -0.764 | 1.372 | -0.557 | 0.289 |
| Target Sex M | -18.378 | 3413.358 | -0.005 | 0.498 |
| Understory Height | -0.540 | 0.851 | -0.634 | 0.263 |

The estimated species-level posterior probabilities of alarm calling behavior ranged from 0.01 to 0.36. In some cases, birds that I did not expect to have an above-average alarm call probability (e.g., *Ammodramus aurifrons, Sporophila caerulescens, and Volatinia jacarina*) likely had their output boosted due to phylogenetic proximity to species that produced alarm calls in my experiments. Additionally, the non-phylogenetic species effects had substantial variability (SD = 1.64, 95% credible interval: 0.12-3.52) (i.e., not well explained by phylogeny), and phylogenetic relatedness was only minimally influential (SD = 0.27, 95% credible interval: 0.18-0.69), meaning closely related species behave similarly, but the variation is modest. However, when I calculated phylogenetic signal of alarm call probability using Pagel's lambda (Pagel, 1999), my results showed a very strong phylogenetic signal ($\lambda = 1.047$, $p < 0.00001$) (Pearse, Davies, and Wolkovich, 2025), and this trait is not randomly distributed, instead highly conserved by phylogeny. A lambda value greater than 1 is uncommon, but not impossible (Revell, Harmon, and Collar 2008), and is likely explained by high variance between families but low variance within them (Phillips et al., 2018; Cadotte, Hamilton, and Murray, 2009; Böhning-Gaese and Oberrath, 1999). The relatively distinct foraging strategies across clades is another explanation (Pearman et al., 2014) and shares a similar pattern of variance in my data. I also calculated Blomberg's K for phylogenetic signal (Blomberg, Garland, and Ives 2003), which also showed significant trait conservation for alarm calling ($K = 1.56$, $p = 0.001$) greater than expected under Brownian motion (Adams 2014).

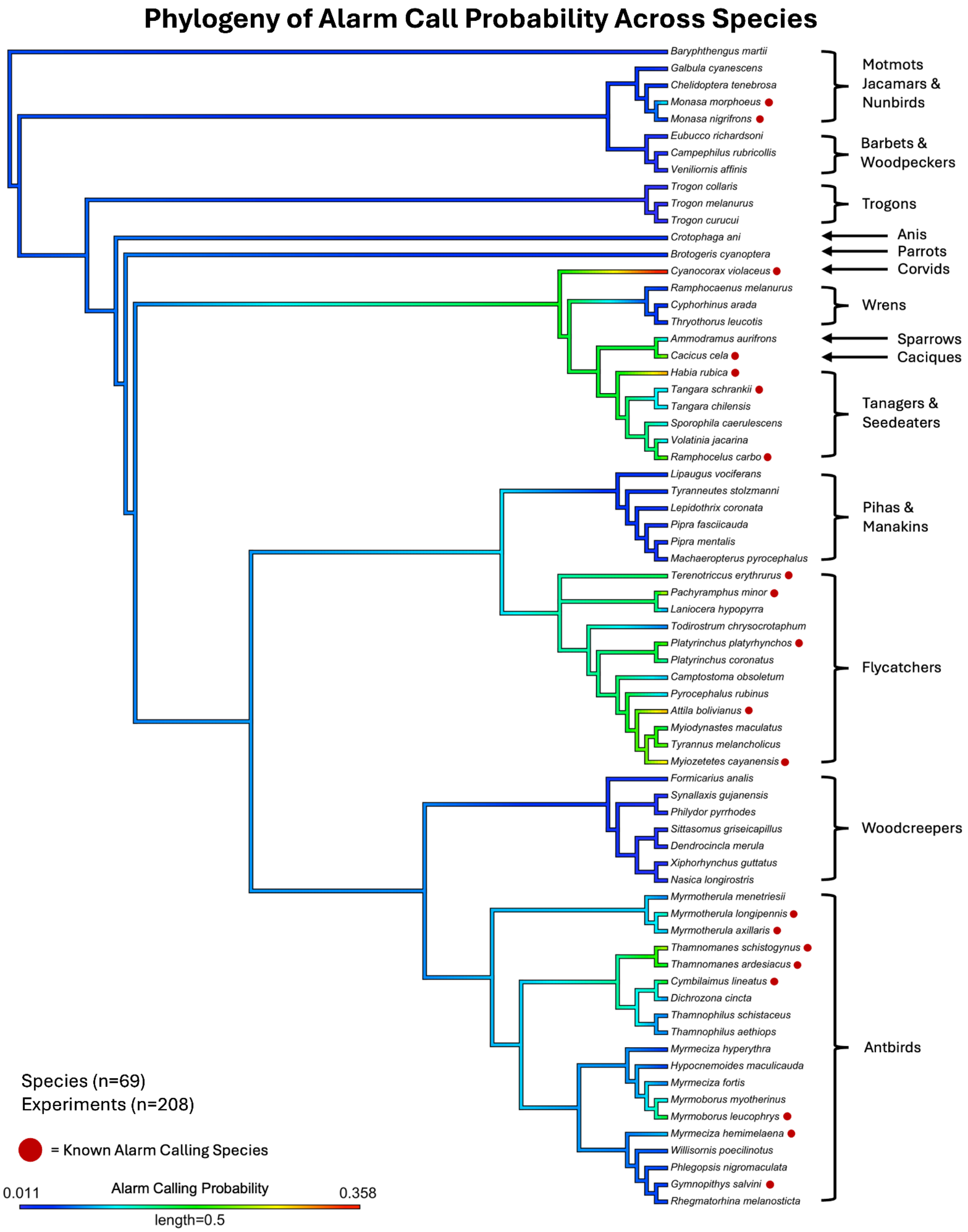


**Fig. 1. Phylogenetic Gradient of Avian Alarm Call Probability**: Bayesian posterior probability of alarm calls, visualized as a continuous color gradient, with lower probabilities depicted in blue and higher probabilities in red. This tree depicts phylogenetic relationships to show how alarm call probabilities vary across species. The red dots indicating known alarm calling species refers to species that gave alarm calls during an experimental trial.

Next, when sociality was the sole predictor of alarm calling in phylogenetic regression, it was significant (p = 0.001), however, it only explained 11% of the variance (R2 = 0.11, ΔAICc = 16.117). When foraging strategies were added to the model along with sociality 51% of the variance was explained (R2 = 0.512, ΔAICc = 0.000). When I incorporated average body mass, the variance explained increased to 53% (R2 = 0.53, ΔAICc = 0.267), but body mass was not significant (p = 0.135).

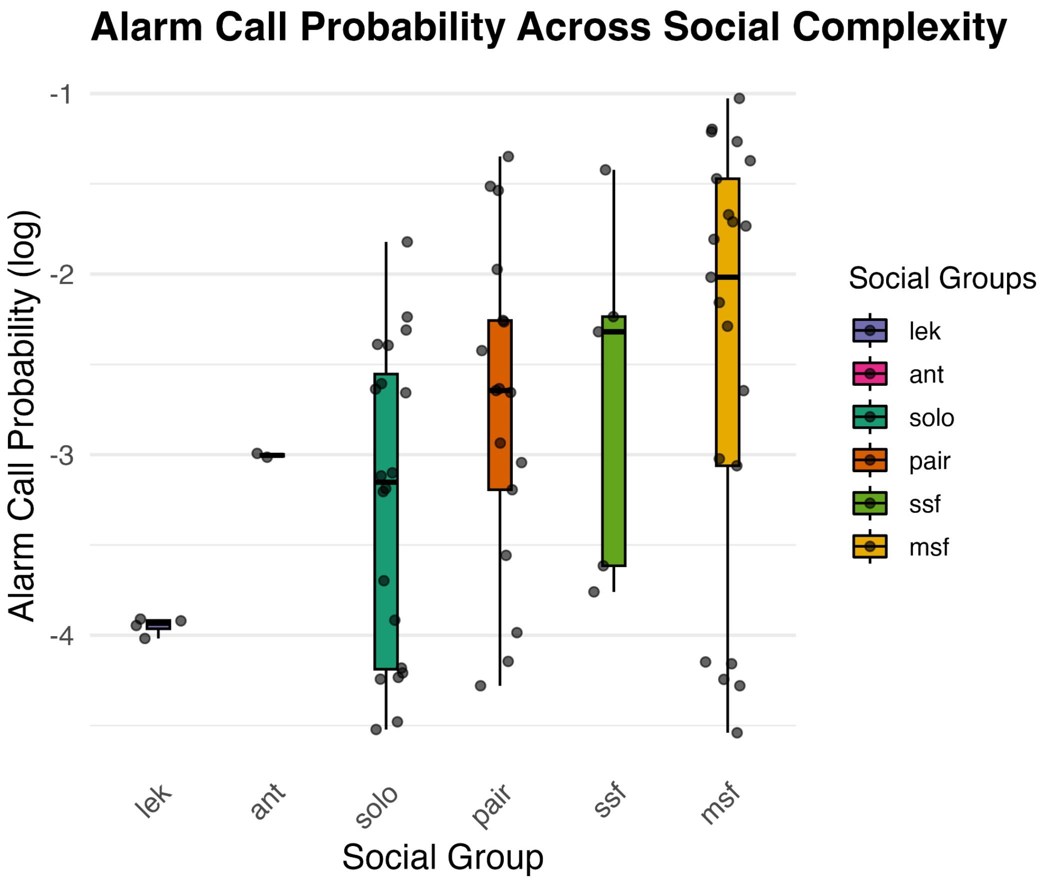


**Figure 2. Alarm Call Probability Across Social Complexity:** Box plots show the distribution of alarm calling probability (log scale) across six social group types. (1) manakin leks (lek), (2) ant-following flocks (ant), (3) solitary individuals (solo), (4) mutual pairs (pair), (5) single-species flocks (ssf), and (6) mixed-species flocks (msf). The points represent unique species.

**Table 5.** Model selection table from phylolm outputs using ΔAICc as the coefficient for best fit.

| Models | Predictors | k | LogLik | AICc | ΔAICc | Weight |
|---|---|---|---|---|---|---|
| 2 | Social Group + Foraging Strategy | 12 | -36.2253 | 106.0220 | 0.0000 | 0.5332 |
| 1 | Social Group + Foraging Strategy + Mass | 13 | -34.8353 | 106.2888 | 0.2668 | 0.4666 |
| 3 | Social Group | 2 | -56.9784 | 122.1387 | 16.1167 | 0.0002 |

The final component of my analysis used post-hoc pairwise comparisons for the phylolm models for different foraging strategies.Some strategies had larger effect sizes than others (see Fig. 3 and 4). Birds that foraged by sallying were significantly more likely to produce alarm calls than all other foraging-substrate groups ($p < 0.0001$), but species that sallied in the air were not different from those that sallied for green leaves ($p = 0.7$). Likewise, species that gleaned from green leaves also showed a higher alarm call propensity across most other groups. Other foraging strategies had lower alarm call probability. Birds that probe bark for food had the lowest overall probability. For birds that use gleaning as their primary strategy, the highest overall probability was for the green leaf substrate, and gleaning for other substrates (e.g., dead leaf, fruit, and ground) had lower probability. Within the ground foraging strategy, neither strategy I tested was significantly associated with alarm calling probability. Finally, the pounce strategy, which, in my data, was only present in ant-following birds, had slightly higher alarm probability, albeit nonsignificant.

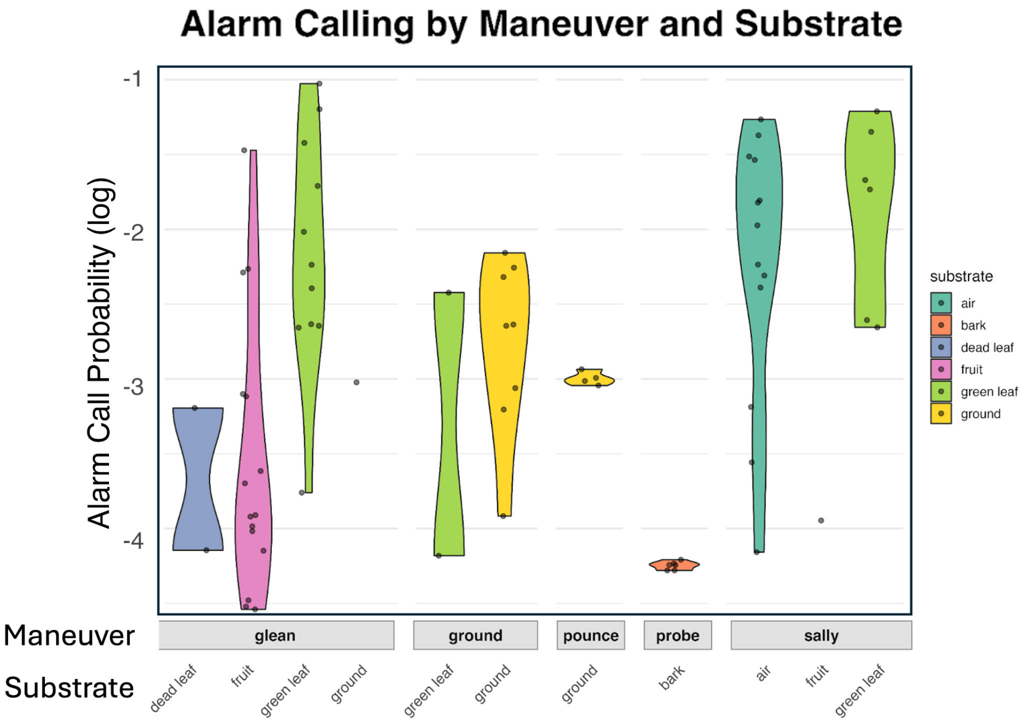


**Fig 3. Alarm Calling Probability Based on Foraging Maneuver and Substrate:** Box plots show the distribution of alarm call probability (log scale) across foraging behaviors. Foraging strategies are grouped by maneuver (top facet labels) and further divided by substrate type along the x-axis.

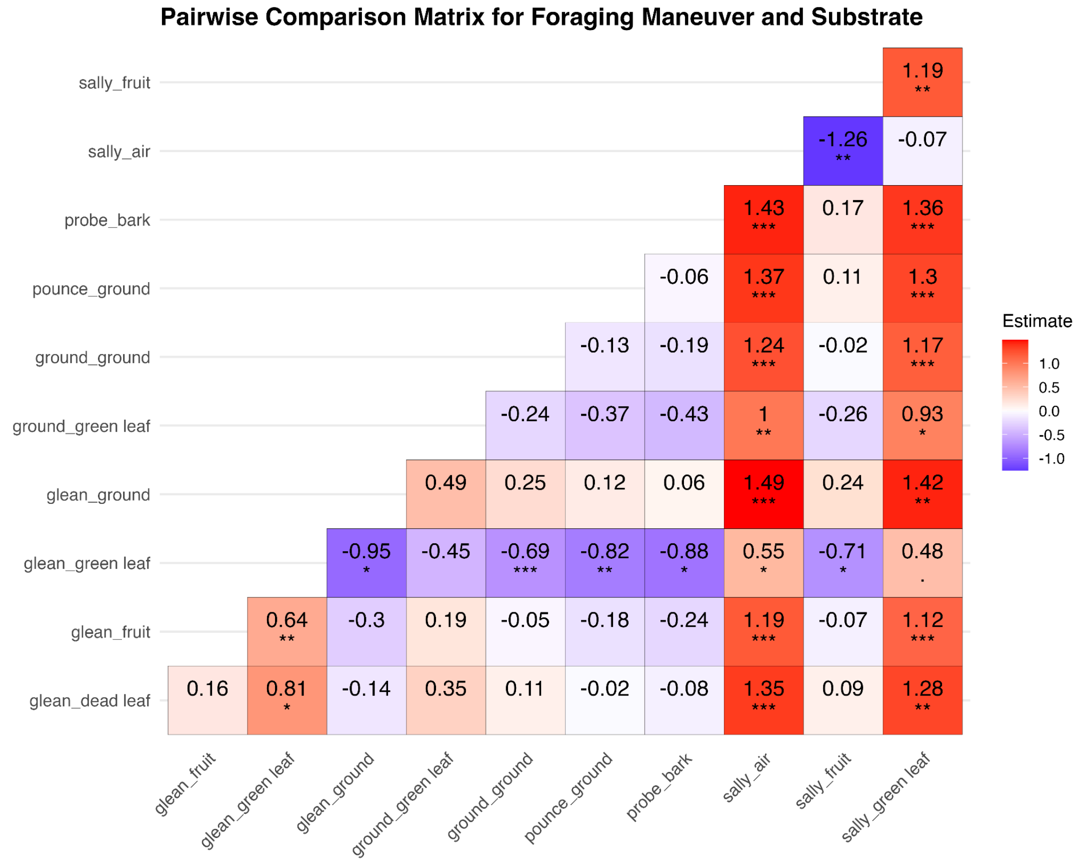


**Fig 4.** A post-hoc pairwise comparison matrix showing comparisons between all maneuver and substrate categories. Only the lower triangle was needed, and the numbers are slope estimates from the linear models comparing the x-axis to the y-axis. The color gradient has red for positive estimates, indicating a higher probability of alarm calling, and blue is the opposite, indicating a reduced probability. The stars represent p-value significance( ***, $p \leq 0.001$; **, $p \leq 0.01$; *, $p \leq 0.05$; ., $p \leq 0.1$).

Furthermore, my *a priori* predictions for the differences in alarm call propensity amongst solitary individuals, mutualistic groups, and competitive groups were well supported. Solo birds produced alarm calls rarely. Alarm calling propensity was much higher in mutualistic groups (e.g., pairs, single-species flocks, and mixed-species flocks). Lastly, competitive groups (e.g., manakins and ant-followers) showed very low alarm call propensity. For manakins, I conducted the experiments across five different species: *Pipra fasciicauda, Pipra mentalis, Tyranneutes stolzmanni, and Machaeropterus pyrocephalus, Lepidothrix coronata*; not one of the manakin species exposed to the predator produced an alarm call, and the majority of the target individuals either flew away or froze in place. In ant-following flocks, there was almost no alarm propensity demonstrated, except for one instance where a male *Oneiliornis salvinii* produced an alarm, coincidentally with a female of that species present.

## Discussion

Contrary to my ecological hypotheses predicting that ecological conditions would influence alarm call propensity, my analyses indicate that such factors do not drive variation in patterns of alarm calling. Previous findings (Jones and Robinson 2021, Suhonen 1993) suggested vegetation density as influencing anti-predator behavior, including alarm call propensity in birds. Across all model combinations tested, no ecological predictor significantly accounted for variation in alarm calling. Though, I found a weak trend for alarm calling to increase with greater vegetation density in the dusky-throated antshrike (*T. ardesiacus*) (estimate = 0.808, p = 0.07). These results are contradictory to what has been expected given the hypothesized vulnerability of species in different vegetation densities (Thiollay and Jullien 1998).

Although I did not find an effect of vegetation, rainforests may not have sufficient variation in vegetation density to be important for alarm calling.. Rather, these effects may be more pronounced across habitats that have more extreme examples of vegetation, but such comparisons would need to control for other functional traits such as those found in this study.

At the evolutionary level, my phylogenetic analysis suggests that alarm calling behavior is strongly associated at the clade-level, but not as strong at the species-level.The phylogenetic signal in my analysis indicated that closely related species (i.e., within families) were more similar in alarm-calling propensity than expected under Brownian motion, suggesting strong evolutionary conservatism of this behavior across lineages, and certain clades (e.g., antshrikes, flycatchers, and several oscines) have distinct clustering of species that alarm with higher propensity. Additionally, there are also several groups on the phylogenetic tree that show lower, near-zero likelihood (e.g., woodcreepers, manakins, and ant-followers). In one study, Böhning-Gaese and Oberrath (1999) compared functional traits for 151 bird species to quantify phylogenetic effects, and one of their key findings was that such effects were weak within families (i.e., species-level) but strong when comparing families to one another.. This pattern suggests that alarm calling may be influenced by evolutionary history and that variation in behavioral strategies may be shaped by functional ecological traits associated with taxonomic clades. Thus, my experiments suggest that alarm calling to aerial predators is better explained by evolutionary processes than ecological contexts.

Consistent with my expectations, sociality and foraging strategy were strong predictors of patterns of alarm call production. One of the primary benefits of increasing social complexity is a greater degree of anti-predator defense. Numerous studies have documented the benefits of group formation in avoiding predators (Boinski and Garber 2000 ). More specifically, alarm calling is frequently employed within groups to warn group members of approaching predators (Goodale et al. 2017, Jiang et al. 2023; Goodale and Kotagama 2005). While I tested for the patterns of alarm calling using a general classification for group complexity, I have not assessed variation in audience effects, such as species diversity or kin/non-kin associations, that may be driven by the composition of group membership (Sherman 1977, Smith 1986, Gyger 1990, Demartsev et al. 2023, Meaux et al. 2023). For example, dominance hierarchies are known to influence alarm call variation within groups of conspecifics such tits, whereas kinship has also widely been documented to drive variation in alarm calling (Sherman 1977, Smith 1986). The extent to which audience effects are driven by variation in heterospecific species composition within flocks is much less well known and merits further investigation (Ridley et al. 2007, Bai et al. 2020, Krama et al 2023). The roles of competitors versus species contributing to group dilution (Turner and Pitcher 1986) or confusion (Krakauer 1995) may influence the degree to which audience effects drive patterns of alarm call production in heterospecific groups (Coppinger et al. 2020, Meaux et al. 2023) and this topic surely will provide insight into the behavioral mechanisms driving variation in alarm calling due to social group composition.

Antipredator behavior varied with social context, with solitary individuals, mutualistic groups, and competitive groups showing different propensities to alarm, consistent with my a priori predictions. When individual birds had no receivers present, they only rarely produced alarm calls, which suggests that alarm calling in the absence of receivers may be disadvantageous for the caller's survival, and choosing to remain silent is a good strategy. Mutualistic groups, which may potentially involve reciprocal altruism (Trivers 1971), hint at both the antipredator value of having a larger group size, but also potentially that heterospecific receiver presence could be influential. In the context of competitive groups, it may not be beneficial to alert others to threats because alarm calling in this social system is likely disadvantageous because fewer competitors might lead to more food resource availability as well as potentially greater breeding opportunity. It may be in the interest of the individual to allow group members to experience predation and exhibit selfish defensive behavior (Hammer et al. 2023; Krama et al. 2023). However, the safety benefits of grouping in this strategy are still likely explained by dilution and confusion effects. In ant-following flocks, for example, which are directly competitive over a shared feeding resource, there may be limited propensity for alarm calling. Though, it may be limited or highly directional between mutual pairs in order to thwart competitive eavesdroppers. Additionally, lekkingmanakins may have no reason to alarm, because the many males are vying to attain the alpha position (Robbins 1985) in the flock, thereby increasing their chance to breed with a limited number of females. To my knowledge, this is the first direct experimental study that exposed manakins to a predator stimulus in order to gauge their antipredator response behaviors. Olson and Blumstein (2010) found that when Yellow-bellied Marmots form large all-male groups, they reduce their alarm calling behavior. Beyond that, the specific relationship between competitive social grouping strategies and alarm calling remains little explored.

My results for foraging strategy were consistent with my predictions based on previous work on how this behavior influences vigilance and vulnerability (Martínez et al. 2016). Species that were previously shown to be less likely to eavesdrop–those that catch insects by searching the air around them–are likely to double up the cost of foraging while maintaining vigilance (Martinez and Zenil 2012). While birds that employ this foraging strategy are less likely to be reliant on eavesdropping, they may also be more likely to make alarm calls, which is precisely what I found. While this is found in other systems, such as with Fork-tailed Drongos (Goodale and Kotagama 2008) other species that alarm call do not flycatch but similarly perch upright, such as the Pied Babbler (Ridley, Nelson-Flower, and Thompson 2013). Interestingly, while I was not able to sample canopy species, a well-known alarm caller in this system is the White-winged Shrike Tanager (*Lanio versicolor*), which, although in the tanager family, perches upright and sallies through the air to catch insects (Munn 1985). In addition, while true for my system, it is particular to a forest system where many species are not gregarious in big monospecific flocks (Terborgh et al. 1990). Indeed, where I found resemblance to gregariousness in monospecific groups, my results were consistent with what has been found in other regions where conspecific groups of birds are likely to give alarm calls (Soard and Ritchison 2009). The relationship between alarm calling and large conspecific groups is possibly a consequence of having 'many eyes' being vigilant, such as as that found in wintering parids in temperate regions, and fulvettas in subtropical Asia (Freeberg and Harvey 2008, Sridhar et al. 2009, Soard and Ritchison 2009, Meaux et al. 2023).

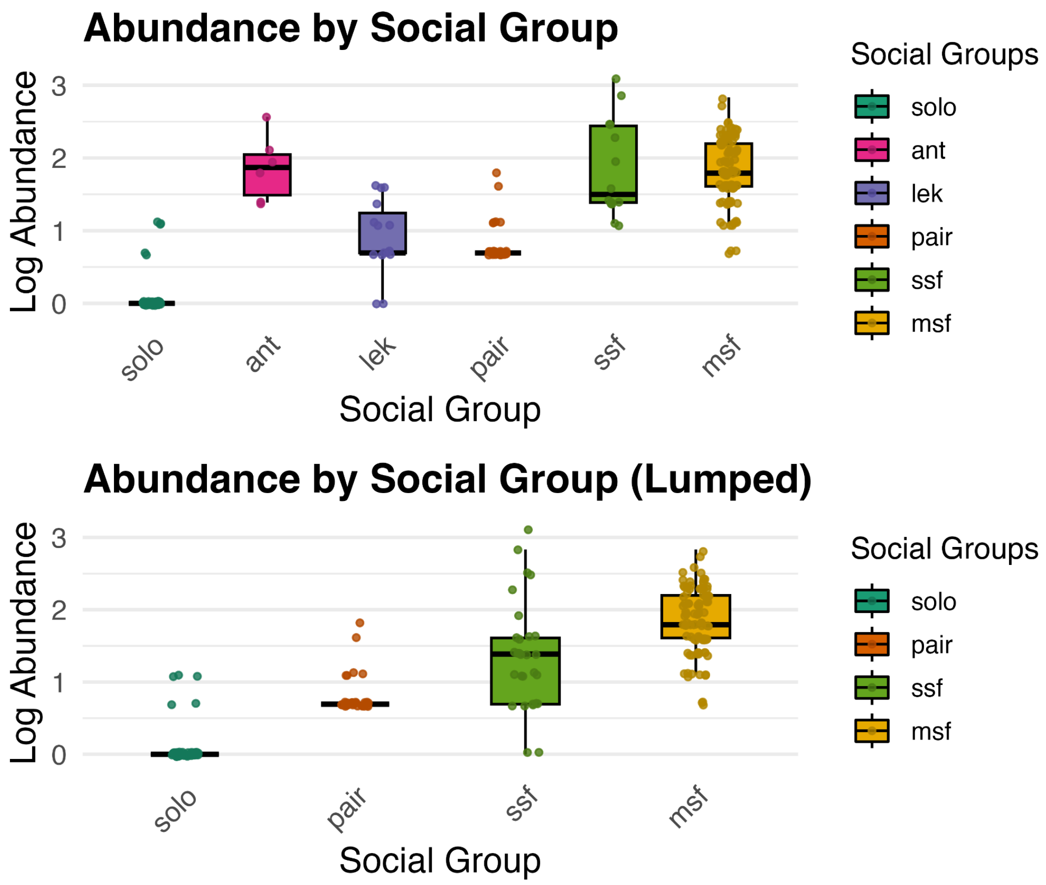
While I tested the relative importance of extrinsic and intrinsic factors on aerial alarm calling, I have only assessed one context of communication for predator threats. For example, while mobbing is widespread among bird species, the extent to which certain species incite mobbing has recently shown asymmetries, suggesting that certain species play more important roles than others (Lima et al. 2018; Hetrick and Sieving 2012; Carlson et al. 2020; Liao et al. 2024). However, few of these studies have addressed the extent to which species traits may explain patterns in alarm calling behavior specifically and anti-predator behavior in general (Caro 2005, Lima et al. 2018, Jiang et al. 2023). While there appears to be shared ancestry in the degree to which certain species mob (e.g., Paridae, Owens and Freeberg 2007, Lima et al. 2018), results in this context suggest that foraging guild and body mass were better predictors of species that mob.

While many of these species produce alarms, the degree to which they are used by other species has not been tested. Thus, the extent to which these different species are key information providers is currently not known (Hetrick and Sieving 2012, Carlson et al. 2020). Measuring the responses of suites of species to different alarm calls would provide much insight into the relative importance of different functional traits in driving the quality of threat information across individuals and species that share predators. Additionally, I was not able to assess many species in the canopy, such that the degree to which that community responds to similar predator stimuli is clearly underestimated.

This may be especially true for migrants because they may lack familiarity with resident social groups on wintering grounds. It has been observed that migrants may initially exhibit more solitary behavior until they integrate into existing social groups, and another possibility explaining why migrants could be solitary is that they may experience territorial aggression from groups already present in the area year-round (Munoz and Colorado 2021).

Understanding who produces alarm calls and the relative importance of use by other species will allow for a broader understanding of how information scales up from individuals and groups to the level of the community (Goodale and Magrath 2024). Previous work has suggested that logged forests and forest fragmentation lead to degradation in group structure (Mokross et al. 2014, Zou et al. 2018) and that information use among species also becomes degraded (Hua and Sieving 2016). Thus, understanding the ecological and evolutionary drivers of alarm calling will allow for a better mechanistic understanding of how anthropogenic change can drive variation in information flow (Hua et al. 2024, Diniz and Duca 2021, Kunc and Schmidt 2019, Schmidt 2017). By linking functional trait diversity in animal communities to information, this will allow for better prediction of changes in the information landscape. Experimental approaches that link behaviors to functional traits will allow for a more comprehensive understanding of how diversity in animal communities influences information availability and use.

## Supplements



**Supplementary Figure 1.** Box plots displaying observed flock abundance (log) of individual birds across social groups (1) solitary individuals (solo), (2) ant-following flocks (ant), (3) manakin leks (lek) , (4) mutual pairs (pair), (5) single-species flocks (ssf), and (6) mixed-species flocks (msf). The points represent unique species.. The top figure shows all groups. The lower figure lumped competitive groups with their analogous mutualistic groups–lek with ssf, and ant with msf.

**Supplementary Table 1.** A list of all species that were targeted in an experimental trial. For each species, there are summaries of their auditory reactions into three categories. (i.e., alarm, call, or quiet). The sum total of experimental trials for any given species is represented by n. Alarm mean rate is the mean positive alarm reactions across all trials for that species. Overall the mean alarm rate across all species was 0.25. Sample sizes across species have relatively high variability (mean = 2.99, SD ± 4.62, min = 1, max = 34). The second part of the table shows the foraging strategies for each species subdivided into maneuvers and substrates.

| | **Audio Reaction** | | | | | **Foraging Strategy** | |
|---|---|---|---|---|---|---|---|
| **Species** | **Alarm** | **Call** | **Quiet** | **n** | **Mean Alarm Rate** | **Maneuver** | **Substrate** |
| *Ammodramus aurifrons* | | | 2 | 2 | 0.00 | ground | ground |
| *Attila bolivianus* | 1 | | | 1 | 1.00 | sally | green leaf |
| *Baryphthengus martii* | | | 1 | 1 | 0.00 | glean | fruit |
| *Brotogeris cyanoptera* | | 1 | | 1 | 0.00 | glean | fruit |
| *Cacicus cela* | 2 | 1 | | 3 | 0.67 | glean | green leaf |
| *Campephilus rubricollis* | | | 1 | 1 | 0.00 | probe | bark |
| *Camptostoma obsoletum* | | | 1 | 1 | 0.00 | sally | air |
| *Chelidoptera tenebrosa* | | | 1 | 1 | 0.00 | sally | air |
| *Crotophaga ani* | | 1 | | 1 | 0.00 | glean | green leaf |
| *Cyanocorax violaceus* | 1 | | | 1 | 1.00 | glean | green leaf |
| *Cymbilaimus lineatus* | 1 | | | 1 | 1.00 | sally | green leaf |
| *Cyphorhinus arada* | | | 1 | 1 | 0.00 | ground | ground |
| *Dendrocincla merula* | | | 2 | 2 | 0.00 | probe | bark |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Dichrozona cincta* | | | 2 | 2 | 0.00 | ground | ground |
| *Eubucco richardsoni* | | | 1 | 1 | 0.00 | glean | fruit |
| *Formicarius analis* | | | 2 | 2 | 0.00 | ground | ground |
| *Galbula cyanescens* | | 1 | 2 | 3 | 0.00 | sally | air |
| *Gymnopithys salvini* | | | 3 | 3 | 0.00 | pounce | ground |
| *Habia rubica* | 11 | 2 | 2 | 5 | 0.73 | glean | green leaf |
| *Hypocnemoides maculicauda* | | 1 | 6 | 7 | 0.00 | glean | ground |
| *Laniocera hypopyrra* | | | 1 | 1 | 0.00 | sally | green leaf |
| *Lepidothrix coronata* | | 2 | 2 | 4 | 0.00 | glean | fruit |
| *Lipaugus vociferans* | | | 1 | 1 | 0.00 | glean | fruit |
| *Machaeropterus pyrocephalus* | | | 1 | 1 | 0.00 | glean | fruit |
| *Monasa morphoeus* | 2 | | 2 | 4 | 0.50 | sally | air |
| *Monasa nigrifrons* | | | 6 | 6 | 0.00 | sally | air |
| *Myiodynastes maculatus* | | | 1 | 1 | 0.00 | sally | air |
| *Myiozetetes cayanensis* | 1 | | | 1 | 1.00 | sally | air |
| *Myrmeciza fortis* | | | 1 | 1 | 0.00 | ground | ground |
| *Myrmeciza hemimelaena* | 1 | | 5 | 6 | 0.17 | ground | green leaf |
| *Myrmeciza hyperythra* | | 4 | 5 | 9 | 0.00 | ground | ground |
| *Myrmoborus leucophrys* | 5 | | 2 | 7 | 0.71 | glean | green leaf |
| *Myrmoborus myotherinus* | | | 2 | 2 | 0.00 | glean | green leaf |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Myrmotherula axillaris* | 1 | 2 | 4 | 7 | 0.14 | glean | green leaf |
| *Myrmotherula longipennis* | 3 | 2 | 4 | 9 | 0.33 | glean | green leaf |
| *Myrmotherula menetriesii* | | | 1 | 1 | 0.00 | glean | green leaf |
| *Nasica longirostris* | | 1 | | 1 | 0.00 | probe | bark |
| *Pachyramphus minor* | 1 | | | 1 | 1.00 | sally | green leaf |
| *Philydor pyrrhodes* | | 1 | | 1 | 0.00 | glean | dead leaf |
| *Phlegopsis nigromaculata* | | | 2 | 2 | 0.00 | pounce | ground |
| *Pipra fasciicauda* | | | 9 | 9 | 0.00 | glean | fruit |
| *Pipra mentalis* | | | 4 | 4 | 0.00 | sally | fruit |
| *Platyrinchus coronatus* | | | 1 | 1 | 0.00 | sally | air |
| *Platyrinchus platyrhynchos* | 1 | | | 1 | 1.00 | sally | air |
| *Pyrocephalus rubinus* | | | 1 | 1 | 0.00 | sally | air |
| *Ramphocaenus melanurus* | | | 1 | 1 | 0.00 | glean | fruit |
| *Ramphocelus carbo* | 4 | | 2 | 6 | 0.67 | glean | fruit |
| *Rhegmatorhina melanosticta* | | | 1 | 1 | 0.00 | pounce | ground |
| *Sittasomus griseicapillus* | | | 1 | 1 | 0.00 | probe | bark |
| *Sporophila caerulescens* | | | 1 | 1 | 0.00 | ground | ground |
| *Synallaxis gujanensis* | | 1 | 1 | 2 | 0.00 | ground | green leaf |
| *Tangara chilensis* | | 1 | | 1 | 0.00 | glean | fruit |
| *Tangara schrankii* | | | 1 | 1 | 0.00 | glean | fruit |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Terenotriccus erythrurus* | 1 | | 1 | 2 | 0.50 | sally | air |
| *Thamnomanes ardesiacus* | 13 | 10 | 11 | 34 | 0.38 | sally | green leaf |
| *Thamnomanes schistogynus* | 2 | | | 2 | 1.00 | sally | air |
| *Thamnophilus aethiops* | | | 1 | 1 | 0.00 | glean | green leaf |
| *Thamnophilus schistaceus* | | | 1 | 1 | 0.00 | glean | green leaf |
| *Thryothorus leucotis* | | 1 | | 1 | 0.00 | glean | dead leaf |
| *Todirostrum chrysocrotaphum* | | | 1 | 1 | 0.00 | sally | green leaf |
| *Trogon collaris* | | | 2 | 2 | 0.00 | glean | fruit |
| *Trogon curucui* | | | 1 | 1 | 0.00 | glean | fruit |
| *Trogon melanurus* | | | 2 | 2 | 0.00 | glean | fruit |
| *Tyranneutes stolzmanni* | | | 2 | 2 | 0.00 | glean | fruit |
| *Tyrannus melancholicus* | 1 | | 1 | 2 | 0.50 | sally | air |
| *Veniliornis affinis* | | | 1 | 1 | 0.00 | probe | bark |
| *Volatinia jacarina* | | | 3 | 3 | 0.00 | ground | ground |
| *Willisornis poecilinotus* | | 1 | 1 | 2 | 0.00 | pounce | ground |
| *Xiphorhynchus guttatus* | | | 3 | 3 | 0.00 | probe | bark |
| Grand Total | 52 | 33 | 121 | 206 | 0.25 | | |

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