

Deconstructing the landscape of fear in stable multi-species societies

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Abstract. Animal distributions are influenced by variation in predation risk in space, which has been described as the “landscape of fear.” Many studies suggest animals also reduce predation risk by eavesdropping on heterospecific alarm calls, allowing them to occupy otherwise risky habitats. One unexplored area of study is understanding how different species’ alarms vary in quality, and how this variation is distributed in the landscape. We tested this phenomenon in a unique system of avian mixed species flocks in Amazonian rainforests: flock mates (eavesdropping species) strongly associate with alarm-calling antshrikes (genus *Thamnomanes*), which act as sentinel species. Up to 70 species join these flocks, presumably following antshrike behavioral cues. Since flocks in this region of the Amazon are exclusively led by a single antshrike species, this provides a unique natural system to compare differences in sentinel quality between flocks. We simulated predation threat by flying three species of live trained raptors (predators) towards flocks to compare sentinel probability to (1) produce alarm calls, and (2) encode information about magnitude and type of threat within such alarm calls. Our field experiments show significant differences in the probability of different sentinel species to produce alarm calls and distinguish predators. This variation may have important fitness consequences and shape the “landscape of fear” for eavesdropping species.

Key words: eavesdropping networks; ecology of information; fitness landscape; landscape of fear; predation-risk; sentinel quality; spatial ecology.

INTRODUCTION

Interactions between predators and prey lie at the foundation of community ecology. Recent work has shown that the indirect effects of predator threat have major community level consequences which influence prey distribution in a “landscape of fear” (Lima 1998, Laundré et al. 2010, Magrath et al. 2015). While many species select habitat based on individual assessment of foraging opportunity and predation risk (Heithaus et al. 2009, Willems and Hill 2009, Morosinotto et al. 2010), eavesdropping on the behavioral cues of heterospecific neighbors allows individuals to save energy and mitigate risk without the added cost of gathering information first-hand (Seppänen et al. 2007). This method of gauging local conditions allows prey species to share vigilance in risky habitat (Powell 1989, Gil et al. 2016). Through the production of social signals, sentinel species greatly affect the structure of communities of species at risk from similar predators (Sieving et al. 2004, Goodale et al. 2010, Schmidt et al. 2010). Thus, variation in how sentinel species provide information about predators across a landscape may be a key component of basic habitat quality and this may have direct consequences affecting survival and fitness for eavesdropping species (Gil et al. 2016).

Studies of prey distribution in the presence and absence of predators have shown that prey assess and respond to predation risk (Laundré et al. 2001). It has also been reported that prey rely on predator information from other species, social information, to make decisions on habitat use (Ridley et al. 2014). However, it is still not well understood whether or how social information quality varies, especially in regards to the relationship between predator risk and habitat heterogeneity. Such information is vital given that predator risk likely varies across landscapes (Mönkkönen et al. 2007, Morosinotto et al. 2010). A graded response to predators has been proposed through studying the variability of alarm signal structure (Templeton et al. 2005, Sieving et al. 2010), and correlated behavioral changes in eavesdropping species (Templeton and Greene 2007, Hetrick and Sieving 2012), but general rarity and variation of observable live predator-prey interactions precludes a standardized measure of prey species ability to provide accurate threat information (Leavesley and Magrath 2005, Fallow and Magrath 2010). Such tests require the manipulation of predator behavior in a natural setting. Given the overwhelming logistical difficulty of doing so, prey response across species to various predator contexts have rarely been directly compared in the field (Leavesley and Magrath 2005).

We explored the extent to which species vary in their probability to emit alarm calls to predator threats and distinguish different types of threats, in terms of predator size and distance to prey, across two habitats that potentially vary in predator risk in an Amazonian rainforest. These habitats were occupied by mutually exclusive

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congeners (Bluish-slate Antshrike *Thamnomanes schistogynus* and Dusky-throated Antshrike *Thamnomanes ardesiacus*; habitat specialists) that were the primary alarm calling birds in their respective flocks (Munn and Terborgh 1979, Munn 1986, Martínez and Zenil 2012). We provide evidence that the core group of permanent species of flock members that associate with these sentinel antshrikes are identical in composition across these different habitats (habitat generalists), thus providing a model system for isolating the effects of differences in sentinel quality and thus, variation in the information landscape, for associate species. We used live raptors to examine the extent to which these different alarm calling birds produced alarm calls and evaluated different predator contexts. We tested two hypotheses, (1) variation in the fear landscape (habitat “riskiness”) is mediated by the information landscape (vigilance of alarm calling birds) and (2) species’ alarm signals vary with predator context (predator size and predator distance to alarm caller). We predicted that the Bluish-slate Antshrike, that occupied forest with more open gaps, was likely to produce more alarm calls and provide more specific information (specific information about size and distance) within its alarm calls than the Dusky-throated Antshrike. We also predicted that both species would provide additional information about threat, providing details of predator size and distance to predator. This encoded detailed information could be communicated through the number of urgent notes in calls. Because smaller aerial predators are more maneuverable in the complex habitats found in Amazonian rainforests, we expected both sentinel species would use more urgent notes for smaller predators (referential information; Macedonia and Evans 1993, Gill and Bierema 2013). We also expected that more urgent notes would be produced when predators flew closer to flocks (magnitude of threat; Leavesley and Magrath 2005, Hetrick and Sieving 2012). Variation in the information landscape may be a key component of risk attenuation in heterogeneous habitat. Consequently, the information landscape may ultimately optimize prey decision-making in a landscape of fear.

MATERIALS AND METHODS

Study site

Experimental trials were conducted during the dry season from 14 June and 24 July of 2016 at the Pantiacolla Field station in the foothill tropical forests of south eastern Peru. The station sits on the north bank of the Alta Madre de Dios River at 12°39'2.0" S 71°13'48" W. The locality of Pantiacolla is characterized as moist, tropical forest. The local habitats include tracts of bamboo, floodplain forests, mature foothill transitional forests, and mature terra firme forests. Study flocks were generally limited to two distinct forest types; terra firme dominant forest and terra firme forest mixed with bamboo patches.

Experimental trials

Simulated predation attempts were performed using trained birds of prey presented by professional falconers, to treatment birds in situ. In this study site we have mapped and described ~30 flocks, and banded up to 70% of the individuals for the majority of these flocks. Previous studies in this system have shown that individuals of core flocking species are permanently associated with a single flock (Munn and Terborgh 1979, Jullien and Thiollay 1998). Each day, antshrike led flocks were located by a single “scout” researcher and followed within 15 m for more than 30 min prior to treatment. Data on flock composition was collected during this period, including GPS location at every 10-min interval and species composition at every 30-min interval (Martínez and Gomez 2013). This method allowed us to collect home range data for each flock over the course of the field season. Radio and compass was used by a second group of researchers to locate the scout researcher. When the second group of researchers arrived to the proximate treatment flock, the single scout researcher left the site and began following the subsequent treatment flock. In this manner up to ten trials could be completed per day. Three researchers performed the stimulus presentation of the live bird of prey after the flock resumed normal foraging behavior following any disturbance produced by the scout and stimulus researchers’ change of positions, or after any other disturbance seen to interrupt the normal foraging behavior of the flock, including the presence of nearby predators and territorial disputes with neighboring mixed flocks. The primary observer maintained visual contact with the focal Antshrike from a distance of 10 to 15 meters, while recording real-time behavioral observations vocally into a handheld voice recorder (Olympus VN-702PC, Tokyo, Japan) using behavioral codes outlined in (Remsen and Robinson 1990), including Look, Flight, Dive, Sally-Hover, Sally-Strike. The second observer recorded the focal bird’s vocal activity for one minute prior to the presentation of the bird of prey to one minute after presentation, using a parabola mic constructed around an omnidirectional condenser microphone (Audio-Technica ATR3350, Tokyo, Japan) coupled with a digital recorder (Roland R-05, Los Angeles, USA) at a sampling rate of 44.1 kHz and 24-bit resolution. The third researcher handled the trained bird of prey, and after a hand signal from the primary observer, released the bird of prey towards a flight path that would best result in a prey/predator distance within the pre-determined categories of near (0–4 m), medium (4–8 m) and far (8–12 m). In the instance where the raptor did not fly the predetermined distance, the trial was repeated on a different day. A maximum of one trial per flock per day was performed to best avoid a focal bird’s overexposure to the stimulus. The raptors used in the experiment were trained to only feed out of the hand of the falconer, and thus were not accustomed to hunting their own prey.

None of our study birds were harmed by the raptors in our study. Control treatments followed all pre-raptor flight procedures, except when the hand signal from the primary observer was given, a small branch (~50 cm) was thrown within 10 m of the focal bird instead of a live raptor, controlling for effects of observer's presence and observer's actions during the trials. In other systems, a stick is used to generate alarm calls of birds (Goodale and Kotagama 2005) but in our system, only weak alarm calls were generated on two occasions, most likely from the noise of the stick hitting branches nearby.

Three species of trained raptor were used in the trials. Our aim was to determine whether predator size influences the type of threat information that birds produce using a novel large predator, a novel small predator, and a native small predator. Differences among the two smaller predators would suggest that prey species recognize differences in predator species. Differences between the two smaller predators and the large predator would suggest that prey distinguish threats based on body size, regardless of the predator species. The largest raptor used was a juvenile female Harris hawk, *Parabuteo unicinctus* (730 g), a non-native species whose size and flight characteristics closely resemble native hawks in the genus *Buteo* and *Leucopternis*. The second largest raptor used was a juvenile female Bi-colored Hawk, *Accipiter bicolor* (368 g), a native species who naturally specializes in preying upon small passerines like those in the mixed flocks under study. The smallest raptor used was an adult male Aplomado Falcon *Falco femoralis* (218 g), a non-native species whose size and flight characteristics are similar to the native *Falco* species.

Two species of focal bird were presented with birds of prey, Dusky-throated and Bluish-slate Antshrikes. These species are congeners that share similar foraging ecologies and are similar in body size (18.0 vs. 17.5 g, Martínez unpublished data, Munn and Terborgh 1979, Martínez and Robinson 2016), and are vulnerable to similar predators (Munn and Terborgh 1979, Munn 1986). Each mixed flock was led by a single antshrike species, with 8 flocks of each sentinel type representing a total of 16 treatment flocks. The three species of raptor were presented a minimum of three times (far, medium and close trials) plus control to 16 focal antshrikes of two flock types, resulting in a semi-factorial design of (3 raptor species \times 3 presentation distances \times 2 flock types + 1 control) 160 trials performed across 16 different flocks. The order in which flocks were visited as well as the treatments presented to each flock were both randomized.

Canopy height and cover measures were recorded by visiting 20 GPS points per flock ($n = 320$) after the live raptor portion of the trials had finished. Points were selected at random from available home range points previously collected. At each point, a photo was taken from 2 m above the ground of the canopy using a Sony Alpha 65 mirrorless camera paired with a Sony DT 2.8/30 Macro lens for later analysis using the GLAMA light

analysis mobile application, which provided adjusted canopy cover estimates (Tichý 2015). Canopy height at each point was measured using a Bushnell Pro Sport 450 laser range finder. Measurements were taken to the highest available reading at each point.

Statistical analyses

We used GPS point location data for each flock to estimate home ranges by creating a spatially-explicit density surface through Kernel Density Estimation. We calculated flocking occurrence by deriving the percentage of intervals that a species was present over the total number of intervals a flock was censused. We then calculated a mean percent occurrence that a species was present in each flock type (either those led by Bluish-slate or those led by Dusky-throated Antshrike). We then compared the species occurrences of the two communities of flocks using the Bray-Curtis Dissimilarity Index (using species occurrences as an abundance metric). The index provides a value bounded between 1 and 0 where values close to one indicate high similarity and values close to zero indicate low similarity in species composition between two communities. We then compared the observed value of dissimilarity derived from the Bray-Curtis Dissimilarity Index to a null distribution of Bray-Curtis values generated through bootstrapping of the original data (through 10,000 simulations). By comparing the observed values of dissimilarity to the population of expected values, we could then determine whether the level of dissimilarity we observed was more or less than expected due to chance.

We analyzed the dynamics of alarm calling by measuring two response variables: by calculating the proportion of predator trials in which different sentinels produced alarm calls and by calculating the number of urgent notes that alarm calling birds produced during alarm calls. Alarm calls that convey predation threat vary in length and are composed of several variants of a single note type which we define as "urgent notes" (Munn 1986, Templeton et al. 2005, Martínez and Zenil 2012, Fig. 1). We modeled these responses by fitting the data to Generalized Linear Mixed Models (GLMM) where we used predator type, the type of sentinel (alarm-calling bird) and the minimum distance to the predator as fixed effects and individual flock as a random effect. In the first case we modeled the proportion of predator flights that elicited alarm calls using a binomial probability distribution and in the case of number of urgent notes we modeled the data using a Poisson probability distribution. We checked for overdispersion in the Poisson model, and we checked the goodness of fit of both models by evaluating plots of residuals of GLMMs (Dunn and Smyth 1996, Hartig 2017). We used an information theoretic approach, using Akaike's Information Criterion (AIC), where we identify a candidate set of models that are most likely to describe the observed data (Burnham and Anderson 2004). In identifying these

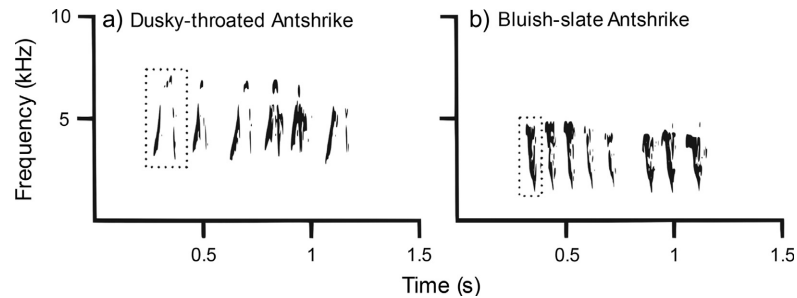


FIG. 1. Spectrograms of alarm calling birds, (a) Dusky-throated Antshrike and (b) Bluish-slate Antshrike, composed of individual urgent notes (highlighted in boxes).

models, we select the candidate set of models guided by the criteria of choosing models with a delta AIC of <8 compared to the best model (Burnham et al. 2011).

To evaluate differences in canopy cover and canopy height we fitted a GLMM and a Linear Mixed Model respectively, using flock type as a fixed effect and each individual flock as a random effect in each case. For canopy cover we fit a model using a binomial distribution and for canopy height we fit a model using a Gaussian distribution which we checked for violations of assumptions of normality. We conducted likelihood ratio tests to compare the fits of models for canopy cover and canopy height against null models.

All data analyses were conducted in R version 3.3.2 (R Core Team 2016). We used the lme4 package (lmer and glmer), for fitting generalized linear models, the vegan package for community-wide analyses, and DHARMA for evaluating goodness of fit for GLMM models.

RESULTS

We estimated home range sizes for the 16 flocks used in our study with 90% KDEs (Fig. 2). We compared the two flock communities using a Bray-Curtis analysis and found an observed dissimilarity index that was low

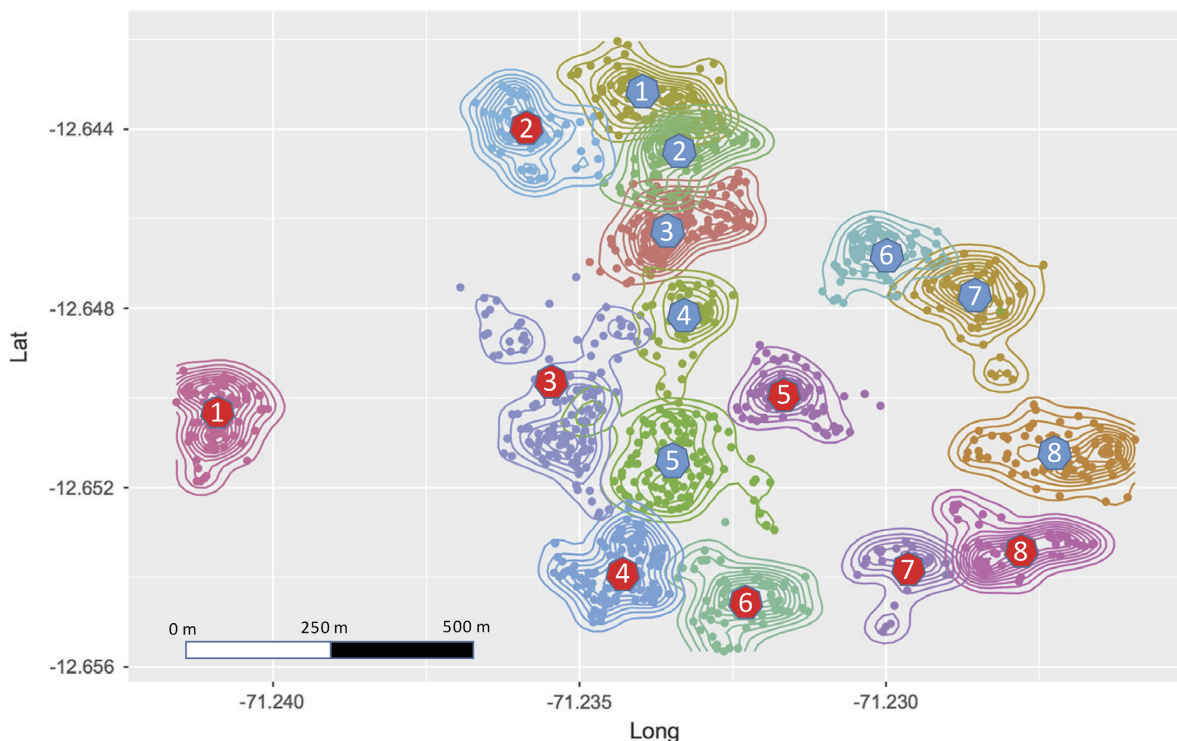


FIG. 2. Home ranges of eight different flocks in the Pantiacolla field site that are led by either Bluish-slate Antshrike (red numbers, $n = 8$) or Dusky-throated Antshrike (blue numbers, $n = 8$). Each color represents an individual flock territory.

(0.36), suggesting that these two flock communities are very similar ($P < 0.0001$) when compared to a population of expected dissimilarity indices generated by bootstrapping the data (10,000 simulations). Except for the mutually exclusive presence of the two alarm calling species, the flock composition amongst these two flock types is nearly identical (Fig. 3).

We found that the type of alarm calling bird, the type of predator and distance to closest alarm calling were all important in explaining variation in the probability of alarm call production as they were components of the best model, and each variable was important in two of the three best candidate models (Table 1). The Bluish-slate Antshrike was much more likely to alarm call than the Dusky-throated Antshrike (Table 1, Fig. 4a, b). Smaller predators (*A. bicolor* and *F. femoralis*), were much more likely to generate alarm calls than *P. ubucinctus* (Table 1b, Fig. 4a, b). In addition, alarm calling birds were much more likely to produce alarms as predators flew closer (Fig. 4a, b).

In terms of alarm urgency, our set of candidate models suggested that all three variables (raptor proximity, size, and species) were likely to explain the patterns in our observed data even though the best model included only raptor type: (Table 2). We show all three variables simultaneously in the model predictions (Fig. 5a, b). Our results suggest that the Bluish-slate Antshrike produced more urgent notes than the Dusky-throated Antshrike, and in both sentinel species, smaller raptors elicited more urgent notes than larger raptors (Fig. 5a, b). The effects of distance to the alarm calling bird was less important in determining the number of urgent notes elicited.

Our results suggest no variation in canopy cover but large differences in forest height between the two flock types. Vegetation cover of the forest showed no differences within home-ranges of the two flock types (LRT_{canopy cover:null model}, $X^2 = 0.2$, $df = 1$, $P = 0.7$; mean \pm standard error [SE] percent canopy cover for Dusky-throated and Bluish-slate Antshrike flocks = $76.3 \pm 1.2\%$ and $77.0 \pm 1.1\%$ respectively, $n = 160$ per

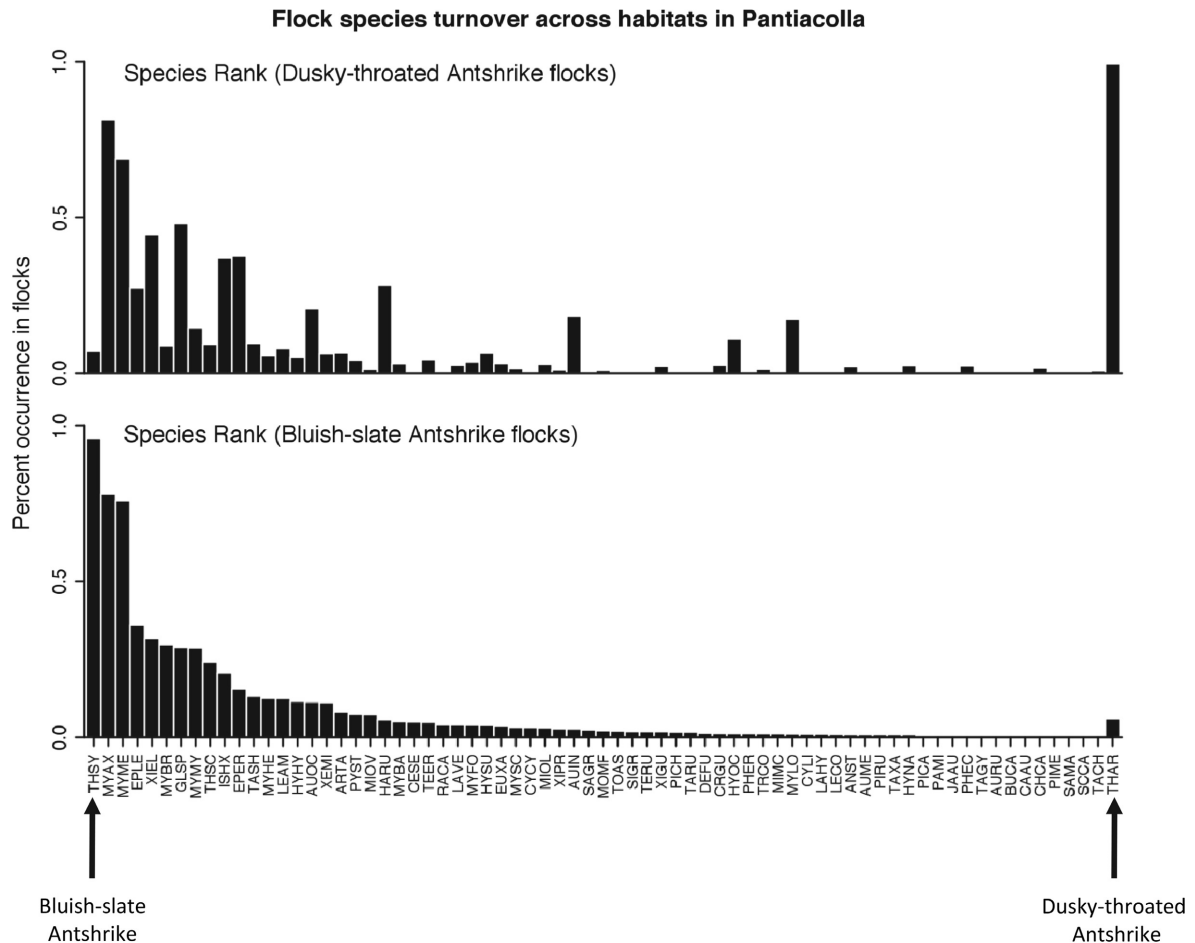


Fig. 3. Flock species composition according to sentinel type present in flock. Mean percent flocking occurrence for each species across flocks led by Dusky-throated Antshrike ($n = 8$), and Bluish-slate Antshrike ($n = 8$). Flocking occurrence was based on the presence/absence of a species in flock based on half hour census intervals. In total flocks were followed from 4 to 20 h each. Full species names corresponding to codes are found in Appendix S1: Table S1.

TABLE 1. Evaluation of the effects of alarm caller and predation context on predator detection.

Model	Model terms	<i>k</i>	logLik	AICc	ΔAICc	ω_i	Deviance	Marginal R^2	Conditional R^2
1	Raptor + Flock Sentinel + Distance	7	−107.5	229.7	0.0	0.8	215.1	0.34	0.37
2	Raptor + Flock Sentinel	6	−110.6	233.7	4.1	0.1	221.3	0.27	0.38
3	Distance + Raptor	6	−111.1	234.6	5.0	0.1	222.2	0.30	0.34
4	Raptor	5	−114.0	238.3	8.6	0.0	228.0	0.24	0.35
5	Flock Sentinel + Distance	4	−123.9	255.9	26.3	0.0	247.7	0.11	0.12
6	Flock Sentinel	3	−127.0	260.1	30.4	0.0	254.0	0.04	0.13
7	Distance	3	−128.1	262.4	32.8	0.0	256.3	0.07	0.08
8	Null Model	2	−130.9	265.9	36.3	0.0	261.9	0.00	0.09

Notes: Model selection results of Generalized Linear Mixed Models on the effects of alarm caller type, predator type (species/body size) and distance from alarm caller on the probability of generating an alarm call using a binomial probability distribution. Individual flock was used as a random effect. We report conservative AIC estimates (AICc) due to small sample sizes.

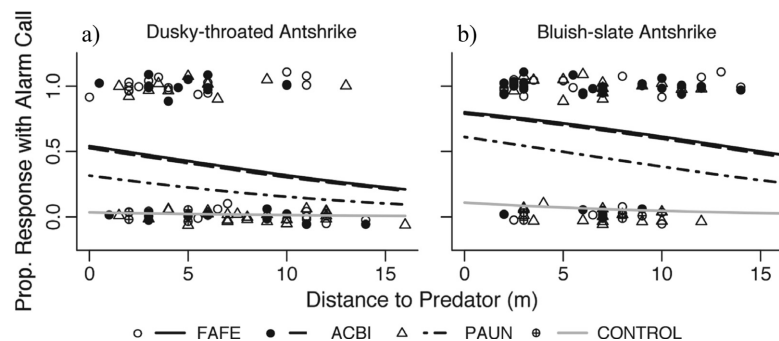


FIG. 4. Probability of alarm calling in the presence of predators. Results of model predictions from the best candidate model using Generalized Linear Mixed Models with a binomial distribution for (a) Dusky-throated Antshrike, and (b) Bluish-slate Antshrike, to different predator types and different distances ($n = 192$ trials in total). Values were back-transformed, and even though the response was recorded as binary, data is plotted with a small offset for clarity. Prop. Response with Alarm Call = probability of responding with an alarm call (proportion of positive responses), points shown are individual predicted values and lines are based on predicted mean values. ACBI = *Accipiter bicolor* (Small Predator), FAFE = *Falco femoralis* (Small Predator), PAUN = *Parabuteo ubucinctus* (Large Predator), and Control = Stick.

TABLE 2. Evaluation of the influence of alarm caller and predation context on length of alarm calls.

Model	Model terms	<i>k</i>	logLik	AICc	ΔAICc	ω_i	Deviance	Marginal R^2	Conditional R^2
1	Raptor	5	−219.4	449.5	0	0.5	438.9	0.20	0.25
2	Raptor + Sentinel Type	6	−219.3	451.4	1.9	0.2	438.5	0.21	0.24
3	Raptor + Distance	6	−219.4	451.7	2.2	0.2	438.8	0.20	0.25
4	Raptor + Sentinel Type + Distance	7	−219.2	453.6	4.1	0.1	438.4	0.21	0.24
5	Null Model	2	−228.6	461.4	11.9	0.0	457.3	0.00	0.07
6	Sentinel Type	3	−228.1	462.5	13.0	0.0	456.3	0.02	0.06
7	Distance	3	−228.6	463.5	14.0	0.0	457.3	0.00	0.08
8	Sentinel Type + Distance	4	−228.1	464.6	15.1	0.0	456.2	0.02	0.06

Notes: Model selection results of Generalized Linear Mixed Models on the effects of Alarm Caller Type, Predator Type (Species/Body Size) and Distance from Alarm Caller on the number of urgent notes elicited in alarm responses using a Poisson probability distribution. Individual flock is used as a random effect. We report conservative AIC estimates (AICc) due to small sample sizes.

flock type, Table 3). In contrast vegetation height showed very large differences between the forests occupied between the two flock types (LRT_{height model:null model}, $\chi^2 = 27.8$, $df = 1$, $P < 0.0001$; mean forest height ± 1 SE for Dusky-throated and Bluish-slate Antshrike flocks = 22.1 ± 0.6 and 14.4 ± 0.6 , $n = 160$ per flock type, Table 3).

DISCUSSION

Our results show that sentinel species vary in the probability of producing alarm calls to aerial predator threats. These alarm calling birds, are mutually exclusive in relation to habitat use, and thus influence the degree of habitat riskiness for a group of commonly shared

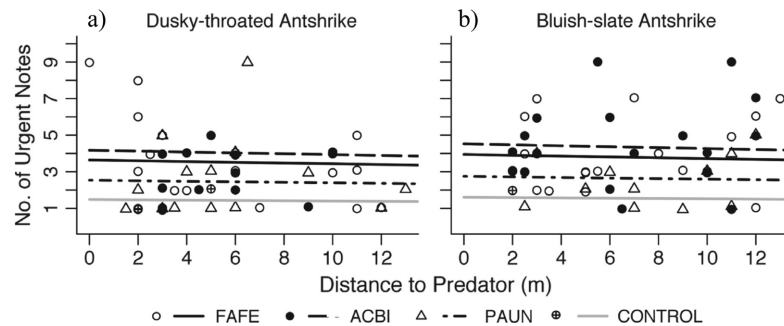


FIG. 5. Differential responses of alarm birds to different predator contexts. Results of model predictions from the best candidate model that includes sentinel type, raptor size, and distance to alarm calling bird, using Generalized Linear Mixed Models with a Poisson distribution, for responses of (a) Dusky-throated Antshrike and (b) Bluish-slate Antshrike to different predator types and different distances ($n = 101$ trials total). Values were back-transformed, and data points are plotted with small offset for clarity. Response = Number of urgent notes produced by a sentinel bird in a trial, points shown are individual predicted values and lines are based on predicted mean values. ACBI = *Accipiter bicolor* (Small Predator), FAFE = *Falco femoralis* (Small Predator), PAUN = *Parabuteo unicinctus* (Large Predator) and Control = Stick.

TABLE 3. Evaluation of canopy heights used by different sentinel birds.

Model	β	95% CI	df	Marginal R^2	Conditional R^2
(a) Canopy cover				0.01	0.01
Intercept	1.18	(1.0, 1.3)	1,319		
Sentinel type	0.04	(-0.2, 0.2)	2,318		
(b) Canopy height				0.24	0.26
Intercept	22.1	(20.8, 23.5)	1,319		
Sentinel type	-7.71	(-9.6, -5.8)	2,318		

Notes: Model results using a Generalized Linear Mixed Model and Linear Mixed Models respectively to evaluate a) canopy cover and b) forest heights used by flocks led by either Dusky-throated or Bluish-slate Antshrikes. Model estimates for the single predictor variable, Flock Type as a fixed effect and individual flock as a random effect. The model for canopy cover was fitted using a binomial distribution while the model for canopy height was fitted using a Gaussian distribution. df = numerator degrees of freedom (based on fixed effects), and residual degrees of freedom, respectively.

eavesdropping species found across habitats. The Bluish-slate Antshrike, which is found in younger patches of lower-canopy forest, had a higher probability of producing alarm calls to predators. While our study does not distinguish between sentinel quality and habitat in affecting vigilance, earlier studies have confirmed that the Bluish-slate Antshrike is the more prominent alarm caller where they co-occur in flocks (Munn and Terborgh 1979, Munn 1986, Jullien and Thiollay 1998), suggesting interspecific variation in vigilance. We also found that sentinels provided context on predator size and distance in their alarms. For example, both sentinels increased the number of urgent notes used in alarms when predators were closer to the flock and to smaller aerial predators compared to larger ones.

We found that rate of alarm call production was influenced by predator body size with more overall alarms with smaller predators. We also found that the quality of the alarm, number of urgent notes, was influenced by predator body size, where smaller predators elicited more urgent notes from sentinels. These results are consistent with previous work that showed that predator size influenced evaluation of predation risk (Templeton et al. 2005, Preisser and Orrock 2012). Our results also

provide evidence supporting the hypothesis that information on the magnitude of threat may be encoded in alarm signals (Leavesley and Magrath 2005, Sieving et al. 2010). The ability of associate species (in the flock) to interpret encoded information from sentinels about predators has been well established in temperate systems (Hetrick and Sieving 2012, Magrath et al. 2014), but has not been well described in the neo-tropics. In Amazonian tropical forests, ant-shrike alarms are used by a large assemblage of species, up to 70 species, that consistently eavesdrop and rely on them for vigilance (Munn 1986, Martínez et al. 2016). We recognize that the raptors we use may differ in other aspects and not only in size (taxonomic group, plumage pattern, silhouette, flight pattern, etc.) and that this may have influenced our results, and thus we exercise caution in the interpretation of our findings.

Bluish-slate and Dusky-throated Antshrikes (the alarm calling birds) are mutually exclusive, but their flocks are made up of the same generalist species (Fig. 3). The variation in predator alarm production and predator information encoded in the alarms of these sentinels suggests that information quality may vary by habitat. There are numerous examples of how variation

in the “information landscape” influences animal decision making. For example, migrating birds have been shown to use resident species to gather information about the environment for decisions on where to nest (Thomson et al. 2003, Forsman et al. 2007). Assessments of predation risk can affect movement decisions (Turcotte and Desrochers 2003), foraging decisions (Gil et al. 2017) the tendency for animals to remain in groups (Rodríguez et al. 2001), and can ultimately influence reproductive success and overall fitness (McNamara and Dall 2010, Zanette et al. 2011). Eavesdropping species change foraging habitat to riskier areas when a sentinel species is detected, presumably affecting overall foraging strategy and fitness of the eavesdropping species (Ridley et al. 2014).

Earlier studies suggest that early successional stage habitats occupied by Bluish-slate Antshrikes are likely to be more productive (Robinson and Terborgh 1995). Thus in these habitats, eavesdropping species would receive greater benefits in terms of foraging resources, and would receive greater predator vigilance. In fact, we found that sentinel species in these areas did provide more alarm calls in the presence of predators. There may also be added benefits to species who occupy habitats with sentinels who provide lower predator vigilance, such as availability of nesting sites, that may counterweigh the benefits of occupying riskier habitats (Morris and Davidson 2000). Differences in sentinel alarm-calling may also generate source-sinks for associate species. Eavesdropping species from high quality sentinel areas may produce more offspring and help colonize lower fitness areas with low quality sentinels. This could indicate a fitness landscape in part defined by information “rich” vs. information “poor” habitats.

One limitation of our study is that we do not measure response of other flock members to different quality alarm calls, but data from a subsequent experiment suggests that there are differences in the value associated with the alarm calls of these species: eavesdropping species respond more to the alarm calls of the Bluish-slate Antshrike, regardless of the sentinel with which they normally associate. Additionally, while we focus on two common sentinel species, there are other alarm calling birds in tropical lowland rainforests, and they may also contribute to predator vigilance (Magrath et al. 2007). The landscape of fear has been defined as a means of quantifying a species perceived risk of predation in order to predict how individuals are distributed throughout the landscape (Willems and Hill 2009, Coleman and Hill 2014). Sentinels with different levels of vigilance and alarm call complexity (encoded information about predators) can generate peaks and valleys in the landscape of fear and may be a significant component in shaping the fitness landscape of animal species.

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LITERATURE CITED

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