Local predation pressure predicts the strength of mobbing responses in tropical birds

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Abstract   Many birds join cooperative mobbing aggregations and collectively harass predators. Individuals participating in these ephemeral associations benefit by deterring the predator, but also incur energetic costs and increased risk of predation. Explaining the evolution of mobbing is challenging because individuals could prevail by selfishly seeking safety while allowing others to mob. An important step in understanding the evolution of mobbing is to identify factors affecting its expression. The *ecological constraints model* suggests that animals are more likely to cooperate under adverse environmental conditions, such as when local predation pressure is high. We tested this prediction by comparing the mobbing responses of several species of birds to the local abundance of their primary predator, the ferruginous pygmy-owl *Glaucidium brasilianum*. We used acoustic playback to elicit mobbing responses in environments where owls were common, uncommon, or rare. Stimuli were either the song of a ferruginous pygmy-owl or the mobbing calls of three of the owl's common prey species. During each playback, we characterized mobbing responses by noting the number of species and individuals that approached the loudspeaker, as well as the closest approach by any bird. Mobbing responses to both stimuli were strong in locations where Ferruginous Pygmy-owls were common, intermediate where owls were uncommon, and weak where they were rare. This pattern persisted even after controlling for differences in species richness and composition among the three environments. Results support the *ecological constraints model* and provide strong evidence that intense predation pressure increases the expression of cooperative mobbing in tropical birds   [*Current Zoology* 58 (5): 781–790, 2012].

Keywords   Antipredator behavior, Alarm signal, Cooperative defense, Learning, Mobbing, Tropical bird

Cooperation among organisms is difficult to explain because cooperators incur costs while providing competitors with benefits and a selective advantage (Haldane, 1932; Fisher, 1958; Hamilton, 1963; Maynard Smith, 1964; Trivers, 1971; Zahavi, 1995; Dugatkin, 1997; Fletcher et al., 2006; Foster et al., 2006; Ekman, 2007). Despite this apparent altruism, cooperation is common in nature. For example, some animals jeopardize their own safety by producing conspicuous alarm signals that warn others of impending danger (reviewed in Zuberbühler, 2009). In other species, such as wild turkeys *Meleagris gallopavo* and long-tailed manakins *Chiroxiphia linearis*, males routinely forego reproduction in favor of helping other males attract mates (McDonald and Potts, 1994; Krakauer, 2005). Among cooperatively breeding animals, some individuals may help raise unrelated offspring by assisting other parents with nest construction, thermoregulation, food provisioning, and predator defense (Brown, 1987; Cockburn, 1998). Kin selection can explain cooperation among relatives, but it cannot explain cooperation among unrelated individuals or individuals from different species (Hamilton, 1964).

A critical step in understanding the evolution of cooperation is to identify the factors that affect its expression. The *ecological constraints model* predicts that cooperation is more likely to occur under stressful environmental conditions because the costs of acting alone under these conditions are prohibitively high (Emlen, 1982). This prediction is supported by computer simulation studies and empirical studies that both document positive correlations between environmental adversity and the expression of cooperation (Andras et al., 2003). For example, Emlen (1982) showed that white-fronted bee-eaters *Merops bullockoides* are more likely to help others raise offspring when insects are rare, but to breed independently when insects are common. Similarly, Callaway et al. (2002) showed that alpine plants inhibit the growth, reproduction, and survival of neighboring plants when living in benign low-elevation environments, but facilitate these traits when living in stressful high-elevation environments. Environmental adversity

therefore appears to be a critical factor affecting the expression of cooperation in a wide range of species, although the precise mechanisms linking environmental adversity to the expression of cooperation remain unclear.

Predation is a potent selective force that has shaped a wide range of anti-predator behaviors among prey (Lima and Dill, 1990). Among these behaviors, mobbing is particularly fascinating because often-unrelated individuals from one or more species cooperatively expel predators from the immediate area by harassing them with conspicuous vocalizations, rapid and frequent movements, and direct physical attacks (Altmann, 1956; Curio, 1978; Hurd, 1996). Mobbing can be costly due to energy expenditure, time lost for foraging, and predation risk (Curio and Regelmann, 1986; Sordahl, 1990). Furthermore, conspicuous mobbing vocalizations can attract additional predators that attack mobbing individuals (Ostrow, 2006) or depredate their nests (Krama and Krams, 2005; Krams et al., 2007). Possible benefits of mobbing are to acquire information about the predator, such as its size or location, teach young birds about predators, deter the predator from the area, and reduce the probability of the predator returning to the unsuccessful hunting ground (Curio, 1978; Curio et al., 1978; Pettifor, 1990; Flasskamp, 1994; Pavey and Smyth, 1998; Templeton et al., 2005). Despite these potential benefits, however, the ecological conditions that promote mobbing behavior are not well characterized (Curio, 1978; Dugatkin and Godin, 1992; Ostreiher, 2003; Graw and Manser, 2007; Grim, 2008; Krams et al., 2008).

The *ecological constraints model* suggests that cooperative behavior is more likely to occur under adverse environmental conditions (Emlen, 1982). Although the model was originally developed to explain cooperative breeding, its general theoretical argument suggests that other cooperative behaviours, such as mobbing, are also more likely to occur under adverse environmental conditions, such as when local predation pressure is high. Only two studies have examined this relationship, however, and they reached opposite conclusions. Forsman and Mönkkönen (2001) showed that boreal forest passerines exhibit a stronger mobbing response when local predation pressure is low, whereas Krams et al. (2010) showed that breeding pied flycatchers *Ficedula hypoleuca* exhibit a stronger mobbing response when local predation pressure is high. The relationship between mobbing and environmental adversity in general, and between mobbing and local predation pressure in

particular, is therefore unclear and requires further investigation.

In this study, we test whether mobbing behavior of small birds varies in relation to local predation pressure. We used the local abundance of ferruginous pygmy-owls *Glaucidium brasilianum* as an indicator of local predation pressure and overall environmental adversity, since this owl is one of the predominant predators of small birds (Stiles and Skutch, 1989; Carrera et al., 2008). It is also mobbed by a wide range of tropical avian species (Reudink et al., 2007), which makes it ideal for studying mobbing behavior. In our experiment, we simulated the presence of a ferruginous pygmy-owl by broadcasting standardized acoustic stimuli through a loudspeaker in locations where ferruginous pygmy-owls were common, uncommon, or rare. Stimuli were either vocalizations produced by a ferruginous pygmy-owl or the combined mobbing calls of three of the owl's common prey species. We predicted that the frequency and intensity of mobbing would be positively correlated with the local abundance of ferruginous pygmy-owls. This is the first study to test the *ecological constraints model* using mobbing behavior in tropical birds and differences in predation pressure among large-scale geographic regions, and thus provides new insight into the function and evolution of this unique cooperative behavior.

1   Materials and Methods

We conducted the experiment at six study sites in Costa Rica between January and April 2010. The six sites were separated from each other by a minimum of 37 km, and varied according to their local abundance of ferruginous pygmy-owls. Ferruginous pygmy-owls are year-round residents of Costa Rica, and were common in the mangroves near Chomes (10°02′ N, 84°54′ W, 5 m above sea level) and in Palo Verde National Park (10°20′ V, 85°20′, 15 m above sea level) (Stiles and Gill, 1988; Stiles and Skutch, 1989), uncommon at the Universidad de Costa Rica campus (09°56′ N, 84°02′ W, 1200 m above sea level) and at Londres, Quepos, Puntarenas Province (09°29′ N, 84°02′, 200 m above sea level) (Biamonte et al., 2011; unpublished data), and rare in El Copal Biological Reserve (09°46′ N, 83°46′ W, 1000 m above sea level) and Santa Rosa National Park (10°54′ N, 85°42′ W, 100 m above sea level) (Causey and Trimble, 2005; unpublished data).

1.1   Stimuli

We created two playback stimuli that simulated the

presence of a ferruginous pygmy-owl. The first was the owl's song. The second was a multispecies bout of mobbing calls produced in response to the owl by two migratory species (Tennessee warbler *Oreothlypis peregrina*; Wilson's warbler *Cardellina pusilla*) and one resident species (rufus-tailed hummingbird *Amazilia tzacatl*). These three species were common at all of our study sites during the experimental period (Stiles and Skutch, 1989; Garrigues and Dean, 2007). We included both types of playback stimuli in our experiment to increase the probability of eliciting mobbing behavior.

Recordings used to construct the playback stimuli were obtained at a remote site (Getsemaní, Heredia Province, Costa Rica: 10°02′ N, 84°06′ W, 1300 m above sea level; 13 km to nearest study site) to ensure that they were unfamiliar to the subjects used in our experiment. They were recorded with a digital recorder (Marantz PMD 661; 44.1 kHz sampling rate, 16-bit amplitude encoding, WAVE format) and a Sennheiser ME 66 microphone (super-cardioid/lobar pick-up pattern; 40 – 20000 Hz frequency response, ± 2.5 dB) during naturally occurring bouts of singing and mobbing. From the initial recordings, we used CoolEdit 2000 (Syntrillium Software Corporation, Phoenix, Arizona, USA) to select a single owl song and a single bout of mobbing calls that had high signal-to-noise ratios and no overlapping background sounds. For the bout of mobbing calls, we selectively deleted all of the owl's vocalizations. Both stimuli were then filtered with a 1-kHz high-pass filter. Finally, we constructed a 4-min playback stimulus from each recording. The owl song, which was 5.4 s in duration and contained 15 repeated elements, was repeated at a natural rate of 1 song every 9 s for a total of 4 min. The mobbing sequence, which was 2 min in duration, was repeated two times to create a continuous 4-min bout of mobbing calls. We generated a single owl song stimulus and a single mobbing call stimulus so that variation in subjects' responses could be attributed to differences in local predation pressure and not to variation in stimulus characteristics (Sandoval, 2011). Including only one exemplar of each call type was justified in this study because the effect of call-type on mobbing responses was not the focus of our study. The final stimuli were saved as WAVE files (44.1 kHz sampling rate, 16-bit amplitude encoding) and transferred onto a CD for playback in the field.

1.2 Playbacks

We broadcast playback stimuli at 8 to 13 locations within each of the six study sites (*n* = 53 playback locations in total), where Ferruginous Pygmy-owls were common (*n* = 15 locations), uncommon (*n* = 15 locations), or rare (*n* = 23 locations). The six study sites were sampled in a random order. All playback trials within a given site were conducted on two consecutive days between 07: 00 h and 10: 00 h, which corresponds to a period of high activity in birds. We separated playback locations within a study site by a minimum of 200 m to minimize the probability of the same individuals responding at multiple locations.

We selected playback locations that were typical of where a ferruginous pygmy-owl would perch and sing, such as along trails and forest edges (Stiles and Skutch, 1989; personal observation). After finding a suitable location, we attached a loudspeaker (Radio Shack Accurian pliable speaker) to a bush or tree branch 1.5 to 2.5 m above the ground and in close proximity to other vegetation. Flags were placed on all sides of the speaker at a distance of 5 m to facilitate our estimates of the distance between the speaker and approaching birds. The observer connected the loudspeaker to a digital playback device (Sony CD Walkman, model D-E351), selected one of the two 4-min playback stimuli, and broadcast it through the loudspeaker at 82 dB SPL (measured 2 m from the loudspeaker with a Sper Scientific mini sound level meter, model 840014; 32-130 dB response range; slow response; C-weighting). This amplitude approximates the natural amplitude of owl songs and mobbing calls, as determined aurally in the field. During the 4-min playback, the observer stood quietly 10 m away from the loudspeaker and observed avian mobbing responses (described below). After the playback stimulus ended, the observer waited until no birds had been seen within 5 m of the loudspeaker for at least 5 min, and then broadcasted the second 4-min playback stimulus. We alternated the presentation order of the two playback stimuli among playback locations to control for possible order effects.

During each 4-min playback trial, we quantified avian responses using four behavioral measures: (1) *latency* of the first bird to approach to within 5 m of the loudspeaker, (2) *minimum distance* from the loudspeaker of any bird, (3) *maximum number of birds*, which was the sum of the maximum number of individuals of each species observed simultaneously within 5 m of the loudspeaker, and (4) *number of species* observed within 5 m of the loudspeaker. We used 5 m as the criterion for participation in a mobbing event because, beyond this distance, dense vegetation at the majority of our playback locations would have precluded us from accurately monitoring the movements of small

birds. If no birds approached to within 5 m of the loud-speaker throughout the 4-min trial, we assigned values of 240 s for latency and 10 m for minimum distance (beyond 10 m we could not be confident that birds were absent).

1.3 Statistical analysis

Preliminary analyses revealed that our four behavioral response measures were highly intercorrelated (Spearman correlation analysis: all $n = 106$, all $|r| > 0.68$, all $P < 0.001$; Table 1). To avoid conducting multiple non-independent tests, we reduced the four original response variables using a principal component analysis (Table 1). A single principal component with an eigenvalue greater than one explained 83.9% of the variance observed among the original four variables. We labeled the component *mobbing response*. Higher mobbing response scores corresponded to shorter latencies, closer minimum approach distances, and more individuals and species responding to the playback.

Table 1   Details of the principal component analysis used to describe avian mobbing responses during 53 playback trials with two treatments per trial

Variable	latency	Minimum distance	Number of birds	Number of species	Mobbing response
Latency	1.00	.	.	.	-0.92*
Minimum distance	0.85*	1.00	.	.	-0.88*
Number of birds	-0.74*	-0.68*	1.00	.	0.92*
Number of species	-0.77*	-0.71*	0.95*	1.00	0.94*
Eigenvalue					3.3
Variance explained (%)	84.0	77.6	85.0	88.2	83.7

Pearson correlation coefficients are provided for the four original variables and the single derived principal component labeled "mobbing response" (* indicates $P \leqslant 0.001$). Variance explained describes the percentage of each variable's variance that is explained by the principal component (i.e., communalities), as well as the total variance among the four original variables that is explained by the principal component. Analysis was based on the correlation matrix and unrotated components were extracted when eigenvalues exceeded one. Sampling adequacy was assessed using Bartlett's test, and the hypothesis that the correlation matrix contained only zero-correlations was rejected ($\chi_6^2 = 457.2$, $P < 0.001$). Component scores were generated using the regression method.

Mobbing responses to the two playback stimuli broadcast at each location (i.e., owl song, mobbing call) were not independent (Spearman correlation analysis: n = 53; $r = 0.68$, $P < 0.001$). We therefore tested for the effects of owl-abundance on mobbing response using a repeated measures ANOVA. We included owl abundance as a between-subject factor (common, uncommon, rare) and the type of playback stimulus as a within-subject factor (owl song, mobbing call). The order in which playback treatments were broadcast did not significantly affect the probability of response (i.e., the probability that at least one bird approached to within 5 m of the loudspeaker; sign test: $n = 53$, $P = 0.66$) and was not included in the analysis.

The richness of avian species varied among the six study sites from more than 350 species in El Copal Biological Reserve (a location where Pygmy-owls are rare) and Londres (a location where Pygmy-owls are uncommon) to fewer than 200 species at Universidad de Costa Rica (a location where Pygmy-owls are uncommon) and the mangroves at Chomes (a location where Pygmy-owls are common) (Stiles and Gill, 1988; Biamonte et al., 2011; unpublished data). This variation did not confound our analysis because species richness and the local abundance of ferruginous pygmy-owls did not covary (Stiles and Gill, 1988; Biamonte et al., 2011; unpublished data). A concern, however, is that species richness could affect the number of species responding to playbacks, and thus obscure the effect of local predation pressure on mobbing response. To remove this potentially obscuring effect, we conducted a second repeated measures ANOVA that was based on the subset of species ($n = 26$ species) that was present at all of our study sites. Thus, the species richness and species composition of this subset of data were identical among the six study sites. In this second analysis, we used the maximum number of these birds observed simultaneously within 5 m of the loudspeaker as the response variable. We did not calculate a principal component, as in the first analysis, because we did not know the latency or the minimum approach distance for the subset of species being analyzed.

All analyses were two-tailed and results were considered statistically significant when $P \leq 0.05$. For both repeated measures ANOVAs, we reported effect sizes as partial eta-squared ($\eta^2_{partial}$; Cohen, 1973). Where an overall model was statistically significant, we compared the response variable among the three levels of owl abundance by conducting three post-hoc pairwise comparisons. We controlled experimentwise error by applying a Bonferroni correction for multiple comparisons ($\alpha_{corrected} = 0.017$).

2 Results

Playbacks elicited mobbing behavior from a wide range of birds, including 58 species from 16 families (Table 2). Mobbing response was significantly affected by the local abundance of Ferruginous Pygmy-owls and the type of stimulus that was broadcast through the loudspeaker (repeated measures ANOVA: whole-model, $F_{3,50} = 9.60$, $P < 0.001$; abundance of Ferruginous Pygmy-owls, $F_{2,50} = 19.54$, $P < 0.001$, $\eta^2_{partial} = 0.44$; type of stimulus, $F_{1,50} = 27.94$, $P < 0.001$, $\eta^2_{partial} = 0.36$; interaction, $F_{2,50} = 0.07$, $P = 0.935$, $\eta^2_{partial} = 0.00$; Fig. 1a). Post-hoc analyses revealed that mobbing response differed significantly between each of the three predator environments; it was strong in locations where Ferruginous Pygmy-owls were common, intermediate where Ferruginous Pygmy-owls were uncommon, and weak where Ferruginous Pygmy-owls were rare (Fig. 1A). In addition, mobbing response was stronger in response to the mobbing call stimulus than in response to the owl song stimulus (Fig. 1A).

We observed a similar pattern when we considered only the subset of species that was present at all of our study sites. As with mobbing response, the maximum number of birds observed simultaneously within 5 m of the loudspeaker was significantly affected by the local abundance of ferruginous pygmy-owls and the type of stimulus broadcast through the loudspeaker (repeated measures ANOVA: whole-model, $F_{3,50} = 4.35$, $P = 0.001$; abundance of ferruginous pygmy-owls, $F_{2,50} = 5.39$, $P = 0.008$, $\eta^2_{partial} = 0.18$; type of stimulus, $F_{1,50} = 12.04$, $P = 0.001$, $\eta^2_{partial} = 0.19$; interaction, $F_{2,50} = 1.38$, $P = 0.262$, $\eta^2_{partial} = 0.05$; Fig. 1B). Post-hoc analyses showed that more individuals approached the loudspeaker when Ferruginous Pygmy-owls were common or uncommon versus when they were rare (Fig. 1B). As with mobbing response, more birds approached in response to the mobbing call stimulus than in response to the owl song stimulus (Fig. 1B).

3 Discussion

Our simulations of an avian predator elicited mobbing responses from a wide range of tropical birds (Table 2). In general, local predation pressure was an excellent predictor of the strength of mobbing responses, with birds exhibiting stronger mobbing responses in locations where predatory ferruginous pygmy-owls were common and weaker responses where ferruginous pygmy-owls were rare. This pattern persisted even after controlling for variation in species richness and species

composition among our study sites. Results are therefore consistent with the *ecological constraints model*, which states that adverse environmental conditions, such as high predation pressure, cause greater cooperation among animals (Emlen, 1982). Our study relied on natural variation in local predator abundance, so it is also possible that stronger mobbing caused reduced predator abundance at certain study sites. We argue against this alternative interpretation, however, because mobbing typically deters predators only from the immediate vicinity, such as the mobber's territory, and not from larger geographic regions, such as the study sites examined in our experiment (Pettifor, 1990; Pavey and Smyth, 1998). Furthermore, this alternative interpreta-
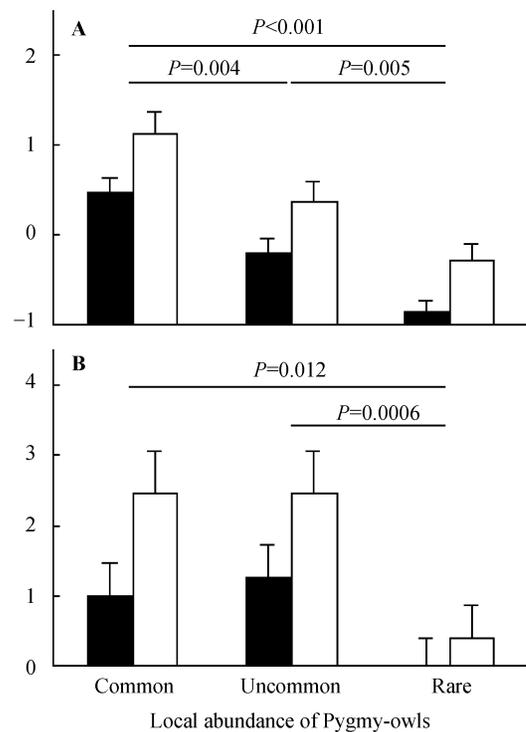

Fig. 1 Responses of Costa Rican birds (mean + SE) to predator stimuli in environments where Ferruginous Pygmy-owls were common (*n* = 15 locations), uncommon (*n* = 15 locations), or rare (*n* = 23 locations)

Playback stimuli were either songs produced by a Ferruginous Pygmy-owl (black bars) or the combined mobbing calls of three of the owl's common prey species (white bars). **A**. Mobbing response is a principal component that incorporates latency, minimum distance, maximum number of birds, and number of species (see text for definitions of these variables). **B**. Maximum number of birds is the sum of the maximum number of birds of each species observed simultaneously within 5 m of the loudspeaker; only the 26 species that were present at all playback locations were included in this measure. Statistically significant differences between predator environments are indicated by horizontal lines and associated *P*-values. Both response measures were significantly greater in response to the mobbing call stimulus than in response to the owl song stimulus.

Table 2 Details of the 58 species that responded during 53 playback trials with two treatments per trial

Family	Scientific name	Common name	Resident/migrant	Common	Uncommon	Rare	Total
Cardinalidae	*Saltator caerulescens*	Grayish saltator	Resident	.	.	2	2
Cuculidae	*Crotophaga sulcirostris*	Groove-billed ani	Resident	.	.	2	2
Emberizidae	*Arremonops rufivirgatus*	Olive sparrow	Resident	.	2	.	2
Emberizidae	*Atlapetes albinucha*	White-naped brush-finch	Resident	.	.	1	1
Emberizidae	*Melozone leucotis*	White-eared ground-sparrow	Resident	.	.	1	1
Emberizidae	*Peucaea ruficauda*	Stripe-headed sparrow	Resident	1	.	.	1
Emberizidae	*Sporophila americana*	Variable seedeater	Resident	.	5	1	6
Emberizidae	*Sporophila torqueola*	White-collared seedeater	Resident	.	4	1	5
Emberizidae	*Volatinia jacarina*	Blue-black grassquit	Resident	.	.	1	1
Emberizidae	*Zonotrichia capensis*	Rufous-collared sparrow	Resident	.	.	2	2
Fringillidae	*Euphonia imitans*	Spot-crowned euphonia	Resident	.	.	1	1
Furnariidae	*Glyphorhynchus spirurus*	Wedge-billed woodcreeper	Resident	1	.	1	2
Furnariidae	*Lepidocolaptes souleyeti*	Streak-headed woodcreeper	Resident	.	2	.	2
Furnariidae	*Sittasomus griceicapillus*	Olivaceus woodcreeper	Resident	1	.	.	1
Icteridae	*Icterus pustulatus*	Streak-backed oriole	Resident	.	3	.	3
Icteridae	*Quiscalus mexicanus*	Great-tailed grackle	Resident	.	1	.	1
Parulidae	*Dendroica pensylvanica*	Chestnut-sided warbler	Migrant	1	.	.	1
Parulidae	*Dendroica petechia*	Yellow warbler	Resident/Migrant	.	11	.	11
Parulidae	*Geothlypis poliocephala*	Gray-crowned warbler	Resident	.	.	2	2
Parulidae	*Oreothlypis peregrina*	Tennessee warbler	Migrant	1	.	.	1
Parulidae	*Parkesia noveboracensis*	Northern waterthrush	Migrant	.	3	.	3
Parulidae	*Parula pitiayumi*	Tropical parula	Resident	1	.	.	1
Picidae	*Melanerpes hoffmannii*	Hoffmann's woodpecker	Resident	.	1	2	3
Polioptilidae	*Polioptyla albiloris*	White-lored gnatcatcher	Resident	1	13	.	14
Thraupidae	*Chlorophanes spiza*	Green honeycreeper	Resident	.	.	2	2
Thraupidae	*Coereba flaveola*	Bananaquit	Resident	.	.	1	1
Thraupidae	*Cyanerpes cyaneus*	Red-legged honeycreeper	Resident	.	.	1	1
Thraupidae	*Cyanerpes lucidus*	Shining honeycreeper	Resident	.	.	2	2
Thraupidae	*Tangara larvata*	Golden-hooded tanager	Resident	.	.	2	2
Thraupidae	*Thraupis episcopus*	Blue-gray tanager	Resident	.	.	5	5
Thraupidae	*Thraupis palmarum*	Palm tanager	Resident	.	.	2	2
Tityridae	*Pachyramphus aglaiae*	Rose-throated becard	Resident	.	1	.	1
Trochilidae	*Amazilia boucardi*	Mangrove hummingbird	Resident	.	2	.	2
Trochilidae	*Amazilia rutila*	Cinnamon hummingbird	Resident	.	1	.	1
Trochilidae	*Amazilia saucerrotei*	Steely-vented hummingbird	Resident	.	1	1	2
Trochilidae	*Amazilia tzacatl*	Rufous-tailed hummingbird	Resident	.	.	3	3
Trochilidae	*Chlorostilbon canivetii*	Canivet's emerald	Resident	.	1	.	1
Trochilidae	*Microchera albocoronata*	Snowcap	Resident	2	.	.	2
Trochilidae	*Thalurania colombica*	Violet-crowned woodnymph	Resident	.	.	1	1
Trochilidae	unknown hummingbird	unknown hummingbird	Resident	.	1	.	1
Troglodytidae	*Campylorhynchus rufinucha*	Rufous-naped wren	Resident	.	4	.	4
Troglodytidae	*Thryothorus modestus*	Plain wren	Resident	.	.	2	2
Troglodytidae	*Thryothorus pleurostictus*	Banded wren	Resident	.	4	.	4
Troglodytidae	*Troglodytes aedon*	House wren	Resident	.	.	5	5
Turdidae	*Catharus ustulatus*	Swainson's thrush	Migrant	1	.	.	1
Turdidae	*Turdus grayi*	Clay-colored thrush	Resident	.	.	5	5
Tyrannidae	*Empidonax minimus*	Least flycatcher	Migrant	1	.	.	1
Tyrannidae	*Mionectes oleagineus*	Ochre-bellied flycatcher	Resident	.	.	2	2
Tyrannidae	*Myiarchus nuttingi*	Nutting's flycatcher	Resident	.	5	.	5
Tyrannidae	*Myiarchus panamensis*	Panama flycatcher	Resident	.	2	.	2
Tyrannidae	*Myiarchus tyrannulus*	Brown-crested flycatcher	Resident	1	4	.	5
Tyrannidae	*Myiozetetes similis*	Social flycatcher	Resident	.	2	1	3
Tyrannidae	*Todirostrum cinereum*	Common-tody flycatcher	Resident	.	3	.	3
Tyrannidae	*Tolomyias sulphurescens*	Yellow-olive flycatcher	Resident	2	3	.	5
Tyrannidae	*Tyrannus melancholicus*	Tropical kingbird	Resident	.	3	.	3
Tyrannidae	*Zimmereus villisimus*	Paltry tyrannulet	Resident	.	.	2	2
Vireonidae	*Hylophylus decurtatus*	Lesser greenlet	Resident	.	3	.	3
Vireonidae	*Vireo flavoviridis*	Yellow-green vireo	Migrant	2	.	.	2
Vireonidae	*Vireo pallens*	Mangrove vireo	Resident	.	1	.	1

Shown is the number of trials per treatment in which at least one individual approached to within 5 m of the playback speaker. Treatments correspond to locations where Ferruginous Pygmy-owls were common, uncommon, or rare.

tion does not explain why mobbing responses would differ among study sites in the first place.

The positive correlation between local predation pressure and the strength of mobbing responses is consistent with a recent study on breeding Pied Flycatchers (Krams et al., 2010). In that study, the authors experimentally manipulated predation pressure within a subject's territory by repeatedly presenting taxidermic mounts of either a predatory tawny owl *Strix aluco* or a non-predatory mistle thrush *Turdus viscivorus*. Following the manipulation, they elicited a mobbing response at a neighboring flycatcher's nest and found that the subject was almost twice as likely to assist its neighbor in its mobbing response if local predation pressure had previously been increased. In contrast, our results contradict a study on forest passerines in which the authors elicited mobbing responses at increasing distances (30–720 m) from the active nests of predatory Eurasian Sparrowhawks (*Accipiter nisus*; Forsman and Mönkkönen, 2001). They found that more species joined the mobbing aggregations at greater distances from nests, where predation pressure was lower. We suggest that this contradictory result was because predation pressure was highly localized around Sparrowhawk nests and that prey simply avoided those particular high-risk areas. Predation pressure in our study was not localized around a fixed point, so prey could only avoid high-risk areas by emigrating to completely different geographic regions. Similarly, the pied flycatchers studied by Krams et al. (2010) would have been unable to avoid high-risk areas because those areas were established close to the flycatchers' nests only after their eggs had already hatched. Avoiding risky areas would have required the flycatchers to abandon their nestlings (Krams et al., 2010).

Our study showed that the strength of mobbing responses varied in relation to local predation pressure, but it did not identify the mechanism underlying this relationship. One possibility is that mobbing behavior is phenotypically plastic and that individuals adjust their mobbing responses according to local predation pressure. A simple cognitive mechanism, for example, could allow birds to monitor predators and select adaptive mobbing responses that are tailored to local risk (Bouskila and Blumstein, 1992). Learning could also provide the necessary link, since many antipredator behaviors are experience-dependent. For example, animals living in environments devoid of predators (e.g., islands) often do not express appropriate antipredator behaviors,

but can be taught to do so through repeated interactions with introduced predators (Griffen et al., 2000; Čapek et al., 2010). In our study, the weak mobbing responses observed in locations where Ferruginous Pygmy-owls were rare could simply be the result of the local birds lacking experience with this avian predator. Finally, a physiological mechanism could also generate phenotypic plasticity and provide the link between mobbing behavior and local predation risk. In many vertebrates, acute exposure to predators (Cockrem and Silverin, 2002; Barcellos et al., 2007; Thaker et al., 2009a), as well as chronic exposure to predator-rich environments (reviewed in Clinchy et al., 2011), can elevate glucocorticoid stress hormones. This, in turn, can increase the expression of antipredator behavior (Kalynchuk et al., 2004; Thaker et al., 2009a,b), which could explain why mobbing behavior was stronger in locations with greater predation pressure.

Genetic differences among study sites, as opposed to phenotypic plasticity, could also explain the observed relationship between mobbing behavior and local predation pressure. Antipredator behavior is known to have a strong genetic basis in a variety of taxonomic groups (but see Blumstein et al., 2010), including birds (Bize et al., 2012), amphibians (Storfer and Sih, 1998; Kishida et al., 2007), arachnids (Riechert and Hedrick, 1990), branchiopods (Watt and Young, 1992), and reptiles (Garland, 1988). Furthermore, genetically based antipredator behavior is often absent or diminished among populations that have been isolated from predators over evolutionary time (Riechert and Hedrick, 1990; Storfer and Sih, 1998; Abjornsson et al., 2004; Kishida et al., 2007). It is therefore possible that the genes responsible for mobbing behavior had been lost from those populations where Ferruginous Pygmy-owls were rare. However, we suggest that genetic differences probably do not explain our results. First, there were no reproductive barriers between populations at our six study sites (Stiles and Skutch, 1989; Garrigues and Dean, 2007), so gene flow would have impeded the evolution of genetically distinct responses. Second, several species observed in our study were migratory (Table 2) and would have lacked the local genetic structure that would have adapted them to local predator conditions.

Mobbing behavior was stronger in response to the mobbing call versus owl song stimulus, yet we expected birds to respond more strongly to the owl song stimulus because it provides a definitive and specific cue that a Ferruginous Pygmy-owl is nearby. In contrast, mobbing

calls are not produced by the predator and consequently provide less reliable information about a predator's presence. A possible explanation is that mobbing calls indicate not only that a predator is present, but also that other prey perceive it as an immediate threat. Since a predator is more dangerous in some situations than in others (Howland, 1974; FitzGibbon, 1989; Stankowich and Blumstein, 2005), information about its level of threat can allow prey to respond optimally during all encounters (e.g., Griesser et al., 2008; Wilson and Evans, 2012). Mobbing calls also indicate that other birds are already responding to the predator and that the risk of predation would be distributed among multiple individuals (Hamilton, 1971). Diluted predation risk could therefore explain why individuals were more likely to approach the mobbing call versus owl song stimulus. Another possible explanation is that the structural characteristics of the two stimuli, independent of their information content, evoked differential responses from receivers. For example, signaling sequences with a greater duty cycle (i.e., more vocalization per unit of time) often evoke stronger responses from birds (Wilson and Mennill, 2011). In our study, the mobbing call stimulus had a higher duty cycle than the owl song stimulus (100% versus 60%), which could explain why it evoked a stronger response. We interpret the effect of stimulus type on mobbing response with caution, however, because it was not the focus of our study, and consequently, our experiment did not involve multiple exemplars of each stimulus type.

In conclusion, our study provides new insight into the evolution of cooperative behavior. In particular, we show that birds exhibit stronger mobbing responses when predators are locally abundant than when they are rare. Furthermore, we show this relationship for the first time in a tropical environment, which expands the ecological conditions and taxonomic groups in which this relationship has been described. Our findings support the *ecological constraints model* and provide strong evidence that intense predation pressure increases the expression of cooperative mobbing behavior in tropical birds.

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