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Original Article

Predation risk drives the expression of mobbing across bird species

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Many species approach predators to harass and drive them away, even though mobbing a predator can be deadly. However, not all species display this behavior, and those that do can exhibit different behaviors while mobbing different predators. Here we experimentally assessed the role of social and ecological traits on the expression of mobbing behavior in a bird community in SE Brazil (n = 157 species). We exposed birds to models of two morphologically similar diurnal owls that pose different risks, and assessed which species engaged in mobbing. Among those that mobbed, we evaluated how they adjusted their mobbing behavior depending on the predator type. We tested the hypothesis that only species that are at risk and can afford to mob engage in this antipredator behavior. We found that species that engaged in mobbing are in the body mass range of potential prey, forage in the understory or in the canopy, and form flocks. A species' social system did not influence its mobbing behavior. Furthermore, species that engaged in mobbing formed larger mobbing assemblages when facing a high-risk predator, but mobbed more intensely when facing a low-risk predator. Our findings support our predictions, namely that the expression of mobbing is limited by its costs.

Key words: **antipredator behavior, birds, mobbing, predation risk, prey–predator interaction.**

INTRODUCTION

Predation is an important selective force, facilitating the evolution of antipredatory adaptations, such as mobbing behavior. During mobbing, potential prey approach a potential predator to harass and sometimes even attack it, with the primary function of driving the predator away (Curio et al. 1978a; Caro 2005). Thus, mobbing is likely to be adaptive (Curio et al. 1978a; Vieth et al. 1980), reducing the immediate risk for the mobber (Pavey and Smyth 1998). Moreover, moving-on a predator may limit the future risk of attacks (Flasskamp 1994). However, mobbing can be costly since predators may kill prey during mobbing (Sordahl 1990; Motta-Junior 2007).

A large number of field studies investigated the costs and benefits of mobbing in single species, showing that this behavior can increase the chances of survival for the mobber, their offspring, and their relatives (Shields 1984; Pavey and Smyth 1998; Griesser and Suzuki 2017). Also, mobbing can serve as an opportunity to recruit partners for future mobbing events (Krams et al. 2008). Generally, it is expected that the costs and benefits of mobbing vary across species, influencing its expression (Dugatkin and Godin 1992; Pavey and Smyth 1998; Krama and Krams 2005). However, we lack comparative studies that investigate the influence of ecological and social traits on the expression of mobbing across species, and how these factors influence this behavior depending on the risk posed by a predator. Accordingly, it remains unclear why only some species but not others engage in mobbing when encountering certain predators.

Here we take a comparative, phylogenetically-controlled approach to assess correlates of mobbing behavior in birds. We exposed a bird community in SE Brazil to models of 2 diurnal perch-hunting owls that differ in their risk. We examined which social and ecological traits are associated with engagement in mobbing, testing 4 nonexclusive hypotheses:

1) *Size matters hypothesis*: We predicted that only species that are potential prey should engage in mobbing. Predators can only kill prey of a given body size (Valcu et al. 2014), and thus only species that fall within the size range of potential prey should engage in mobbing.

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2) *Safe niche hypothesis*: We predicted that ground-dwelling species should be less likely to mob perch-hunting owls than species that forage in the understory or canopy. Ground-dwelling species are more vulnerable to perch-hunting predators with a top-down hunting strategy (Ekman 1986; Suhonen 1993), as they are more easily killed by these predators and have less possibilities to escape in case of an attack.
3) *Safety in numbers hypothesis*: We predicted that being in a group minimizes the per capita risk of being killed (Hamilton 1971; Hogan et al. 2017). Thus, solitary species are less likely to mob than group-living and flocking species due to the higher risk during mobbing.
4) *Social facilitation hypothesis*: We predicted that mobbing may provide a social learning opportunity to recognize predators (Curio et al. 1978b) for family members (Griesser and Suzuki 2016, Griesser and Suzuki 2017). Thus, family living species (including cooperative breeders; Griesser et al. 2017) are predicted to mob more than nonfamily living species.

Furthermore, among the species that do engage in mobbing, we tested the "mobbing plasticity hypothesis", which predicts that birds can recognize the risk posed by predators (Caro 2005) and adjust their mobbing behavior accordingly. Thus, species that engage in mobbing are predicted to mob a more dangerous predator more intensely and in larger mobbing assemblages. Moreover, since mobbing can be used as nest defense (Arnold 2000) we predicted that birds would mob more intensely during the breeding season than during the nonbreeding season (Shedd 1982; Shedd 1983).

METHODS

This study was carried out on Cauaia Ranch, Minas Gerais State, SE Brazil (19°28`S 44°01`W) between February 2011 and February 2012. The study site is part of the Environmental Protection Area Carste Lagoa Santa, where semideciduous forests and Brazilian savannah patches dominate the landscape, forming a mosaic of pastures, marshes, deciduous forests, and temporary lagoons.

We exposed the local bird community to models of 2 diurnal owl species that are morphologically similar but differ in their risk to birds: a Ferruginous Pygmy-owl (*Glaucidium brasilianum*) that represents a high-risk predator, that is, 43% of its diet consists of birds (Carrera et al. 2008), and a Burrowing Owl (*Athene cunicularia*) that represents a low-risk predator, that is, 95% of its diet consists of arthropods (Zilio 2006), but occasionally eats birds (Motta-Junior 2006). Both owls have a preference for small-sized prey: Ferruginous Pygmy-owls hunt prey weighing on average 43.7 g (min-max: 12.5–225.0 g) (Carrera et al. 2008; Earhart and Johnson 1970), and Burrowing Owls hunt prey weighing on average 39.2 g (min-max: 0.07–210 g, with 60% of their diet composed of prey weighting 0.07–20 g) (Nabte et al. 2008).

We chose 18 experimental locations that were at least 250 m apart to reduce the risk of resampling the same individuals on the same day (Bibby et al. 2012). In each location, we performed 5–6 experiments per model following a Latin square design, resulting in 96 experiments per model. For each experiment, we selected a different location in a relatively open area on the forest edge. We placed the predator model on a 1.5 m high pole, 2 m away from an approximately 3 m high tree. We attached marks at 2, 5, 10, and 15 m in all 4 cardinal directions from the model, facilitating the assessment of the distance between mobbers and the model. Experimental locations were selected to allow the observer good visibility of at least 20 m in all directions around the model.

We placed a speaker on the ground below the model to playback vocalizations of the model species (30 s calls, 15 s silence, during 10 min) to simulate the presence of a live predator. During the experiment, an observer was positioned 10–15 m away from the model wearing camouflage clothing. We recorded the behaviors and distance to the predator model of all present individuals. All trials were conducted between 06h00 and 12h00 local time, corresponding to the time of the day with the highest activity of birds. No trials were conducted on rainy days.

We recorded all species observed in the experimental locations 3 min before each experiment (576 min of observation) to assess the bird species present in the study site. We also included all species that mobbed the models during the trials (1920 min of observation).

We obtained data on the body mass, diet, foraging strata, flocking behavior, and social system of the species from handbooks (del Hoyo et al. 2015). Species were categorized according to their foraging strata: ground, understory, or canopy; their flocking habits: species that live in stable group or joins flocks, or solitary species; and to their social system: nonfamily living, family-living (offspring delay dispersal > 50 days beyond independence (Drobniak et al. 2015)), or cooperatively breeding species (Cockburn 2006). Species whose social system is unknown were not considered for the analysis including this variable.

We assigned the mobbing status of a species based on the response in all experiments using a categorical variable with 2 levels: 1) mobber: a species that mobbed during at least one experiment; 2) nonmobber: a species that is present at the study site but was never observed mobbing).

We assessed the mobbing intensity of all individuals that engaged in mobbing on an increasing ordinal scale from 1 to 7 (adapted from Chandler and Rose 1988; Motta-Junior and Santos-Filho 2012)). Mobbing intensity was ranked based on the mobber's distance from the model (in meters), and its behavior (emitting calls or not, and/or visual displays such as flapping wings, rattling the tail feathers, ruffling the crown feathers, and/or repetitive movements with wings, tail, or head): 1) an individual was > 10 m away from model making visual displays and/or giving warning calls or being silent, 2) an individual was ≤ 10 m and > 5 m away making visual displays and/or giving warning calls or being silent, 3) an individual was ≤ 5 m and > 2 m away being silent, 4) an individual was ≤ 5 m and > 2 m away making visual displays and/or giving warning calls, 5) an individual was ≤ 2 m away being silent, 6) an individual was ≤ 2 m away making visual displays and/or giving warning calls but not attacking the model, and 7) an individual was physically attacking the model.

Statistical analyses

We used the software R 3.3.2 for the statistical analyses (R Core Team 2016), using Generalized Linear Mixed Models in the package MCMCglmm (Hadfield 2010). This method allowed us to perform phylogenetic regression analyses (Ives and Garland 2014) of response variables that do not follow a Gaussian error distribution. To test our hypotheses we ran 3 separate models to assess the influence of independent factors on 1) whether species mob or not (mobbers vs. nonmobbers, categorical variable with 2 levels), 2) the mobbing intensity (an ordinal scale [rank scale 1–7, see above], and 3) the mobbing assemblage size (a discrete numerical variable). The "MCMCglmm" statistical R package uses Markov chain Monte Carlo (MCMC) probabilistic sampling technique, making the analysis of complex models possible (Hadfield 2012). Furthermore, the use of "MCMCglmm" allowed us to include random variables in the models, and to control for the influence of phylogeny (Hadfield 2012; Ives and Garland 2014).

We included a consensus tree at the species level of a recent phyla-wide avian phylogeny (Jetz et al. 2012) as a random effect to control for phylogenetic nonindependence. The MCMCglmm models were run for 100,000 iterations, with a 1000 burn-in period and samples drawn every 100 iterations. Our models resulted in comparable effective sample sizes for all factors (~1000), and visual inspection of trace plots indicated proper mixing of the models.

To test the 4 hypotheses regarding the influence of ecological and social traits on whether or not species engage in mobbing behavior, we included the following species-specific explanatory variables into the model: body mass (log-transformed, in grams), foraging strata, flocking habits, social system. We also included the encounter rate per minute as a covariate to control for the influence of relative species abundance. We used a categorical mixed model using the logit link function in MCMCglmm. For this model, we excluded species for which the social system is unknown. Thus, the analysis was conducted with a reduced dataset of 145 species, of which 67 species mobbed.

Within the species that mobbed, we assessed the factors that influenced mobbing assemblage size and mobbing intensity with separate models. For the former, we performed a phylogenetically-controlled Poisson-distributed generalized linear mixed model with log link, using MCMCglmm. We included the following explanatory variables in this model: predator model (high-risk, low-risk), season (breeding season (September to February), nonbreeding season (March to August)), and the maximum mobbing intensity during an experiment of each individual (ordinal scale from 1 to 7). To test mobbing intensity we performed a phylogenetically-controlled ordinal generalized linear mixed model with a probit function, using MCMCglmm. We included the maximum mobbing intensity of each individual as the response variable and the following explanatory variables: predator model (high-risk, low-risk), season (breeding season (September to February), nonbreeding season (March to August)), and the mobbing assemblage size. In addition to phylogeny, we included in both models the location and the date of each trial as a random effect to control for repeated sampling in the same location. For these models, we included all 79 species that mobbed at least once.

We used the package "car" (Fox and Weisberg 2011), to test for collinearity using the generalized variance inflation factor (GVIF) (Supplementary Appendix S2), which revealed that the factors in our models have a low collinearity (all GVIFs are smaller than 1.32). We tested specific hypotheses based on our a priori predictions and thus only the terms that represent these hypotheses were included and nonsignificant terms were retained in the models. We note that the inclusion of the nonsignificant terms did not influence the qualitative interpretation or significance of the other parameters.

RESULTS

We observed 157 bird species in the study area (Supplementary Appendix S1), of which 79 species (50.31%) mobbed in at least one of the experiments. Overall, 26 species mobbed both models, 50 species only mobbed the high-risk model (Ferruginous Pygmy-Owl), while 3 species only mobbed the low-risk model (Burrowing Owl).

Bird species with smaller body mass were more likely to mob (Table 1, Figure 1a). Species that forage in the understory or canopy were more likely to mob than species that forage on the ground (Table 1, Figure 1b). Moreover, species that flock or live in stable groups were more likely to mob than solitary species (Table 1, Figure 1c). The social system did not influence whether species engaged in mobbing (Table 1). Also, the relative abundance of a species (encounter rate) did not influence whether it engaging in mobbing (Table 1).

Birds adjusted their mobbing behavior depending on the risk posed by a predator. The mobbing assemblage was larger when birds mobbed the high-risk predator model than the low-risk one (Table 2, Figure 2), but mobbing intensity and the mean body mass of species that mobbed did not influence the number of individuals in a mobbing assemblage (Table 2). Furthermore, birds mobbed more intensively when mobbing the model of a low-risk predator than the high-risk one (Table 3, Figure 3), and individuals of smaller species mobbed more intensively than individuals of larger species (Table 3).

DISCUSSION

Our results revealed that particularly species that are potential prey engage in mobbing, but only if they can afford to do so. Accordingly, ground-living species that experience the highest risk of being killed by perch-hunting owls, and solitary species that cannot benefit from safety in numbers, were less likely to mob. In contrast, species that utilize safer parts of the habitat (understory or canopy), and species that benefit from safety in numbers, were more likely to engage in mobbing. Species that engaged in mobbing adjusted their behavior depending on the risk posed by the predator. In the presence of the high-risk predator, larger mobbing assemblages formed, but individuals took less risks than in the presence of a low-risk predator, confirming findings from previous studies (Maloney and McLean 1995; Veen et al. 2000; Griesser 2009).

Size matters hypothesis

It has been suggested that potential prey particularly mob predators (Hartley 1950; Dutour et al. 2016; Forsman and Mönkkönen 2001), but this hypothesis has so far not been tested across species. Our results lend support to this hypothesis, showing that species that engage in mobbing are lighter than species that do not mob, and thus, are within the prey body-size range of the two owl species (i.e., weight less than 200 g (Motta-Junior 2006; Carrera et al. 2008; Lima and Neto 2008)).

Safer niche hypothesis

In support of this hypothesis, terrestrial species were less likely to mob than understory or canopy-living species. The owl models used in this study are perch-hunters that attack with a top-down strike, and consequently, terrestrial species are under the highest risk (Lima and Dill 1990; Kullberg and Ekman 2000; Hedenstrom 2001). Accordingly, they may have evolved alternative strategies of dealing with perched predators, for example by relying on camouflage as found in tinamous (Tinamidae) and nightjars (Caprimulgidae). The predation risk should not only vary depending on the strata, but also across different habitats. Since our experiments were conducted in one habitat type only (i.e., relatively open areas at the edge of forest patches), we cannot test this hypothesis. A study on powerful owls *Ninox strenua* showed that they were equally likely to roost in forest patches and in open areas (Pavey and Smyth 1998). However, owls were more frequently mobbed in open habitats during daytime roosting (i.e., their typical hunting area at night), indicating that prey adjust their mobbing behavior depending on habitat-specific risks.

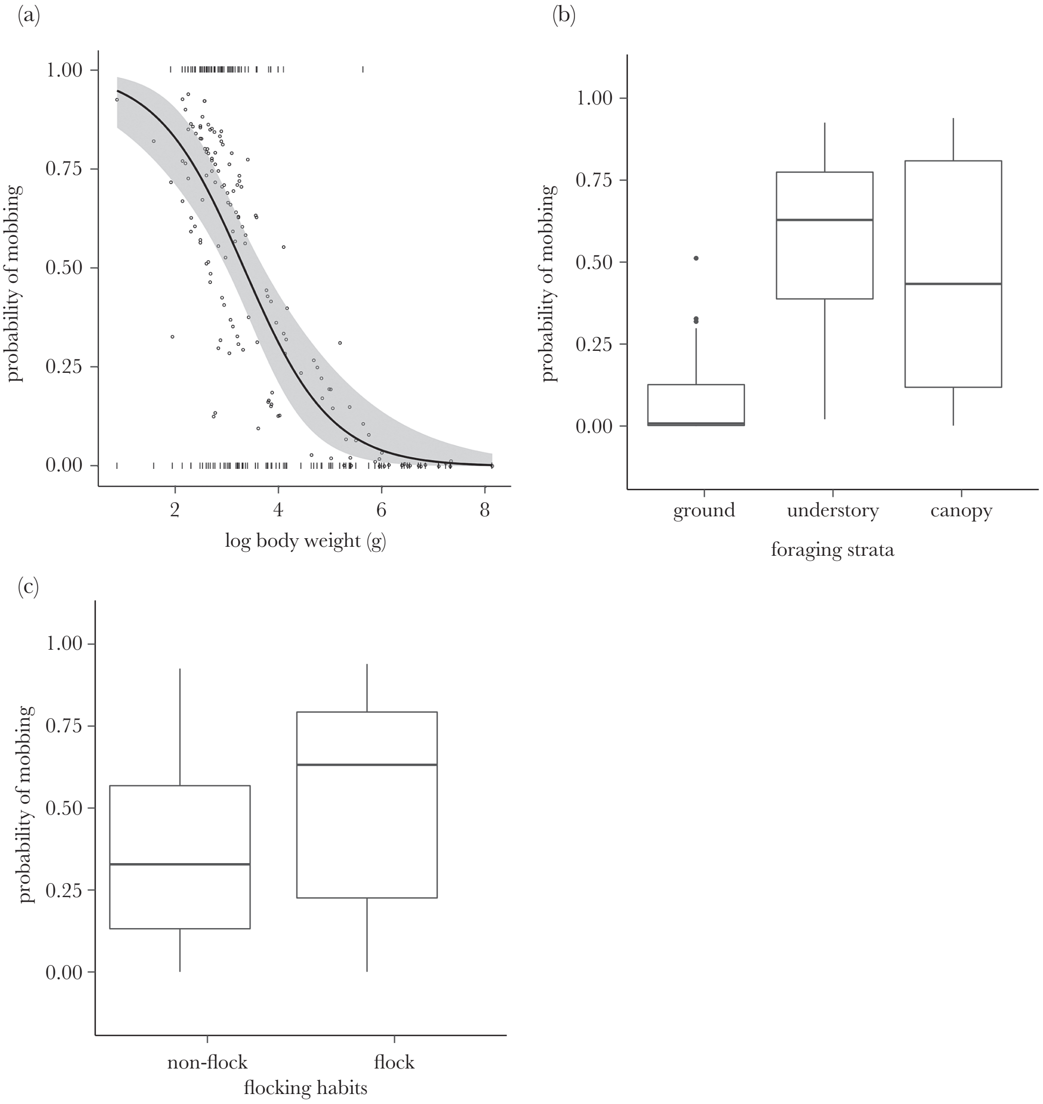

Figure 1

(a) Probability of species mob at least one of the 2 owl models according to the body mass of bird species. Graph based on predicted values from the generalized mixed model using MCMCglmm, the grey area indicates the 95% credible interval. The empty circles are the predict values, while the ticks are the raw values. (b) Probability of species mob at least one of the owl models according to the foraging strata that each species occupy. Graph based on predicted values from the generalized mixed model using MCMCglmm. (c) Probability of species mob at least one of the owl models according to the foraging strata that they occupy. Graph based on predicted values from the generalized mixed model using MCMCglmm.

Safety in numbers hypothesis

A number of studies demonstrated that being in a larger group dilutes the risk to an individual (Hamilton 1971), and reduces the probability of a successful predator attack due to the confusion effect (Miller 1922). In support of this idea, our results showed that gregarious species that join flocks or live in stable groups are more likely to mob than solitary species (Table 1). Thus, even though solitary species could benefit from safety in numbers in a heterospecific mob, they still do not mob. This finding suggests that solitary species may have evolved different strategies of dealing with predators as discussed above, but further studies are required to explore this idea.

Social system hypothesis

Previous studies in a family-living bird species showed that parents mob more intensively in the presence of independent offspring (Griesser and Ekman 2005), and that mobbing provides a social learning opportunity to learn to recognize predators (Griesser and Suzuki 2017). In contrast to our prediction, the social system of a species did not influence their likelihood to engage in mobbing. Clearly, predator mobbing can have social functions also in nonfamily living species, such as providing opportunities to recruit partners for future mobbing events (Krams et al. 2008), to form dispersal coalitions (Maklakov 2002), or to display their quality to potential mates (Cunha et al. 2017a).

Mobbing plasticity depending on the risk

Previous studies showed that birds recognize their predators (Curio et al. 1978b; Griesser and Ekman 2005), and adjust their behavior depending on the specific risks that a predator poses (Griesser 2009; Motta-Junior and Santos-Filho 2012; Tvardíková and Fuchs 2012). In accordance, our findings show that birds

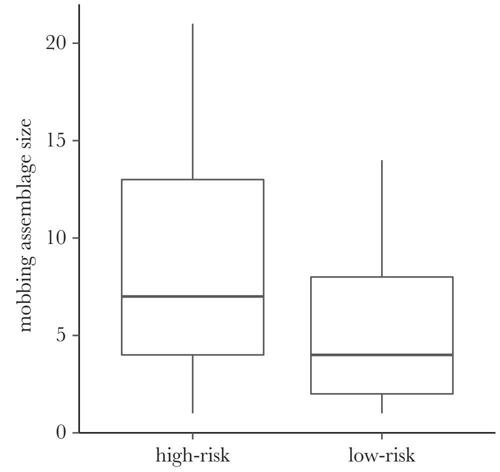

Figure 2

Number of individuals in the mobbing assemblage according to the risk represented by the predator stimuli (high-risk, low-risk). Graphs are based on raw data, bars indicate 95% confidence interval.

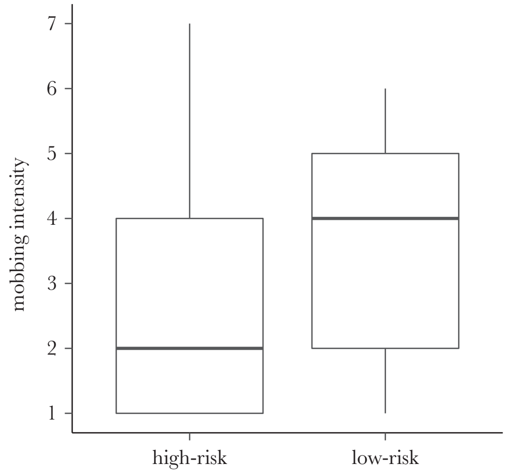

Figure 3

Mobbing intensity according to the risk represented by the predator stimuli (high-risk, low-risk). Graphs are based on raw data, bars indicate 95% confidence interval.

mob less intensely but form bigger assemblages when mobbing a high-risk predator compared to a low-risk predator. A previous study reported that Neotropical birds mobbed a dangerous predator (i.e., striped owl *Asio stygius*) more intensely than a less dangerous predator (i.e., barn owl *Tyto alba*) (Motta-Junior and Santos-Filho 2012). However, these species not only have very different diets, but they are also morphologically distinct and are crepuscular/nocturnal, which may influence the mobbing response of birds. In contrast, we used predator species that are morphologically similar and have diurnal habits. Diurnal owls are a constant threat to most diurnal bird species, therefore the risk of mob a potential threating predator at daytime may be higher than a nocturnal one, which does not impose an immediate threat. Thus, it may be less costly to approach high-risk nocturnal predator than a diurnal high-risk predators. Moreover, the similar plumage of the owls species excludes the possibility that differences in the mobbing behavior were caused by body coloration.

Table 1

Phylogenetically controlled generalized linear mixed model, using MCMCglmm, comparing the effect of body mass (logarithmic scale—g), foraging strata (ground, understory, or canopy), flocking behavior (yes or no), and social organization (nonfamily/cooperative, family living, cooperative), the encounter frequency rate (encounter per min) on the propensity of species to mob or not mob predators

		95% CI		
	Estimate	Lower	Upper	pMCMC
Intercept	2.87	−0.73	6.02	0.11
Body mass	**−2.04**	**−2.75**	**−1.22**	**<0.001**
Foraging strata (ground vs. canopy)†	**3.40**	**0.87**	**5.83**	**<0.001**
Foraging strata (ground vs. understory)†	**2.66**	**0.46**	**4.96**	**0.010**
Flocking behavior (no vs. yes)†	**1.83**	**0.58**	**3.00**	**0.006**
Social organization (nonfamily vs. family)†	0.71	−0.79	1.93	0.30
Social organization (nonfamily vs. coop.)†	1.08	−1.66	4.08	0.49
Encounter frequency rate (encounter/min)	−11.15	−36.03	14.34	0.40
Random effects				
Phylogeny	1.03	0.74	1.30	

Significant *P* values are highlighted in bold.
†Reference level is the first category in these lists.

Table 2

Phylogenetically controlled generalized linear mixed model, using MCMCglmm, comparing the effect of risk posed by a predator, mobbing intensity, season, and body mass on the mobbing assemblage size

		95% CI		
	Estimate	Lower	Upper	pMCMC
Intercept	**0.99**	**0.58**	**1.31**	**< 0.001**
Predator model (high-risk vs. low-risk)†	**0.35**	**0.04**	**0.68**	**0.034**
Mobbing intensity	−0.00	−0.02	0.02	0.76
Season (nonbreeding vs. breeding)†	−0.15	−0.45	0.13	0.30
Body mass	−0.00	−0.05	0.04	0.90
Random effects				
Phylogeny	0.005	0.001	0.01	
Location	0.49	0.33	0.67	
Date	0.03	0.00	0.09	

Significant *P* values are highlighted in bold.
†Reference level is the first category in these lists.

We did not find a difference in the mobbing behavior (intensity and assemblage size) across seasons (breeding vs. nonbreeding). Similarly, a study with drongos (*Dicrurus macrocercus* and *D. leucophaeus*) showed that there was no difference in the frequency that birds mobbed their predators between different seasons (Nijman 2004). Birds may adjust their mobbing behavior according to the season particularly in a nest defense context (Shedd 1982; Shedd 1983). We used predators of adults as stimuli, which pose a risk independent of the season. Moreover, some bird species are year-round territorial, and territoriality seems to influence aggressive behavior

Table 3

Phylogenetically controlled generalized linear mixed model, using Markov chain Monte Carlo technique, comparing the effect of risk posed by a predator, mobbing assemblage size, season, and body mass on the mobbing intensity

		95% CI		
	Estimate	Lower	Upper	pMCMC
Intercept	**2.10**	**0.93**	**3.21**	**< 0.001**
Predator model (high-risk vs. low-risk)†	**−0.75**	**−1.39**	**−0.09**	**0.026**
Mobbing assemblage	−0.01	−0.04	0.08	0.62
Season (nonbreeding vs. breeding)†	−0.08	−0.88	0.78	0.83
Body mass	**−0.004**	**−0.008**	**−0.0006**	**0.032**
Random effects				
Phylogeny	1.00	0.97	1.02	
Location	1.00	0.97	1.03	
Date	0.99	0.97	1.02	

Significant P values are highlighted in bold.

†Reference level is the first category in these lists.

(Hau et al. 2004) and may also influence mobbing behavior, principally during the nonbreeding season.

CONCLUSIONS

Animals can only die once, and thus, prey should adjust their behavior to minimize the risk of immediate death, for example during predator mobbing. Mobbing and other antipredator behaviors generally are studied from the perspective of those that display it. However, to fully understand factors that facilitate the evolution of these behaviors, it is important to compare species that display these behaviors with those that do not display it. Our results show that only species that can afford mobbing, and do not pay too high costs, express this behavior. Clearly, mobbing is only beneficial for species that can be killed by a given predator.

Recent studies showed that predator mobbing also has important social functions, such as learning to recognize predators (Griesser and Suzuki 2017), to advertising their phenotypic quality to potential mates (Cunha et al. 2017a), learning to recognize alarm calls of heterospecifics (Templeton and Greene 2007), and enhancing social bonds (Krams et al. 2008). Thus, mobbing can encompass a range of functions, calling for empirical studies that quantitatively assess the energetic costs and fitness benefits of mobbing across species, further contributing to the understanding of the evolution of risk taking behaviors.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Cunha et al. (2017b).

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