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Fear-based niche shifts in neotropical birds

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Abstract. Predation is a strong ecological force that shapes animal communities through natural selection. Recent studies have shown the cascading effects of predation risk on ecosystems through changes in prey behavior. Minimizing predation risk may explain why multiple prey species associate together in space and time. For example, mixed-species flocks that have been widely documented from forest systems, often include birds that eavesdrop on sentinel species (alarm calling heterospecifics). Sentinel species may be pivotal in (1) allowing flocking species to forage in open areas within forests that otherwise incur high predation risk, and (2) influencing flock occurrence (the amount of time species spend with a flock). To test this, we conducted a short-term removal experiment in an Amazonian lowland rainforest to test whether flock habitat use and flock occurrence was influenced by sentinel presence. Antshrikes (genus *Thamnomanes*) act as sentinels in Amazonian mixed-species flocks by providing alarm calls widely used by other flock members. The alarm calls provide threat information about ambush predators such as hawks and falcons which attack in flight. We quantified home range behavior, the forest vegetation profile used by flocks, and the proportion occurrence of other flocking species, both before and after removal of antshrikes from flocks. We found that when sentinel species were removed, (1) flock members shifted habitat use to lower risk habitats with greater vegetation cover, and (2) species flock occurrence decreased. We conclude that eavesdropping on sentinel species may allow other species to expand their realized niche by allowing them to safely forage in high-risk habitats within the forest. In allowing species to use extended parts of the forest, sentinel species may influence overall biodiversity across a diverse landscape.

Key words: heterospecific eavesdropping; landscape of fear; mixed-species flocks; neotropical rainforest; niche-shift; predation-risk; realized niche; social information; species coexistence.

Introduction

The effect of predation on communities has been a central focus of ecology for over 100 years. Recent studies have shown the cascading effects of predation risk on ecosystems through changes in prey behavior (Lima and Dill 1990, Suraci et al. 2016, Breviglieri et al. 2017). At large spatial scales a *landscape of fear* (Laundré et al. 2010) is described when predation risk shifts the distribution of prey in the landscape changing dominant vegetation, as demonstrated in elk-wolf and ungulate-lion interactions (Laundré et al. 2001, Valeix et al. 2009). Even at smaller scales, significant change arises when predation risk is detected and acted upon. For example, vulnerable size classes of bluegill fish completely change habitat use to safer, more complex, habitat when predators are detected, leading to a variety of ecological changes (Werner et al. 1983, Werner and Hall 1988). Thus, behavioral responses of prey to predators can lead to changes in resource use in space and time, representing a shift in the realized niche of species (Seppänen et al. 2007).

Since predation is such a strong selective force, any advantages prey develop could significantly impact survival. For example, information concerning predator presence is vital, and eavesdropping on heterospecifics for such information can provide distinct advantages (Magrath et al. 2015). Eavesdropping works best in densely populated assemblages (Magrath et al. 2015), and there are many striking examples (e.g., between hornbills and monkeys, Rainey et al. 2004, drongos and babblers, Goodale and Kotagama 2005). Eavesdropping may provide ecological benefits that influence the realized niche of species (Odling-Smee et al. 1996, Harrison and Whitehouse 2011), increasing benefits of those that utilize it (Ridley et al. 2014, Schmitt et al. 2016). Theoretically, eavesdropping may allow expansion of niche space into high predator risk areas, for high gain, but at low cost (Bruno et al. 2003, He et al. 2013, Crotty and Bertness 2015). Building on these previous studies, we define the *fear-based niche shift hypothesis*: threat information produced by sentinel species about shared predators is used by less-vigilant species to increase their realized niche to include higher risk habitats.

Because mixed-species flocks of birds live in close contact with each other in communities where predation risk is high, they are ideal for testing this hypothesis (Goodale et al. 2010). In the Amazon, mixed-species flocks contain stable territories over generations (Martínez and Gomez 2013), and comprise species that occupy different foraging ecologies, suggesting that flocking is not the result of foraging benefits in which species help each other locate food patches (Martinez and Robinson 2016). The flocks mostly consist of 5–8 species, and are hypothesized to be assembled around 1–2 alarm-calling species (genus *Thamnomanes*) which produce predator risk information, primarily related to ambush raptors in the genera *Micrastur* and *Accipter* that is used by the entire flock (Munn 1986, Thiollay and Jullien 1998, Schulenberg et al. 2010). The availability of this information related to predation risk presumably enables heterospecifics

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to safely exploit riskier habitats (Powell 1989, Thiollay and Jullien 1998).

We conducted a direct experimental test of the *fear-based niche shift hypothesis*, and tested whether the presence of the alarm-calling species (*Thamnomanes ardesiacus*) influenced the realized niche of the flock by enabling other flocking species to utilize open (riskier) habitats. We predicted that in the absence of the alarm-calling species, the flock would shift territory use to areas of lower predation risk (denser vegetation cover), and that the remaining flock members would reduce flock occurrence due to a loss of benefits gained from heterospecific vigilance.

Methods

Our objective was to measure the influence of an alarm-calling flocking bird (hereafter referred to as "sentinel") on the realized niche of other species in the flock. We conducted an experiment in which we temporarily removed the alarm calling species and measured the response of other flocking species, by determining (1) whether they shifted in their home range behavior, (2) whether changes in home range behavior reflected changes in vegetation cover at different forest heights and (3) whether the proportion of time species remained in the flock decreased (flock occurrence).

Study site

Our experiment was conducted in tropical lowland forest in southeastern Peru, adjacent to Manu National Park, at Pantiacolla Lodge (Appendix S1: Fig. S1, Latitude 12°39′36″ Longitude 71°13′93″) from June 23rd to August 28th 2014. The study site sits on the north bank of the Rio Alto Madre de Dios, and consists of a combination of mature tierra firme and transitional forests (that share characteristics of both seasonally inundated and tierra firme forests) with patches of bamboo. Flocks used in our experiment were located on upland tierra firme mature forest.

We identified eight flocks and randomly assigned each flock to serve as a control or removal. Many of the birds from these flocks were previously banded in 2013. We surveyed flocks using the methodology described in, Martínez and Gomez (2013), in which we conducted censuses of the presence of all species in the flock at half hour intervals to derive a percent occurrence for each species in the flock. To accomplish this, flocks were censused by teams of two observers from dawn to dusk over 3 d prior to, and 3 d following, the manipulation. In groups designated as removals we removed the members of the target species. In groups designated as controls, we captured and released the target species to simulate handling effects. Two groups of observers simultaneously observed a separate flock each, which were randomly assigned as either removal or control treatments. In this study, we focus on the core species that are permanently associated with these flocks and to which individuals show a high degree of flock fidelity (Munn and Terborgh 1979, Jullien and Thiollay 1998). To measure responses of the flock, we focused observations on *Myrmotherula axillaris* because this species is the most consistent and visible flocking species at our site and throughout southwestern Amazonia. We used the locations of this species to define the centroid for the whole flock. This approach has been used to characterize flock location in past studies (Munn 1985, Mokross et al. 2014, Martinez et al. 2017).

The core group species share a year round roosting site from which the flock leaves every morning to begin actively foraging throughout its home range (Martínez and Gomez 2013).

To capture and remove the pair or family group of *T. ardesiacus*, we set up four to six mist nets at roosting sites, and used playbacks of *T. ardesiacus* to attract them toward the nets. Concurrently, the same procedure was conducted at control flocks, in order to control for the level of disturbance, with the main difference being that once the *T. ardesiacus* were all captured, they were released after netting was complete. The *T. ardesiacus* removed from flocks were held in small aviaries with natural vegetation and fed orthopterans for three days, at which point they were released back into their territories. In three of four removals, floater *T. ardesiacus* appeared within 24–48 h. To prevent them from joining the flock, we used territorial song playbacks which had the effect of driving these floaters away shortly after playback was used. These territorial playbacks were also played at control flocks.

To quantify the location of the flock, a third observer used a GPS device every 10 min to record the center of the flock as defined by *M. axillaris*. At each of these points, the observer also used a range finder to measure canopy height, and visually estimated overall vegetation presence or absence and vine presence or absence at a range of height intervals at the location of the flock (MacArthur and Horn 1969, Sridhar and Sankar 2008). The same observers used to estimate flock location estimated vegetation presence or absence at different height intervals (as in Sridhar and Sankar 2008); and these observers were trained, and field-tested in estimating vegetation height using a handheld rangefinder. The training consisted of intense day-long training and testing for 1 week prior to the study. Vegetation height intervals were 0–1, 1.1–2, 2.1–4, 4.1–8, 8.1–16, 16.1–32, 32+ m. We used doubling height classes (e.g., 1–2, 2–4, 4–8 m) since visual height estimation becomes more imprecise with increasing distance from the observer.

We used Kernel Density Estimation (KDE) to derive Utilization Densities (UD) which are probabilistic models that describe the relative amount of time that an animal spends in any place and as such effectively describes an animal's home range (Worton 1989, Seaman and Powell 1996). KDE is a standard technique used in many studies that describe animal space use patterns. The kernel estimation is essentially a probability density function that describes the probability of how often an animal uses that particular space. The use of KDEs provides an unbiased home range estimator with high biological relevance, particularly for addressing flocks with multiple centers of activity and unknown levels of animal-habitat relationships (Börger et al. 2006). We account for any potential autocorrelation in GPS points by using a smoothed cross-validation bandwidth selector, from the Hscv function in the ks package in R (Duong 2007; Duong 2016). To account for the tradeoff of variance and bias in density surfaces, we compared isopleth estimations at 10%

intervals for each flock. Thus, we used 90% KDE in order to maximize sampling observations used to estimate space use patterns of each flock while minimizing the use of extreme outliers that may generate bias (Börger et al. 2006). We used 90% KDEs to generate UDs before and after removal events for both types of flocks (removal and control). For all flocks we used pre-manipulation data to estimate home range size. We dropped one of our control flocks from the analysis because we had poor spatial sampling due to logistical difficulties.

We compared UDs of pre-manipulation vs. post-manipulation flock use, to determine the proportion of area overlap. Once a proportion of overlap was obtained for each flock, we evaluated if variation in the proportion of overlap in home range movements was explained by the removal of the sentinel species using a beta regression. The beta regression is effective for evaluating cases in which the response variable is continuous and bounded by 0 and 1 as in the case of modeling proportions (Ferrari and Cribari-Neto 2004). Simulations have shown that this statistical approach is robust in providing parameter estimates and model predictions in scenarios with challenging data structures such as low samples sizes or binary predictors with few events (Ogundimu and Collins 2017). The modeling procedures used in a beta regression are similar to those used for generalized linear models and draws inference through maximum likelihood for parameter estimation. In using maximum likelihood approach the mean of the beta distribution is modeled as a linear combination of the independent variables. We subsequently compared a goodness of fit by conducting a likelihood ratio test. We compared our model to a null model, using the mean overlap amongst all flocks without the treatment effect of removal.

We used generalized linear mixed models (GLMMs) to determine whether removal of the alarm calling species affected (1) the degree of vegetation cover used by flocks, and (2) the percent of time species were found in flocks (species flocking occurrence). Vegetation cover was quantified as the presence/absence at different heights for each time interval. We modeled vegetation cover using a binomial distribution in which sentinel removal, trial stage (pre vs. post), and height interval were treated as categorical fixed effects. Individual flock was treated as a random effect. Similarly, because we quantified the presence and absence of species in each flock during multiple time intervals, we used a binomial distribution to model the presence or absence of species in a flock. In the species occurrence model, we treated sentinel removal, trial stage, and species, as categorical fixed effects to evaluate overall occurrence within the flock. In each analyses we used Likelihood Ratio Tests to compare the full model to the null model. We also derive marginal R^2 (proportion of variance explained by the fixed effect) and the conditional R^2 (proportion of variance explained by both fixed and random effects) values (Nakagawa and Schielzeth 2013) for the fitted models, and parameter estimates, and 95% confidence intervals for model terms using restricted maximum likelihood. All GLMMs were conducted using the glmer function in the lme4 package in R. Data analyses were conducted in R version 3.3.2 (R Core Team 2016).

RESULTS

Space use

We analyzed home range sizes of removal and control flocks (n = 7, $\bar{x}$ [SE] 2.76 ha [0.29]), before and after manipulation and found distinct shifts in home range use (territory) in removal flocks (experimental flocks had lower overlap between pre vs. post manipulation while control

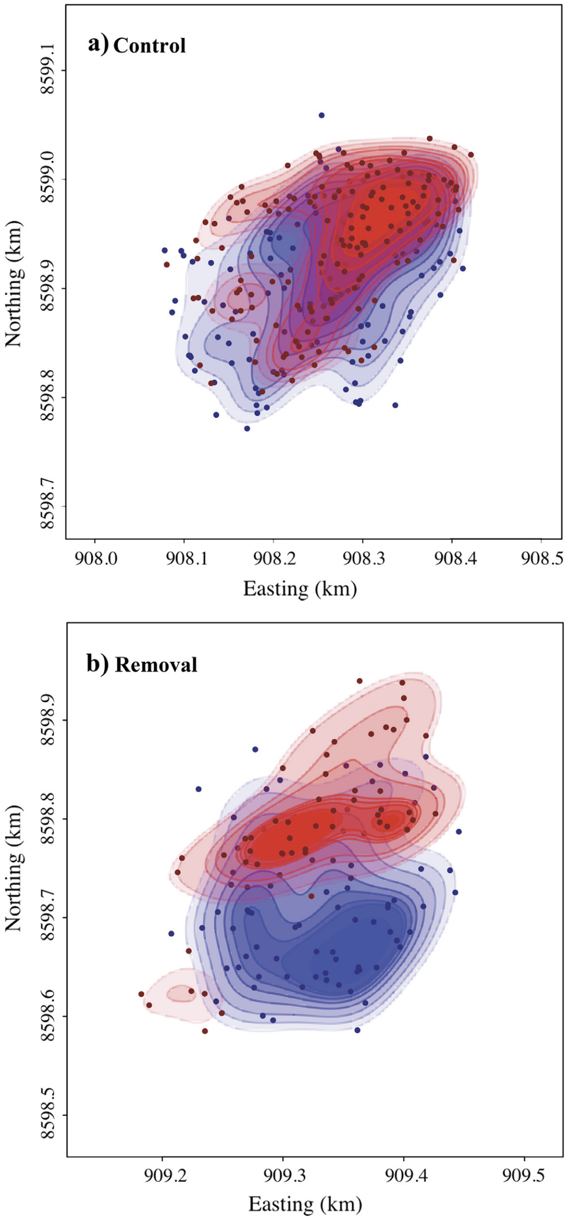

Fig. 1. Home range behavior between flocks with and without removal of sentinel species. A comparison of changes in home range behavior between a control and removal flock, respectively. The home ranges are based on 90% Kernel density estimation derived from mapping points after following flocks three days during the pre trial (red) and post trial (blue). The figures show the patterns for (a) a control flock in which *T. ardesiacus* was not removed from the flock. (b) A removal flock in which *T. ardesiacus*, an alarm calling bird was removed in the post trial. See Appendix S1 for the home range behavior of all control and removal flocks.

TABLE 1. The effect of removal of sentinels on vegetation cover used by flocks.

	k	logLik	Deviance	χ^2	df	P value	Marginal R^2	Conditional R^2	β	95% CI	
(a) Model description											
Null	2	−845	1689.9			–	–	–			
Treatment × Trial Stage × Height Interval	29	−372.5	744.9	945	27	<0.0001	0.14	0.14			
(b) Model terms†											
(Intercept)					1,83				−0.13	−0.27	0.01
Treatment					2,83				0.05	−0.17	0.26
Trial Stage					2,83				0.02	−0.19	0.23
Height Interval					7,83						
Height Interval (1–2 m)									0.18	−0.39	0.02
Height Interval (2–4 m)									0.19	−0.39	0.02
Height Interval (4–8 m)									0.13	−0.33	0.07
Height Interval (8–16 m)									0.19	−0.39	0.02
Height Interval (16–32 m)									0.17	−0.38	0.03
Height Interval (32 m+)									1.87	−2.18	1.56
Treatment × Trial Stage									0.14	−0.43	0.16
Treatment × Height Interval					20,83				0.01	−0.30	0.31
Treatment : Height Interval (1–2 m)									0.02	−0.28	0.33
Treatment : Height Interval (2–4 m)									0.08	−0.38	0.23
Treatment : Height Interval (4–8 m)									0.08	−0.38	0.23
Treatment : Height Interval (8–16 m)									0.10	−0.41	0.21
Treatment : Height Interval (16–32 m)									0.42	−0.93	0.10
Treatment : Height Interval (32 m+)									0.01	−0.30	0.31
Trial Stage × Height Interval					20,83						
Trial Stage : Height Interval (1–2 m)									0.10	−0.21	0.40
Trial Stage : Height Interval (2–4 m)									0.09	−0.21	0.40
Trial Stage : Height Interval (4–8 m)									0.04	−0.27	0.34
Trial Stage : Height Interval (8–16 m)									0.06	−0.25	0.36
Trial Stage : Height Interval (16–32 m)									0.19	−0.50	0.12
Trial Stage : Height Interval (32 m+)									0.58	−1.12	0.05
Treatment × Trial Stage × Height Interval					34,83						
Treatment : Trial Stage : Height Interval (1–2 m)									0.07	−0.49	0.36
Treatment : Trial Stage : Height Interval (2–4 m)									0.04	−0.46	0.39
Treatment : Trial Stage : Height Interval (4–8 m)									0.04	−0.38	0.47
Treatment : Trial Stage : Height Interval (8–16 m)									0.09	−0.34	0.52
Treatment : Trial Stage : Height Interval (16–32 m)									0.32	−0.12	0.75
Treatment : Trial Stage : Height Interval (32 m+)									0.65	−0.11	1.40

Notes: Results of analyses of generalized linear mixed effects models with a binomial error distribution to evaluate the change in structure of forest cover used by the flock after removal of *T. ardesicacus*. In (a) a likelihood ratio test (LRT) to evaluate the model with best fit includes flock type as a random effect. k: number of parameters in the model; logLik: refers to the maximum log likelihood estimate; deviance: absolute deviance; χ^2: Chi-square value from likelihood ratio test; P value: significance level of LRT; Marginal R^2: variation in model accounted for by fixed effects; Conditional R^2: variation in model incorporating both fixed and random effects. In (b) parameter estimates (β) and 95% confidence Intervals (CI) for the fitted model. df: numerator and denominator degrees of freedom.

†Descriptions of models refer to fixed effects only.

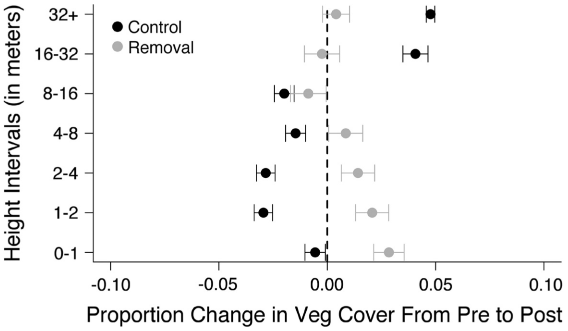

FIG. 2. Change in vegetation cover in forest used by mixed species flocks with and without removal of sentinel species. The effects of generalized linear mixed models with a binomial error distribution to evaluate change in vegetation cover as a function of the presence of a sentinel flock species. At 10-min intervals the location of the flock was recorded and the presence of vegetation cover at different heights of the forest was measured in that location. In the model, we used the interaction of height interval (categorical variable), with treatment and either pre or post observation period as fixed effects. We show back-transformed predicted means and 95% confidence intervals are plotted to show either a net increase or decrease in vegetation cover at each height interval from pre to post manipulation periods. Estimates are based on the fixed effects of the fitted model (Table 1b). Values less than zero indicate a decrease in vegetation cover (more open areas) whereas estimates above zero indicate an increase in vegetation cover (denser areas) corresponding to that height within the forest. Data is based on n = 4 for control and removal groups, respectively.

flocks had much greater overlap pre vs. post manipulation; average home range overlap between pre and post treatment and ±95% Wald type confidence interval [CI], Control = 0.69 ± [0.37, 0.90] vs. Removal 0.08 ± [0.02, 0.28], df = 3, pseudo R^2 = 0.61, Likelihood Ratio Test$_{\text{alt model/null model}}$: χ^2 = 6.03, P = 0.011, between our model and the null, see Fig. 1 for an example of a control and a removal and Appendix S1 for results from all flocks).

The differences in vegetation cover for different forest strata suggest that flocks use different parts of the forest once sentinel birds are removed. Our model for overall vegetation cover suggests an interaction between vegetation cover at specific height intervals and the effect of removal (Table 1a, Fig. 2). The largest change in vegetation cover varied between control and removal flocks at lower height intervals: vegetation cover in parts of the forest used by removal flocks was denser at lower forest heights and more open for control flocks (Table 1b, Fig. 2).

Changes in flock occurrence

Flocking species showed lower flock occurrence after sentinel removal although the effect varied between species (Table 2a,b, Fig. 3). The removal of *T. ardesiacus* resulted in lower flocking occurrence of almost all of the highly attendant flocking species commonly found in these flocks in the absence of *T. ardesiacus*, while the control flocks did not show this pattern (Table 2b, Fig. 3).

DISCUSSION

Our results provide direct experimental evidence in support of the hypothesis that sentinels are central to the formation of stable multi-species flocks of birds. We suggest that association with alarm-calling birds may allow niche expansion of less-vigilant flocking species into riskier habitats. Previous studies have consistently hypothesized that mixed-species bird flocks in tropical forests form as a response to predation pressure (Thiollay and Jullien 1998), but have provided few experimental data in support of the hypothesis that such formations provide differential use of habitats (Alatalo et al. 1985).

In stable multi-species Amazonian bird flocks, predation pressure influences habitat selection; species typically freeze or move to densely vegetated areas when threatened (Martínez et al. 2016). Predation risk may be minimized by predator detection by sentinel species (e.g., antshrikes in genus *Thamnomanes).* These key species are always present in stable multi-species flocks, presumably because they produce specific vocal alarm-calls when predators are present (Munn and Terborgh 1979, Martínez et al. 2016). As we predicted, when the alarm-calling species were removed we found that other flock species shifted habitat use to presumably safer areas with higher vegetation cover and with a higher presence of vines compared to control flocks. Due to logistical and design constraints, we could not test singular removal of alternate species, regardless, our data show that disruption through loss of a core species can potentially influence the realized niche of remaining species. In other multi-species flock systems, species that lose sentinels increase their vigilance in the absence of more vigilant heterospecifics (Sullivan 1984, Dolby and Grubb 2000), and show nutritional stress (Dolby and Grubb 1998, 1999). South African Scimitarbills decreased vigilance by up to 60% and foraged in different habitats in the presence of babblers, who are known for producing predator warning alarms (Ridley et al. 2014). In addition, several studies have shown that the presence of sentinel species, Tufted-Titmice and Carolina Chickadees, can influence space use and movement of associate flocking species (Dolby and Grubb 2000, Sieving et al. 2004, Tubelis et al. 2006). Unlike temperate feeding associations, the species represented in neotropical mixed-species flocks have likely adopted ecological roles dependent on the communication provided by heterospecifics and alarm calling sentinels (Martínez and Gomez 2013), to the extent that many species are obligate mixed-species flock associates (Munn and Terborgh 1979). Our study suggests that flocks use open sections of the forest less often (a realized niche-shift) when sentinels are removed.

It is worth noting that studies from other flock systems (including those led by congeners) suggest that sentinels also benefit from flocks and have been shown to manipulate followers (Munn 1986, Goodale and Kotagama 2006, Radford et al. 2011). Thus, in these systems, flock species may reciprocally make more open sections of the forest useful and beneficial to sentinel species (Odling-Smee et al. 1996). Throughout other parts of Amazonia, *T. schistogynus* is the predominant alarm calling bird in mixed-species flocking systems. Given the evidence that *T. schistogynus* is a more vigilant sentinel (Martinez et al. 2017), we suggest that its influence on the realized niche of other species is significant.

We also predicted a decrease in flock occurrence with the loss of sentinels and our results suggest a decrease in the

Table 2. The effect of sentinel removal on species occurrence.

	k	logLik	Deviance	χ^2	df	P value	Marginal R^2	Conditional R^2	β	95% CI	
(a) Model description											
Null	2	−488.9	977.7			–	–	–			
Treatment × Trial Stage × Species	33	−347.1	694.2	283.5	31	<0.0001	0.14	0.16			
(b) Model terms†											
(Intercept)					1,69				−0.61	−1.02	0.20
Treatment					2,69				−0.29	−0.89	0.31
Trial Stage					2,69				0.02	−0.38	0.42
Species					8,69						
EPER									0.24	−0.15	0.63
EPLE									−2.08	−3.14	1.02
GLSP									−0.49	−0.92	0.06
HYOC									−1.71	−2.38	1.05
MYLO									0.06	−0.35	0.47
MYME									0.35	−0.03	0.73
XIEL									0.08	−0.31	0.47
Treatment × Trial Stage					8,69				0.15	−0.44	0.73
Treatment × Species					26,69						
Treatment × EPER									−0.32	−0.94	0.30
Treatment × EPLE									1.69	0.47	2.90
Treatment × GLSP									−0.70	−1.43	0.02
Treatment × HYOC									1.23	0.35	2.11
Treatment × MYLO									−0.24	−0.96	0.48
Treatment × MYME									−0.04	−0.62	0.53
Treatment × XIEL									−0.99	−1.66	0.32
Trial Stage × Species					26,69						
Trial Stage × EPER									−0.77	−1.33	0.21
Trial Stage × EPLE									−1.53	−3.78	0.73
Trial Stage × GLSP									−0.09	−0.69	0.50
Trial Stage × HYOC									1.55	0.77	2.33
Trial Stage × MYLO									0.27	−0.28	0.82
Trial Stage × MYME									−0.19	−0.71	0.33
Trial Stage × XIEL									−0.03	−0.56	0.50
Treatment × Trial Stage × Species					44,69						
Treatment × Trial Stage × EPER									0.86	0.02	1.70
Treatment × Trial Stage × EPLE									2.68	0.30	5.06
Treatment × Trial Stage × GLSP									0.88	−0.04	1.81
Treatment × Trial Stage × HYOC									−1.34	−2.39	0.29
Treatment × Trial Stage × MYLO									0.40	−0.53	1.32
Treatment × Trial Stage × MYME									−0.10	−0.87	0.67
Treatment × Trial Stage × XIEL									0.66	−0.19	1.51

Notes: Results of generalized linear mixed effects models with a binomial error distribution to evaluate the effects of removal of *T. ardesiacus* on flock occurrence of other flocking species. In (a) a likelihood ratio test to evaluate model with best fit which includes flock type as a random effect. k: number of parameters in the model; logLik: refers to the maximum log likelihood estimate; deviance: absolute deviance; χ^2: Chi-square value from likelihood ratio test; P value: significance level of LRT; Marginal R^2: variation in model accounted for by fixed effects; Conditional R^2: variation in model incorporating both fixed and random effects. In (b) parameter estimates (β) and confidence intervals for the fitted model. df, numerator and denominator degrees of freedom and LRT specifies model comparisons. Where intercept, *C. carmioli*; EPER, *E. erythrura*; EPLE, *E. leucopthalma*; GLSP, *G. spirurus*; MYAX, *M. axillaris*; MYLO, *M. longipennis*; MYME, *M. menetriesii*; XIEL, *X. elegans*.

†Descriptions of models refer to fixed effects only.

amount of time that other highly social species remain in a flock. While all of these species are considered highly dependent on heterospecific vigilance because of their strategy of feeding on nearby substrates (and thus lack of awareness of ambush predators; Martínez et al. 2016), there was significant variation across species. We suggest that future studies

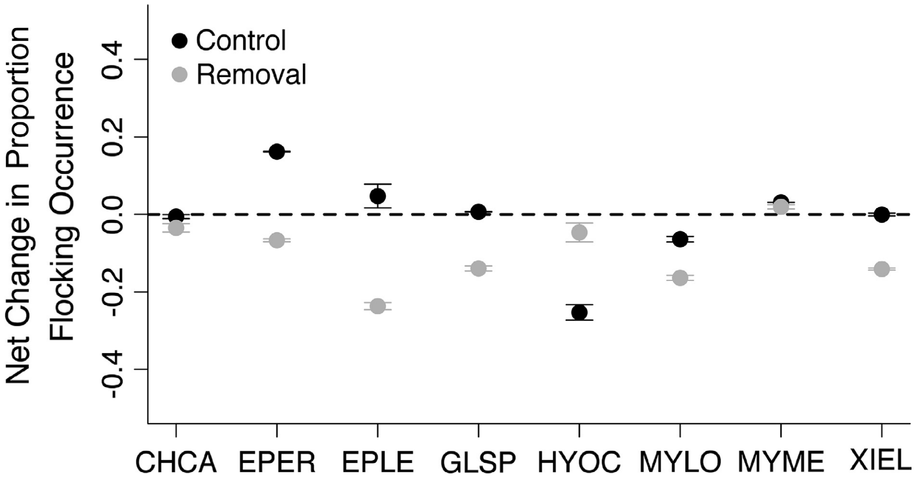

Fig. 3. Change in flock occurrence with and without removal of sentinel species. The effects of removal of the sentinel species on flock occurrence using generalized linear mixed models with a binomial error distribution. We show back-transformed predicted means and 95% confidence intervals which show the difference in the proportion flock occurrence from pre (before removal) to post (after removal) for each flocking species. *M. axillaris* is not shown because it is the reference species for the flock. The estimates indicate the net change in proportion occurrence within the flock from pre to post observation period. Estimates are based on fixed effects of the fitted model (Table 2b). Predicted means and confidence intervals in black = control flocks and grey = removal flocks. Sample sizes are for number of control flocks and removal flocks, respectively: *Chlorothraupis carmioli* (CHCA; *n* = 3, 4), *Epinecrophylla erythrura* (EPER; *n* = 4, 3), *Epinecrophylla leucophthalma* (EPLE; *n* = 2, 3), *Glyphorynchus sprirus* (GLSP; *n* = 4, 4), *Hylophilus ochraceiceps* (HYOC; *n* = 3, 3), *Myrmotherula longipennis* (MYLO; *n* = 3, 2), *Myrmotherula menetriesii* (*n* = 4, 4), *Xiphorhynchus elegans* (*n* = 4, 4).

explore additional functional traits that may explain this variation in reliance on heterospecifics. Our field observations suggest the effect varied by flock. For example, birds from some flocks stayed together as they all shifted to denser vegetation, while in one flock, individuals switched associations and attempted to join canopy flocks led by other sentinel species. The latter observation explains the apparent lack of change in home range behavior for one of the removal flocks (Appendix S1: Fig. S7). Overall, although flocking occurrence did decrease for most species, the flocks remained intact suggesting there are other benefits of staying in the flock even when the alarm calling species are removed. One possible benefit is the flock dilution effect in which safety in numbers results from a decrease in mortality as the number of the group increases (Hamilton 1971, Foster and Treherne 1981). Another possibility is that the remaining species also provide useful information about predators, or that multispecies flocking in general is evolutionarily conserved even in the absence of species that provide key information (Brumfield et al. 2007, Martínez et al. 2016).

The use of alarm-calls and other vocal cues within and between species may be important in the evolution and maintenance of the rich biological diversity we see in tropical bird assemblages. These interactions may provide social information about predators and, vigilant birds may enable other species to inhabit parts of the forest to promote coexistence among species that are both obligate and facultative members of flocks (Powell 1989, Parejo and Avilés 2016). Multi-species flocks in our study area alone include at least 65 bird species joining a single flock (Munn and Terborgh 1979). Additionally, flock territories are stable over multiple generations (Martínez and Gomez 2013), suggesting that they may provide long-term benefits for participating species at evolutionary scales (Odling-Smee et al. 1996, Harrison and Whitehouse 2011). Given that birds provide key ecosystem services (e.g., seed dispersal, controlling plant herbivory), disruption of these these flocks may have cascading effects not only throughout bird assemblages but ecosystems (Suraci et al. 2016, Breviglieri et al. 2017). Understanding how flocking species influence species coexistence in hyper-diverse tropical forests may provide insight into the conservation of remaining intact areas as well as recovery of sites subject to deforestation and degradation.

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Literature Cited

Alatalo, R. V., L. Gustafsson, M. Linden, and A. Lundberg. 1985. Interspecific competition and niche shifts in tits and the goldcrest: an experiment. Ecology 54:977–984.

Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. I. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393–1405.

Breviglieri, C. P. B., P. S. Oliveira, and G. Q. Romero. 2017. Fear mediates trophic cascades: non-consumptive effects of predators drive aquatic ecosystem function. American Naturalist 189. https://doi.org/10.1086/691262

Brumfield, R. T., J. G. Tello, Z. A. Cheviron, M. D. Carling, N. Crochet, and K. V. Rosenberg. 2007. Phylogenetic conservatism and antiquity of a tropical specialization: army-ant-following in the typical antbirds (Thamnophilidae). Molecular Phylogenetics and Evolution 45:1–13.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18:119–125.

Crotty, S. M., and M. D. Bertness. 2015. Positive interactions expand habitat use and the realized niches of sympatric species. Ecology 96:2575–2582.

Dolby, A. S., and T. C. Grubb. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. Animal Behavior 56:501–509.

Dolby, A. S., and T. C. Grubb. 1999. Functional roles in mixed-species foraging flocks: a field manipulation. Auk 116:557–559.

Dolby, A. S., and T. C. Grubb. 2000. Social context affects risk taking by a satellite species in a mixed-species foraging group. Behavioral Ecology 11:110–114.

Duong, T. 2007. ks: kernel density estimation and kernel discriminant analysis for multivariate data in R. Journal of Statistical Software 21:1–16.

Duong, T. 2016. ks: kernel smoothing. R package version 1.10.7. https://CRAN.R-project.org/package=ks

Ferrari, S. L. P., and F. Cribari-Neto. 2004. Beta regression for modeling rates and proportions. Journal of Applied Statistics 31:799–815.

Foster, W., and J. Treherne. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. Nature 293:466–467.

Goodale, E., G. Beauchamp, R. D. Magrath, J. C. Nieh, and G. D. Ruxton. 2010. Interspecific information transfer influences animal community structure. Trends in Ecology & Evolution 25:354–361.

Goodale, E., and S. W. Kotagama. 2005. Alarm calling in Sri Lankan mixed-species bird flocks. Auk 122:108–120.

Goodale, E., and S. W. Kotagama. 2006. Vocal mimicry by a passerine bird attracts other species involved in mixed-species flocks. Animal Behaviour 72:471–477.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31:295–311.

Harrison, N. M., and M. J. Whitehouse. 2011. Mixed-species flocks: An example of niche construction? Animal Behavior 81:675–682.

He, Q., M. D. Bertness, and A. H. Altieri. 2013. Global shifts towards positive species interactions with increasing environmental stress. Ecology Letters 16:695–706.

Jullien, M., and J. Thiollay. 1998. Multi-species territoriality and dynamic of Neotropical forest understorey bird flocks. Journal of Animal Ecology 67:227–252.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the” landscape of fear” in Yellowstone National Park, USA. Canadian Journal of Zoology 79:1401–1409.

Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. Open Ecology Journal 3:1–7.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

MacArthur, R. H., and H. S. Horn. 1969. Foliage profile by vertical measurements. Ecology 50:802–804.

Magrath, R. D., T. M. Haff, P. M. Fallow, and A. N. Radford. 2015. Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. Biological Reviews 90:560–586.

Martínez, A. E., and J. P. Gomez. 2013. Are Amazonian mixed-species flocks stable through two decades? American Naturalist 181: E53–E59.

Martínez, A. E., J. P. Gomez, J. M. Ponciano, and S. K. Robinson. 2016. Functional traits, flocking propensity, and perceived predation risk in an Amazonian understory bird community. American Naturalist 187:607–619.

Martinez, A. E., E. Parra, L. F. Collado, and V. T. Vredenburg. 2017. Deconstructing the landscape of fear in stable multi-species societies. Ecology 98:2447–2455.

Martinez, A. E., and S. K. Robinson. 2016. Using foraging Ecology to elucidate the role of species interactions in two contrasting mixed-species flock systems in northeastern Peru. The Wilson Journal of Ornithology 128:378–390.

Mokross, K., T. B. Ryder, M. C. Côrtes, J. D. Wolfe, and P. C. Stouffer. 2014. Decay of interspecific avian flock networks along a disturbance gradient in Amazonia. Proceedings of the Royal Society B: Biological Sciences 281. https://doi.org/10.1098/rspb.2013.2599

Munn, C. A. 1985. Permanent canopy and understory flocks in Amazonia: species composition and population density. Ornithological Monographs 36:683–712.

Munn, C. A. 1986. Birds that ‘cry wolf’. Nature 319:143–145.

Munn, C. A., and J. W. Terborgh. 1979. Multi-species territoriality in neotropical foraging flocks. Condor 81:338–347.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining *R*2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Odling-Smee, F. J., K. N. Laland, and M. W. Feldman. 1996. Niche construction. American Naturalist 147:641–648.

Ogundimu, E. O., and G. S. Collins. 2017. Predictive performance of penalized beta regression model for continuous bounded outcomes. Journal of Applied Statistics. https://doi.org/10.1080/02664763.2017.1339024

Parejo, D., and J. M. Avilés. 2016. Social information use by competitors: Resolving the enigma of species coexistence in animals? Ecosphere 7:e01295.

Powell, G. V. N. 1989. On the possible contribution of mixed species flocks to species richness in neotropical avifaunas. Behavioral Ecology and Sociobiology 24:387–393.

R Core Team. 2016. A language and environment for statistical computing. R version 3.3.0. https://www.R-project.org/

Radford, A. N., M. B. Bell, L. I. Hollén, and A. R. Ridley. 2011. Singing for your supper: sentinel calling by kleptoparasites can mitigate the cost to victims. Evolution 65:900–906.

Rainey, H. J., K. Zuberbühler, and P. J. Slater. 2004. Hornbills can distinguish between primate alarm calls. Proceedings of the Royal Society B: Biological Sciences 271:755–759.

Ridley, A. R., E. M. Wiley, and A. X. Thompson. 2014. The ecological benefits of interceptive eavesdropping. Functional Ecology 28:197–205.

Schmitt, M. H., K. Stears, and A. M. Shrader. 2016. Zebra reduce predation risk in mixed-species herds by eavesdropping on cues from giraffe. Behavioral Ecology 27:1073–1077.

Schulenberg, T. S., D. F. Stotz, D. F. Lane, J. P. O’Neill, and T. A Parker III. 2010. Birds of Peru: revised and updated edition. Princeton University Press, Princeton, New Jersey, USA.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Seppänen, J. T., J. T. Forsman, M. Mönkkönen, and R. L. Thomson. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology 88:1622–1633.

Sieving, K. E., T. A. Contreras, and K. L. Maute. 2004. Heterospecific facilitation of forest-boundary crossing by mobbing understory birds in north-central Florida. Auk 121:738–751.

Sridhar, H., and K. Sankar. 2008. Effects of habitat degradation on mixed-species bird flocks in Indian rain forests. Journal of Tropical Ecology 24:135–147.

Sullivan, K. A. 1984. The advantages of social foraging in downy woodpeckers. Animal Behaviour 32:16–22.

Suraci, J. P., M. Clinchy, L. M. Dill, D. Roberts, and L. Y. Zanette. 2016. Fear of large carnivores causes a trophic cascade. Nature communications 7. https://doi.org/10.1038/ncomms10698

Thiollay, J. M., and M. Jullien. 1998. Flocking behaviour of foraging birds in a neotropical rain forest and the antipredator defense hypothesis. Ibis 140:382–394.

Tubelis, D. P., A. Cowling, and C. Donnelly. 2006. Role of mixed-species flocks in the use of adjacent savannas by forest birds in the central Cerrado, Brazil. Austral Ecology 31:38–45.

Valeix, M., A. J. Loveridge, S. Chaimaillé-Jammes, Z. Davidson, F. Murindagamo, H. Fritz, and D. W. Macdonald. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology 90: 23–30.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548.

Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk tradeoff. Ecology 69:1352–1366.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

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