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ORIGINAL ARTICLE

The presence of conspecific females influences male-mobbing behavior

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Abstract

Many prey species mob predators to drive them away, thereby reducing their immediate and future predation risk. Given that mobbing is risky, it may also serve as an opportunity for males to advertise their phenotypic quality to females; however, this idea remains untested. We tested this hypothesis with a field experiment in south-eastern Brazil that assessed the response of sexually dimorphic bird species to models of two diurnal owls: a ferruginous pygmy owl (*Glaucidium brasilianum*), which mainly eats small birds, and a burrowing owl (*Athene cunicularia*), which mainly eats invertebrates and thus poses a low risk to birds. Across 19 bird species, the mobbing intensity was higher when facing the less-dangerous owl, and more males engaged in predator mobbing than females. The mobbing intensity of males was higher with a larger number of conspecific females present. This finding indicates that males may use mobbing to display their phenotypic quality to females, suggesting that predator mobbing may be influenced by sexual selection.

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Significance statement

Predation is an important evolutionary force, often leading to an evolutionary arms race between predators and their prey. A puzzling form of prey-predator interactions is predator mobbing. In a wide range of species, prey individuals approach predators and show characteristic visual and acoustic displays. The primary function of mobbing is to drive the predator away; however, it may also serve as an opportunity to advertise phenotypic quality to conspecifics. Field experiments showed that the mobbing intensity of males increased with the number of conspecific females in the audience, suggesting that female choice may influence the evolution of mobbing behavior.

Keywords Anti-predatory behavior · Prey-predator interaction · Mobbing · Sexual selection · Birds

Introduction

Predation is a key cause of mortality in many species, and accordingly, prey species have evolved a number of anti-predatory defenses, such as mimicry, camouflage, predator mobbing, or feigning death (Caro 2005). Prey should benefit from adjusting their responses according to the risk posed by the predator. Indeed, field studies have shown that birds behave differently in response to different predators depending on the risk they pose (Griesser 2009; Motta-Junior and Santos-Filho 2012).

Mobbing is a widespread anti-predatory behavior, which consists of a prey approaching a potential predator to harass it by giving calls, swooping over it, or even physically attacking it. While mobbing is costly (Dugatkin and Godin 1992; Krama and Krams 2005) and potentially lethal (Sordahl 1990), it has been suggested to be adaptive (Curio et al. 1978b). Predators often move away when being mobbed, reducing the immediate and future risk of an attack (Pavey and Smyth 1998). In addition, predator mobbing may serve as an opportunity to receive support during future predator-mobbing events (Krams et al. 2008) or as a social learning opportunity for juveniles (Griesser and Suzuki 2016) to learn to recognize predators (Griesser and Suzuki 2017).

Moreover, mobbing may serve as a costly signal (Maklakov 2002) of phenotypic quality to conspecifics (Arnold 2000), especially potential mates (Curio et al. 1983; Regelmann and Curio 1986). In many species, males are generally more aggressive than females (Francis et al. 1989; Bard et al. 2002) and mob predators more vigorously than females (Curio et al. 1983; Maklakov 2002; Griesser and Ekman 2005). However, it remains unclear why males and females differ in their mobbing behavior, and whether this behavior may be influenced by sexual selection.

Here, we investigate whether the presence of females influences the mobbing intensity of males in 19 bird species. We exposed birds to two sympatric owl species that vary in their risk to birds and measured the size of the mobbing assembly and the mobbing intensity of all individuals that joined the mobbing assembly. We tested the following two non-exclusive hypotheses: (i) if birds recognize the risk posed by a predator and mobbing aims at reducing the immediate risk, the birds will mob a dangerous predator more intensely than a low-risk predator and (ii) if mobbing is a sexually selected behavior, males will mob more intensely when more conspecific females are present, using it as an opportunity to advertise their phenotypic quality.

Material and methods

Study site

This study was conducted on Cauaia Ranch, Minas Gerais State, south-eastern Brazil (19° 28′ S 44° 01′ W) between February 2011 and February 2012, encompassing both the breeding season (October to March) and the non-breeding season (April to September). The landscape at the study site is dominated by a mosaic of semi-deciduous forests, Brazilian savannah areas, and agricultural fields. All the experiments were conducted in the edge of forest patches with sparse tree and bushes, providing perches to birds during mobbing but allowing good visibility of birds in all directions for at least 20 m.

Experimental procedure

We selected 18 locations that were at least 250 m apart to minimize the risk of resampling the same individuals on the same day (Bibby et al. 2012). Within each location, we placed the model on a 1.5-m pole, 2 m away from an approximately 3-m high tree. We used two models of owl species that are similar in their coloration and size but differ in their risk to birds: a ferruginous pygmy owl model (*Glaucidium brasilianum*, body length = 16.8 cm; 43% of its diet consists of birds (Carrera et al. 2008)), and a burrowing owl model (*Athene cunicularia*, body length = 22.4 cm; 95% of its diet consists of arthropods (Zilio 2006) but it occasionally eats birds (Motta-Junior 2006)). An earlier study showed that the size of predators may affect the mobbing intensity of birds (Templeton et al. 2005). Thus, using similarly sized species controls for the influence of body size on mobbing intensity.

We performed 96 experiments with each model throughout the year (five to six experiments in each location per model). The order of the experiments in each location followed a Latin square design, and we randomly chose different experimental sites within each location. To attract birds to the model and simulate the presence of a live predator, we placed a speaker below the model and played back vocalizations of the respective predator species (calling bouts of 30 s followed by 15 s silence). The observer was positioned 10–15 m from the model wearing camouflage clothes. We registered the behaviors of all present individuals and their distance to the predator during 10 min with a voice recorder. It was not possible to record data blind because our study involved observation of wild animals in the field.

We assessed the maximum mobbing intensity for each bird that mobbed the models during the experiment using a scale of mobbing intensity from 1 to 7 (following Chandler and Rose 1988; Motta-Junior and Santos-Filho 2012): (1) an individual was >10 m away from the model making visual displays, emitting warning calls, or being silent, (2) an individual was ≤10 m and >5 m away making visual displays, emitting warning calls, or being silent, (3) an individual was ≤5 m and >2 m away and 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 and 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. Distances between the birds and the model were assessed with the help of distance marks in trees placed in the four main cardinal directions (north, south, east, and west) before the experiment.

In total, 79 different bird species mobbed the models, but we included only 19 species that have conspicuous sexual color dimorphism to assess the response variable in our analyses (Table 1), allowing unambiguous discrimination of females and males in the field. These species belong to six different taxonomic groups which are mostly poorly studied but display a large variety of mating, parental care, and social systems (del Hoyo et al. 2015). Trochilidae (hummingbirds) are typically polygynyous and females alone care for the brood. Galbulidae (jacamars) usually have biparental brood care and males engage in courtship feeding. Picidae

Table 1 Color-dimorphic species included in this study. Taxonomy follows (Jetz et al. 2012)

Taxonomic family	Scientific name	English name
Trochilidae	*Colibri serrirostris*	White-vented violetear
	Chlorostilbon lucidus	Glittering-bellied emerald
	Heliomaster squamosus	Stripe-breasted starthroat
Galbulidae	*Galbula ruficauda*	Rufous-tailed jacamar
Picidae	*Picumnus cirratus*	White-barred piculet
	Veniliornis passerinus	Little woodpecker
	Campephilus melanoleucos	Crimson-crested woodpecker
Thamnophilidae	*Herpsilochmus atricapillus*	Black-capped antwren
Tyrannidae	*Colonia colonus*	Long-tailed tyrant
Thraupidae	*Nemosia pileata*	Hooded tanager
	Lanio pileatus	Pileated finch
	Tangara cayana	Burnished-buff tanager
	Tersina viridis	Swallow tanager
	Dacnis cayana	Blue dacnis
	Hemithraupis ruficapilla	Rufous-headed tanager
	Volatinia jacarina	Blue-black grassquit
	Sporophila nigricollis	Yellow-bellied seedeater
	Euphonia chlorotica	Purple-throated euphonia

(woodpeckers) have biparental brood care and live solitarily, in couples or in small family groups. Thamnophilidae (antbirds) usually have biparental brood care and are family-group living. Tyrannidae (tyrant flycatchers) are presumably monogamous and pair-bonded and have biparental brood care. Thraupidae (tanagers) usually have biparental brood care and extra-pair paternity is common, and are frequently part of mixed flocks or large groups. The specific breeding and social systems have not been studied in the study populations and thus were not considered here. However, given that female choice is predominant in birds (Searcy 1979; Majerus 1986), it is expected that males use any opportunity to advertise their phenotypic qualities to their current mate, future mates, or potential extra-pair mating partners.

Statistical analyses

We used the software R for our analyses (R Core Team 2015). To test the influence of the presence of female and male conspecifics on the maximum mobbing intensity of each individual in the mobbing assemblage, we used a generalized linear mixed model using Markov chain Monte Carlo techniques in the package MCMCglmm (Hadfield 2010). We used the maximum mobbing intensity as our response variable and included the following predictors: predator model (high-risk or low-risk), interaction between the sex of the individual and the total number of conspecific females in the mobbing assemblage, interaction between the sex of the individual and the number of conspecific males in the mobbing assemblage, interaction between the sex of the individual and the number of total individuals in the mobbing assemblage (conspecifics and heterospecifics), and season (breeding or non-breeding). Given that we tested specific hypothesis based on a priori predictions, all non-significant terms were retained in the models. We included a consensus tree of a recent phylum-wide phylogeny (Jetz et al. 2012) and the location of each experiment as random factors to control for species-specific differences in their abundance and mobbing behavior and to control for potential non-independency of the data, since individuals were not marked. The MCMCglmm model resulted in balanced trace plots and an effective sample size of around 1000 for all variables. We checked the model convergence by analyzing the trace plots, the residuals, and the predicted values of the model. We checked for collinearity among the main effects through the variance inflation factor using the package "car" (Fox and Weisberg 2011). All values were <2.2, showing that collinearity among the main effects was negligible (supplementary material).

An ordinal regression model with phylogenetic control was not practicable, due to quasi-separation of the data (i.e., some clades were only represented by a single rank). Therefore, maximum mobbing intensity was analyzed using a linear mixed model. An earlier simulation study showed that ordinal variables with more than five levels can be reasonably assessed using approaches designed for continuous data (Rhemtulla et al. 2012). We note that an ordinal regression in a generalized linear mixed model without phylogenetic control yields qualitatively similar results (supplementary material).

Results

We observed at least one individual of a sexually dimorphic species in 54 experiments. Overall, 165 individuals of 19 sexually dimorphic species approached the predator models (mean number of total individuals − sexually dimorphic and non-sexually dimorphic − per experiment = 13.09, ranging from 1 to 21). The majority of the individuals that mobbed were males ($n = 108$), independent of the predator species. While 126 individuals mobbed the high-risk model, only 39 individuals mobbed the low-risk model. More males mobbed when exposed to both the high-risk predator model (82 males, 44 females) and the low-risk predator model (26 males, 13 females). In most experiments, no conspecific individuals were present in the mobbing assemblage, independent of the sex of the mobber (Table 2). The number of conspecific females varied between 0 and 3 (mean = 1.53), while the number of conspecific males varied between 0 and 7 (mean = 2.27).

Overall, birds mobbed a low-risk predator model more intensively than a high-risk predator model (Fig. 1, Table 3), but

Table 2 Frequency of additional conspecific males and females in mobbing assemblages. The column on the right indicates the sex of the sampled individual. The table is divided by the frequency of additional males (upper part) and the frequency of additional females (lower part)

Number of additional conspecific females in the mobbing assemblage	Number of additional conspecific males in the mobbing assemblage						
	0	1	2	3	4	7	♂
0	38	9	0	0	0	0	
1	27	12	3	0	0	0	
2	1	2	3	0	0	0	
3	1	0	0	4	8	8	
	0	1	2	3	4	8	♀
0	7	28	5	1	0	0	
1	1	2	2	0	0	0	
2	0	3	0	0	3	3	
3	0	2	0	0	0	0	

males and females did not differ in their mobbing intensity (Table 3). We did not find a difference in mobbing intensity between the breeding and non-breeding season (Table 3). Total mobbing assemblage size (counting conspecific and heterospecific individuals) did not influence the mobbing behavior of either sex (Table 3). However, the composition of the audience influenced the mobbing behavior of males. They mobbed more intensely when more conspecific females were present (Fig. 2; Table 3), but the number of males had no influence (Table 3). The mobbing behavior of females did not depend on the audience size or composition (Table 3).

Discussion

Mobbing is an anti-predatory behavior that primarily aims at moving the predator away, reducing both the immediate and future predation risk (Pavey and Smyth 1998). Since mobbing is risky (Sordahl 1990), it may also serve as an honest signal of phenotypic quality (Zahavi and Zahavi 1997), giving males the opportunity to display their quality to potential mates. Our results support this hypothesis, by showing that male birds mob more intensively in the presence of more conspecific females but not in the presence of more conspecific males.

This pattern could reflect two different processes: males may increase their mobbing intensity after more females join a mobbing assemblage or more conspecific females may join the assemblage due to high male-mobbing intensity. However, it is difficult to assess when males perceive the presence of females in the field, which would be critical to understand which of the two processes occurs. Regardless of the order of events, our data show that the mobbing intensity was not related to assemblage size but only to the number of conspecific females, which suggests that mobbing is influenced by sexual selection. This novel finding highlights the general importance of sexual selection and may help to better understand the evolution of anti-predatory behaviors.

It is well known that birds recognize the specific risks predators pose (Curio et al. 1978a; Griesser 2008). In contrast to our prediction, our experiments showed that birds mob a low-risk predator more intensively than a high-risk one, supporting findings from previous studies (Forsman and Mönkkönen 2001; Griesser and Ekman 2005; Griesser 2009). Thus, despite that driving away a high-risk predator is more beneficial, mobbing it is riskier, suggesting that immediate costs influence mobbing intensity.

In a wide range of species, males show more aggression than females (Bard et al. 2002). Our experiment confirms that males were more likely to mob predators (Maklakov 2002; Griesser and Ekman 2005), yet males were sensitive to the number of conspecific females in the mobbing assemblage. Earlier studies showed that males can be sensitive to their audience, adjusting sexual displays depending on the number

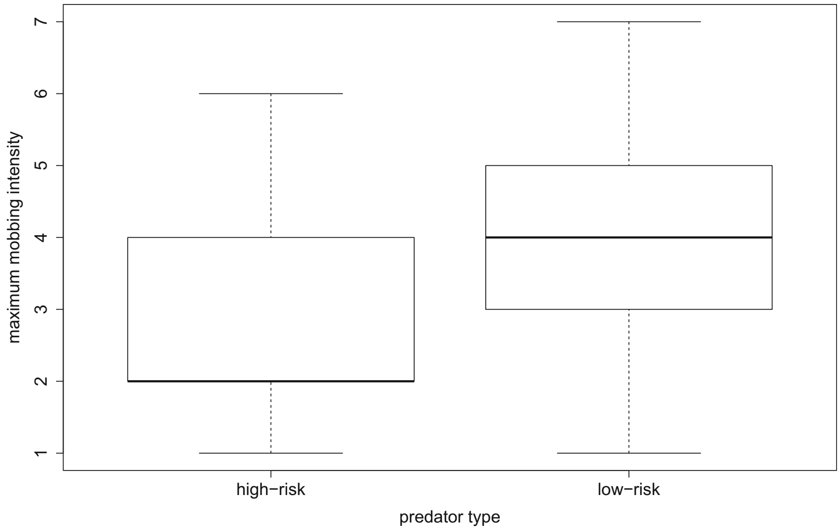

Fig. 1 Birds mobbing intensity according to the predator stimuli. Boxplots showing the median, quartiles of, and maximum and minimum mobbing intensity per treatment

Table 3 Influence of the predator model, sex of the mobber (males or female), the presence of conspecific (females or males), the total number of individuals in the mobbing assemblage (conspecifics and heterospecifics) and season (non-breeding or breeding) on the mobbing intensity of females and males. Significant *p* values are highlighted in italics

	Estimate	95% CI		pMCMC
		Lower	Upper	
Intercept	*2.56*	*1.02*	*3.89*	*0.004*
Sex (female vs. male)[a]	−0.06	−1.16	1.00	0.89
Number of conspecific females in the mobbing assemblage	−0.14	−0.77	0.42	0.63
Number of conspecific males in the mobbing assemblage	−0.06	−0.36	0.24	0.67
Total number of individuals in the mobbing assemblage	0.01	−0.06	0.09	0.74
Predator model (high-risk vs. low-risk)	*0.95*	*0.24*	*1.63*	*0.014*
Season (non-breeding vs. breeding)[a]	−0.13	−0.84	0.45	0.65
Sex (female vs. male)[a] × number of conspecific females in the mobbing assemblage	*1.13*	*0.28*	*1.88*	*0.009*
Sex (female vs. male)[a] × number of conspecific males in the mobbing assemblage	−0.09	−0.48	0.30	0.66
Sex (female vs. male)[a] × total mobbing assemblage	−0.03	−0.11	0.07	0.48
Random effects				
Phylogeny	0.957	0.003	2.84	
Location	0.068	0.002	0.23	

[a] Reference level is the first category in these lists

and/or the quality of (potential) partners (Matos and McGregor 2002; Dubois and Belzile 2012). Clearly, it would be interesting to assess in future experiments whether an increased mobbing effort actually results in a higher mating success for males. If mobbing is costly signaling and therefore sexually selected, we would expect that the audience effect would be higher in polygamous species than in monogamous species (Kirkpatrick et al. 1990). Since the mating and parental care systems for the birds in our study population are not studied, we could not assess their influence on the mobbing intensity of males.

Experiments in chaffinches *Fringilla coelebs* showed that males increased their predator-mobbing effort during the first weeks of the breeding season (Krams and Krama 2002). This result was suggested to reflect interspecific reciprocity, but it may also reflect a benefit of advertising quality to neighbor females (to gain access to extra-pair mating opportunities) or to neighbor males (as a consequence of male-male competition). Similarly, male great tits *Parus major* mob predators more intensely than females (Curio et al. 1983), which may reflect that males are using mobbing to advertise phenotypic qualities. Thus, mobbing could be a sexually selected signal in other species but more experiments are needed to validate the generality of this hypothesis.

Several other factors may influence differences in mobbing behavior in general and between sexes. Temperate birds have been shown to mob more intensely during the breeding season (Shedd 1983), especially when a predator is close to their nest

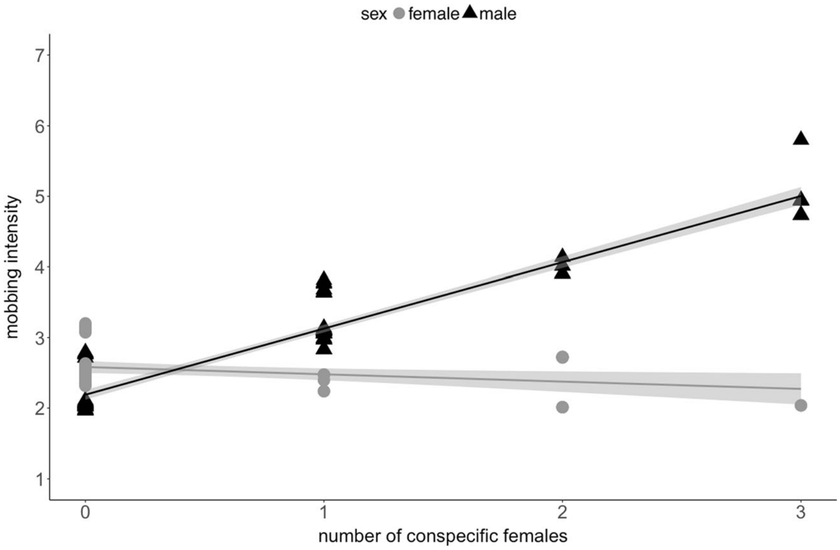

Fig. 2 Mobbing intensity of females and males in relation to the number of conspecific females in the mobbing assemblage based on the predicted values from the model. *Gray areas* represent the 95% credible interval

(Kryštofková et al. 2011). Accordingly, the breeding status can influence the mobbing intensity of males and females across species. However, we did not find a significant difference in mobbing intensity between the breeding and non-breeding season. This result may reflect that tropical and temperate birds differ in their response to nest predators or that the species included in this study breed in different micro-habitats than the ones we chose for our experiment. Furthermore, the mating status of males could influence their mobbing effort, which would be interesting to address in future studies.

To conclude, our results suggest that males across 19 species can use mobbing as an opportunity to display their phenotypic quality to females, highlighting the ubiquitous importance of sexual selection (Andersson 1994). Female choice can be influenced by the motor skills of males, which provides clues about their ability to defend a nest or forage successfully (Barske et al. 2011). Since mobbing a predator is risky, only males with good motor skills that are capable of swiftly escaping can afford to approach a predator, making predator mobbing a potentially honest signal of phenotypic quality (Zahavi and Zahavi 1997).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Ethical statement The study was conducted under research permits issued by the local authorities (Sistema de Autorização e Informação em Biodiversidade).

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