



The effect of mobbing vocalizations on risk perception in common mynas (*Acridotheres tristis*)

Tom Condon¹ · Abbas Hakim¹ · Antonio B. Zenteno Moran¹ · Daniel T. Blumstein¹

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Abstract

Animals emit predator-elicited calls in response to potential predation threats. These vocalizations induce a variety of anti-predator behaviors in conspecific receivers ranging from moving away from predators (alarm calls) to rallying conspecifics to fend them off (mobbing calls). While much is known about the immediate response to alarm calls, less is known about how mobbing calls influence subsequent antipredator decisions. Mobbing calls stimulate harassment of a potential predator. Therefore we predicted that hearing a mobbing call would make animals less likely to immediately flee an approaching threat. To study the potential effect of mobbing vocalizations on risk assessment, we primed common mynas (*Acridotheres tristis*) with a series of different stimuli and studied the variation in their subsequent decisions to flee an approaching human by quantifying flight initiation distance (FID). We found that although mynas increased their rate of locomotion after hearing mobbing calls, their subsequent decision to flee was not influenced. We also found that an individual's propensity to move and look explained some variation in FID. This suggests that while mobbing calls do not influence subsequent decisions to flee, they do affect subsequent behavior.

Keywords *Acridotheres tristis* · Anti-predator behavior · Common myna · Flight initiation distance · Mobbing calls · Risk assessment

Introduction

Predation is an important driver of evolution, creating novel morphological and behavioral antipredator defenses (Caro 2005). Predator–prey interactions are complex and often involve multiple steps (Endler et al. 1986). Behavioral decisions may depend on whether the predator or prey detect the other first. This order of detection influences subsequent decisions about whether to attack, flee, or ignore the other species (Lima and Dill 1990). Prey may face serious consequences for not properly assessing risk. In response to predation, prey may approach the predator in an attempt to drive it off, allowing them to continue foraging (Lima and Dill 1990)

or retreat at the cost of lost foraging opportunities (Ydenberg and Dill 1986). Prey must weigh the costs and benefits of approaching or retreating from predators when deciding how to react (Ydenberg and Dill 1986; Blumstein et al. 2015).

Risk assessment is dynamic and prey must continually monitor the situation to account for new information in their decision making. Playback studies are used to study changes in prey behavior in response to predator vocalizations or sounds (Emmering and Schmidt 2011; Hettena et al. 2013) or in relation to predator-elicited vocalizations (Stone and Trost 1991; Templeton et al. 2005; Hanson and Cross, 2008). Many birds have two types of predator elicited vocalizations: mobbing calls and alarm calls (Caro 2005). Social animals use alarm calls to communicate information about approaching predators to nearby conspecifics and heterospecifics to warn them to escape (Klump and Shalter 1984; Caro 2005; Gil and Bierema 2013; Magrath et al. 2015). Mobbing calls coordinate conspecifics in aggressive responses in an attempt to deter approaching predators (Curio et al. 1978; Hurd 1996; Johnson et al. 2003; Kennedy et al. 2009), however, some animals also respond to heterospecific mobbing calls albeit at a lower intensity (Dutour et al. 2017). The

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✉ Daniel T. Blumstein
marmots@ucla.edu

¹ Department of Ecology and Evolutionary Biology,
University of California, 621 Young Drive South,
Los Angeles, CA 90095-1606, USA

effects of alarm calls on risk perception and subsequent decision-making as well as the behavioral responses to mobbing calls are frequently studied (Stone and Trost 1991; Forsman and Mönkkönen 2001; Lind et al. 2005; Schmist et al. 2008; Suzuki 2012; Magrath et al. 2015; Kalb and Randler 2019), but to our knowledge this is the first study to examine the effect of mobbing calls on subsequent risk perception and escape decisions.

Common mynas (*Acridotheres tristis*) are an ideal species in which to study changes in risk assessment and anti-predator behavior when primed with mobbing call playbacks. Common mynas readily respond to acoustic playbacks (Griffin 2008), including responding to their own vocalizations (Hubbard et al. 2015) which makes them suitable subjects for playback experiments. In addition, studies suggest that mynas aggressively interact with heterospecifics (Fitzsimons 2006; Grarock et al. 2012; Baker et al. 2014). Their potential for aggressive behavior in response to playback makes them an interesting species to study their response to mobbing calls.

Here, we tested whether mobbing vocalizations evoke different behavioral responses in mynas and whether it modified their subsequent risk assessment. To do this, we primed mynas with five exemplars of conspecific mobbing calls or four exemplars of heterospecific non-alarm calls—the song from a sympatric species, red-vented bulbuls (*Pycnotus cafer*), and observed their behavior for 1 min before conducting a simulated predatory approach by having an human observer slowly walk toward the focal subject (Frid and Dill 2002) to measure their flight initiation distance (FID)—the distance between predator and prey when flight is initiated (Cooper and Frederick 2007; Blumstein et al. 2015). We predicted that mynas exposed to conspecific mobbing call playbacks would either approach the observer or tolerate closer approach than mynas exposed to heterospecific non-alarm calls due to previous studies revealing that birds approached the speaker after hearing mobbing call (e.g., Stone and Trost 1991; Hurd 1996).

Methods

Study site

Between 18 January and 5 February 2020, we conducted playback experiments at various locations (Table S1) along roads and open areas in Mo'orea, French Polynesia, between 0700 and 1730 h during periods of low wind (Beaufort ≤ 2), and at times when it was not raining. Mynas were an ideal species to study because they are easy to observe and estimate FID since they are primarily terrestrial foragers (Bates et al. 2014), and because they are abundant where we studied them (Hubbard et al. 2015). To avoid pseudoreplication,

our study sites were 2–9 km apart to account for common myna foraging range; within 2–3 km of their roost (Counsilman 1974). To ensure that we studied unique individuals within study sites, we conducted playbacks at least 30 m apart between focal subjects and did not revisit sites on subsequent days.

Stimulus selection

We used three stimuli in our playbacks. These included five exemplars of myna mobbing vocalizations, to observe how mynas react to their mobbing calls, a silent control, and four exemplars of heterospecific non-alarm calls to test if reactions to the mobbing calls were specifically caused by the conspecific vocalization and not due to hearing a playback in general. We selected our heterospecific non-alarm calls from red-vented bulbuls, a tropical songbird sympatric with common mynas on Mo'orea (Bates et al. 2014) because mynas would recognize the heterospecific non-alarm call and react accordingly. We obtained heterospecific non-alarm call exemplars from a prior study (Hubbard et al. 2015) and conspecific mobbing calls from various sources (Table S2). We eliminated the possibility of familiarity effects, the possibility that mynas may respond more to a call they are familiar with, by using exemplars from outside of Mo'orea for myna (Australia and India) and bulbul (American Samoa, Hawaii, and Pakistan) calls (Hubbard et al. 2015). We found that the playbacks sounded superficially similar to the natural common myna mobbing calls heard on Mo'orea. Each playback track consisted of 30 s of silence followed by 5 s of an exemplar of a treatment and a subsequent 4 min of silence. All playback tracks were edited using Audacity 2.3.3 (AudacityTeam) to remove background noise and select suitable 5 s segments of the vocalizations (Fig. 1). The tracks were exported to an iPhoneXR (Apple, Cupertino, California) and broadcast on a UE Boom 2 speaker (Ultimate Ears, San Diego, California). All stimuli were calibrated to 90–92 dB (measured 1 m from the speaker) using a Radioshack (33–2055, Radioshack, Fort Worth, Texas) Digital Sound Level Meter set to weighting C, peak response.

Experimental setup

We walked through myna habitats and conducted our experiment on relaxed subjects we could approach on foot. Once a suitable subject was identified, a single observer approached the myna to approximate the 15 m starting distance (SD). If the myna was not alerted to the observer's presence, a speaker was then placed and the 30 s silent baseline observation was started followed by 30 s of one of the three playback treatments. Focal observations were conducted by another individual positioned further than 15 m away using binoculars. After 30 s from the start of the playback treatment,

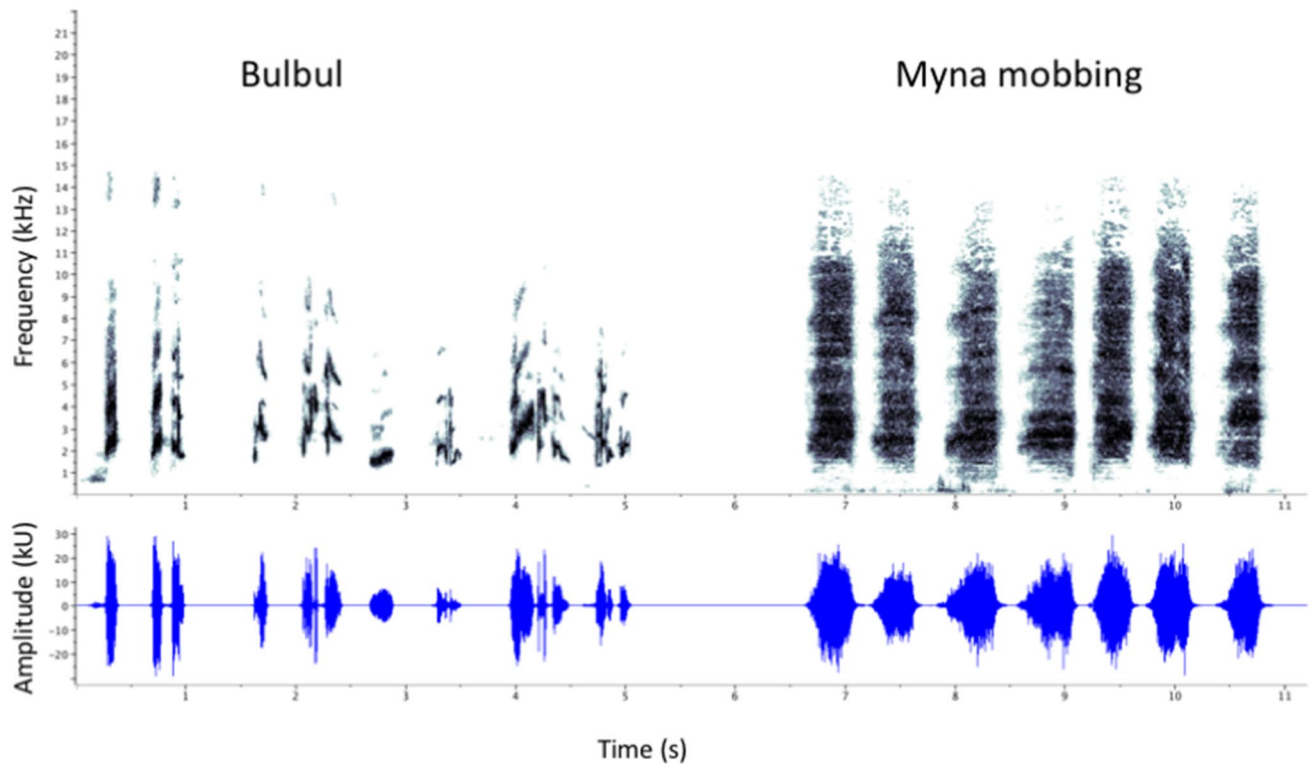


Fig. 1 Spectrograms and waveforms of red-vented bulbul non-alarm vocalization (left) and common myna mobbing vocalizations (right). Spectrograms and waveforms were created using RavenPro

version 1.6.1 (Center for Conservation Bioacoustics, 2019). The spectrogram is a 1024 sample hann spectrogram with a frequency DFT of 2048, 50% overlap, and 512 sample hop size

the focal observation was concluded and the initial single observer approached the myna at a steady pace until the myna fled.

Do mynas respond differently to acoustic treatments?

We aimed to standardize our playback distance to 15 m from mynas, but some subjects moved during the baseline 30 s silence period (19.6 ± 5.9 m; range 7.5–29.2 m). We conducted a continuous recording of the focal subject's behavior during 30 s of silence, followed by a 5 s broadcast of one of the three stimuli treatments, and another 25 s of silence. To avoid observer effects, all behavioral scoring was conducted by a single individual observer (A.Z.) who quietly dictated myna behaviors from an ethogram into an iPhone 6 (Apple, Cupertino, California). Our ethogram was adapted from prior ethograms used to study the proportion of time allocated to behaviors in common mynas (Mahabal 1991; Hubbard et al. 2015) (Table S3).

The same observer then scored all focals in JWatcher (version 1.0; Blumstein and Daniel 2007). Focals were scored as two distinct parts: the baseline 30 s before the playback and the 30 s response from when the playback was first heard. After scoring, we calculated the rates of observed

behaviors during the focal observations in JWatcher (version 1.0; Blumstein and Daniel 2007). We grouped observed behaviors into three categories; looking (head movement in different directions), locomotion (walk, run, fly, hop), and relaxed behaviors (preen and forage). We did not observe any instances of aggressive behaviors and excluded vocalizations in our analyses.

Post-playback period was split into two 15 s time bins. We examined boxplots comparing variation between the 30 s pre and the two 15 s post-playback periods. We chose to proceed with calculations for the 15 s post-playback period to examine immediate behavioral responses to the playbacks. We calculated the change in rates for the three categories above between the 30 s baseline period and the first 15 s of the post-playback period.

Does priming influence subsequent risk assessment?

To measure whether our playback treatment affected risk perception in mynas, we simulated an approaching predator by walking towards mynas (Frid and Dill 2002) to measure FID 30 s after playback began (Adams et al. 2006; Hubbard et al. 2015). Mynas were directly approached at a slow and steady pace of 0.5 ± 0.02 m/s (estimated from 10

measurements). During our approach, we dropped markers (Yee et al. 2013) to measure starting distance (SD), the distance between predator and prey when the predator begins to approach (Blumstein et al. 2015), and alert distance (AD), the distance where prey focuses on an approaching predator, and measured the distances between each marker to the nearest 10 cm using a tape measure.

While we attempted to have a consistent SD of 15 m, mynas frequently moved around during the one min behavioral focal preceding the start of the FID experiment. Some focal subjects were perched above the ground during the FID experiments. For subjects that were in trees or other vertical objects, we calculated FID_{direct} , AD_{direct} , SD_{direct} , and Distance to Speaker_{direct} using the Pythagorean theorem [e.g., $FID_{direct} = (FID^2 + perching\ height^2)$]. Perching height was estimated by “visually rotating the location of the bird into the tree onto the ground, and then measuring the ground distance” (Blumstein et al. 2004: 275).

Statistical analysis

We excluded observations from analysis where mynas were already alert or that were conducted in the presence of known predators (free roaming cats and dogs). We additionally excluded observations that did not have both a focal and FID from analysis. All analyses were conducted in R version 3.6.2 (R Foundation for Statistical Computing).

We tested for potentially confounding variables by running a one-way analysis of variance (ANOVA) on wind speed, percent cloud cover, number of conspecifics within 10 m, Distance to Speaker_{direct}, distance from cover, and height in cover with respect to the different treatments. Additionally, exemplar effects were tested using one-way ANOVAs with difference in rates of the three behaviors (relaxed, looking, and locomotion) as the dependent variable. We accounted for anthropogenic noise, which included passing traffic and nearby construction, by recording either the absence or presence of noise during each experiment. Given that these noises may have affected the mynas perception of the playback experiment, anthropogenic noise was included as a variable in later analyses.

To determine whether mynas responded to the playback, we calculated the 95% confidence intervals (CI) of the difference in rates of our three observed behaviors from the 30 s baseline period compared to the first 15 s post-playback. The rate of a behavior was defined as a number of times a behavior was observed per observation period. 95% CIs that did not include zero were interpreted as mynas significantly changing their behavior in response to the playback.

We fitted general linear models to examine the effects of playback treatment on the change in rate of each of the three behaviors. The models included direct speaker distance, the presence of substantial anthropogenic noise, and playback

treatment. We calculated pairwise comparisons of the means of the differences in the rates of behavior change between the three treatments using the Tukey method via the emmeans package (Lenth 2020). To test assumptions of our linear models, we calculated the residuals using the residual function in R on the fitted linear models for the change in rates of locomotion, looking, and relaxed behaviors between the pre 30 s and the post 15 s. We checked model fit by plotting the residuals in a histogram, examining Q–Q plots, and plotting residuals against the fitted values.

To test if the previous playback experiment affected subsequent FID, and for each behavior, we fitted a linear model for FID_{direct} that included AD_{direct} , playback treatment, anthropogenic noise, the interaction between AD_{direct} and playback treatment, and the residuals from the response to playback model for each behavior. We calculated pairwise comparisons of the means of FID_{direct} using emmeans as above to identify significant differences between treatments. We calculated partial η -squared values to assess the effect size of each fixed effect via the sjstats package (Lüdtke 2020).

All data and code are contained in on-line supplementary material (Table S4, Table S5). Throughout we interpret $p < 0.05$ as significant.

Results

Do mynas respond differently to acoustic treatments?

We conducted focal observations paired with FID experiments on 66 individuals ($n = 21$ for heterospecific non-alarm call treatment, $n = 24$ for conspecific mobbing call treatment, and $n = 21$ for silence treatment). Wind speed [$F(2,63) = 0.208$; $p = 0.813$], percent cloud cover [$F(2,63) = 0.213$; $p = 0.809$], number of conspecifics within 10 m [$F(2,63) = 1.677$; $p = 0.195$], Distance to Speaker_{direct} [$F(2,63) = 1.666$; $p = 0.197$], distance from cover [$F(2,63) = 0.393$; $p = 0.676$], and height in cover [$F(2,63) = 0.855$; $p = 0.43$] did not differ by treatment and thus were not potentially confounding (all ANOVA p -values > 0.178). We did not find exemplar effects for conspecific mobbing calls in the rate of locomotion [$F(4,19) = 0.498$; $p = 0.737$], looking [$F(4,19) = 1.122$; $p = 0.375$], or relaxed behavior [$F(4,19) = 0.335$; $p = 0.851$]. Exemplar effects were also absent for heterospecific non-alarm calls in the rate of locomotion [$F(3,17) = 2.246$; $p = 0.12$], looking [$F(3,17) = 0.503$; $p = 0.686$], and relaxed behavior [$F(3,17) = 0.743$; $p = 0.541$].

Examining the means and CIs, we found that mynas responded to conspecific mobbing calls by increasing their rate of locomotion (95% CI = 0.261–0.025), but there were

Fig. 2 Changes in rate of behaviors in common mynas in response to a playback experiment. **a** Mean ($\pm 95\%$ CI) change in rate of locomotion between 30 s baseline period and first 15 s following playback. **b** Mean ($\pm 95\%$ CI) change in rate of looking between 30 s baseline period and first 15 s following playback. **c** Mean ($\pm 95\%$ CI) change in rate of relaxed behavior between 30 s baseline period and first 15 s following playback. Shared uppercase letters show that means are not significantly different between treatments

no significant changes in response to heterospecific non-alarm calls or silence (CI's included 0; Fig. 2a). Mynas had lower rates of looking in response to the silent treatment (95% CI = -0.033 to -0.113 ; Fig. 2b) and conspecific mobbing calls (95% CI = -0.005 to -0.08 ; Fig. 2b). Mynas did not modify their relaxed behavior in response to the playbacks (all CI's included 0; Fig. 2c).

Our linear models (Table 1) revealed that there were significant differences in the rates of locomotion across treatments [$F(4,61) = 3.099$; $p = 0.022$]; they increased rates of locomotion significantly more in response to hearing conspecific mobbing vocalizations compared to either silence [$t(61) = -2.81$; $p = 0.015$] or heterospecific non-alarm vocalizations [$t(61) = -2.626$; $p = 0.029$]. There were no differences between silence and heterospecific non-alarm vocalizations [$t(61) = -0.187$; $p = 0.981$]. We detected no significant differences in changes of rates of relaxed or looking behavior between the treatments.

Does prior exposure to conspecific mobbing calls influence subsequent risk assessments?

We found a positive relationship between AD_{direct} and FID_{direct} , however, there was no obvious difference in the slope of the regression lines (Fig. 3). Thus, being primed by a conspecific mobbing call playback did not influence subsequent risk perception as comparison of FID between treatments did not differ significantly. The linear model for FID_{direct} was significant [$F(9,56) = 18.92$; $p < 0.001$] and explained 71.2% of the variance (Table 2). We found no direct effect of treatment on FID. Additionally, we found no significant effect of treatment on the rate of looking, but alert distance and the residuals of the differences in looking and locomotion were significant within the FID model (Table 2). Individual mynas that were more inclined to look and locomote had greater FIDs.

Discussion

Mynas engaged in higher rates of locomotion after hearing conspecific mobbing calls, often flying closer to the speaker during the mobbing call playback and, in at least one instance, emitting a mobbing vocalization. Mynas showed no response in rates of relaxed or looking behavior after

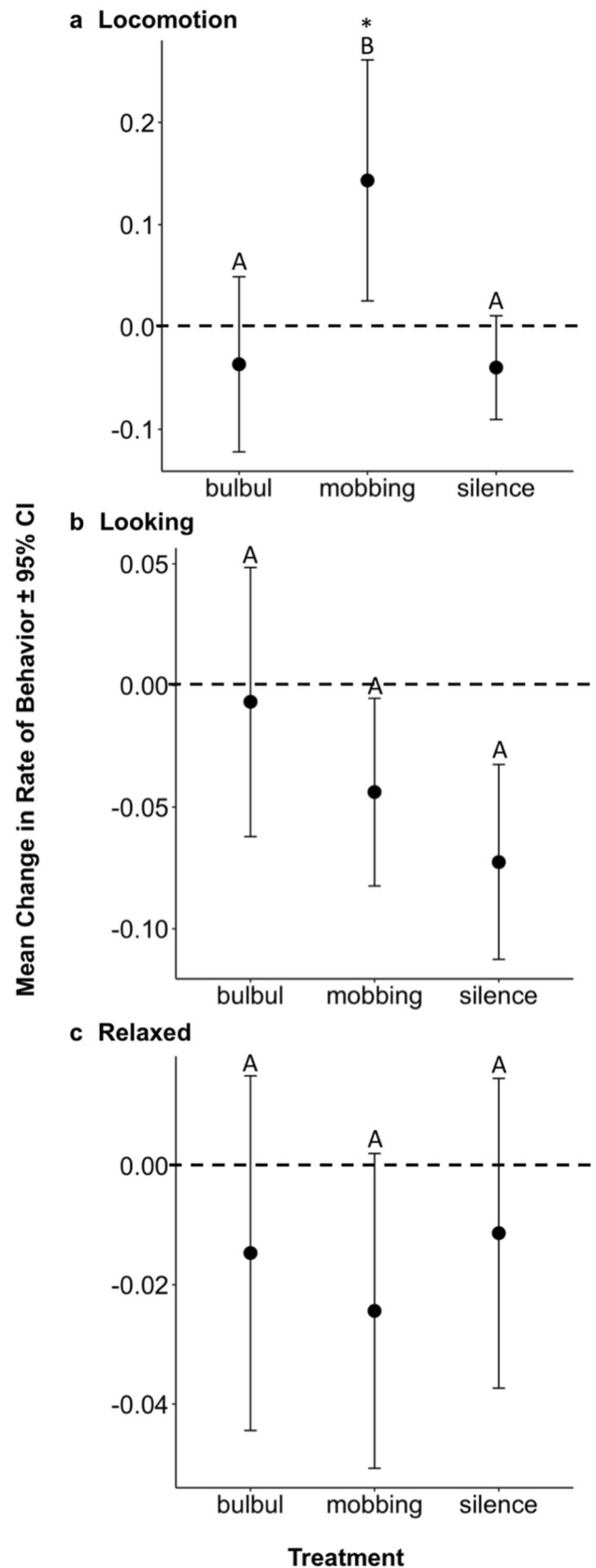


Table 1 Linear models summarizing the behavioral response of mynas to a playback experiment: (a) Locomotion (b) Looking (c) Relaxed

Variables	Estimate	Std. Error	<i>T</i>	<i>p</i>	Partial <i>R</i> ²
(a) Locomotion^a					
Intercept	0.021	0.099	0.215	0.830	
Speaker Distance _{direct}	-0.003	0.005	-0.528	0.599	0.005
Playback Treatment (silence reference)					
Bulbul	0.012	0.066	0.187	0.853	0.146
Mobbing	0.181	0.063	2.881	0.005	
Anthropogenic Noise	-0.048	0.055	-0.873	0.386	0.012
(b) Looking^b					
Intercept	-0.196	0.045	-4.380	<0.001	
Speaker Distance _{direct}	0.007	0.002	3.026	0.004	0.131
Playback Treatment (silence reference)					
Bulbul	0.047	0.030	1.573	0.121	0.040
Mobbing	0.029	0.028	1.022	0.311	
Anthropogenic Noise	0.019	0.025	0.770	0.444	0.010
(c) Relaxed^c					
Intercept	-0.056	0.029	-1.934	0.058	
Speaker Distance _{direct}	0.002	0.001	1.657	0.103	0.043
Playback treatment (silence reference)					
Bulbul	-0.010	0.019	-0.520	0.605	0.009
Mobbing	-0.013	0.018	-0.697	0.488	
Anthropogenic noise	0.009	0.016	0.586	0.560	0.006

Bold values indicate statistically significant terms

^a[*F*(4,61) = 3.099; Adjusted *R*-squared = 0.114; *p* = 0.022]

^b[*F*(4,61) = 3.685; Adjusted *R*-squared = 0.142; *p* = 0.009]

^c[*F*(4,61) = 0.906; Adjusted *R*-squared = -0.006; *p* = 0.466]

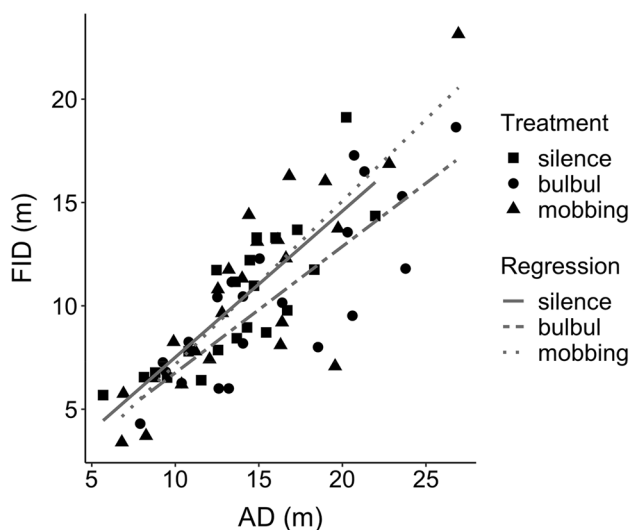


Fig. 3 The relationship between AD_{direct} and FID_{direct} for common mynas previously exposed to silence (square, solid line), bulbul non-alarm vocalization (circle, two-dashed line), and mobbing call (triangle, dotted)

exposure to heterospecific non-alarm calls. This result differs from previous study on mynas (Hubbard et al. 2015), which found that mynas decreased relaxed behaviors during playback of non-alarm calls from conspecifics and heterospecifics, and were also more responsive to a simulated predatory approach (Hubbard et al. 2015). However, these differences may be attributable to the length of time that the playback was presented (30 s) for Hubbard et al. (2015) compared to the priming (5 s) playbacks we employed.

However, these differences may also reflect biological differences in behavior elicited by conspecific mobbing call versus a heterospecific non-alarm call. We found no change in relaxed behavior after exposure to a heterospecific non-alarm call, however, Hubbard et al. (2015) found a decrease in relaxed behavior during a continuous playback using the same exemplars. Prior research also suggests that mynas respond differently to calls temporally in that mynas lose interest in simulated predators if they see them after hearing a distress call whereas mynas resist habituation to a predatory stimulus if they see a simulated predator while hearing a distress call (Griffin 2009). These results may indicate that risk assessment is affected by both the timing of a vocalization in relation to the timing of a predator's approach, and the length of a vocalization.

Table 2 Linear model explaining variation in FID_{direct} following the playback experiment

Variables	Estimate	Std. error	<i>T</i>	<i>p</i>	Partial η^2
Intercept	0.517	1.837	0.282	0.779	
AD_{direct}	0.721	0.125	5.75	< 0.001	0.664
Playback Treatment					
Bulbul	− 0.0854	2.398	− 0.036	0.972	0.023
Mobbing	0.0884	2.288	0.039	0.969	
Anthropogenic noise	− 0.832	0.577	− 1.441	0.155	0.011
Behavior rate residuals					
Looking	7.098	3.048	2.329	0.024	0.014
Relaxed	5.158	4.603	1.121	0.267	0.006
Locomotion	3.716	1.405	2.645	0.011	0.034
Interactions					
AD _{direct} : bulbul treatment	− 0.077	0.158	− 0.487	0.628	0.002
AD _{direct} : mobbing treatment	− 0.007	0.156	− 0.048	0.962	

Bold values indicate that significant variables

Mynas did not change their response to an experimental approach—as FIDs remained similar regardless of the playback they have heard. In addition, we found that neither exposure to conspecific mobbing calls nor to non-alarm vocalizations influenced subsequent risk perception. Great tits (*Parus major*) that heard conspecific mobbing calls resumed foraging as if the threat had disappeared once broadcast of mobbing calls was stopped (Lind et al. 2005). These observations may help to explain why no changes in relaxed behavior were observed following the conspecific mobbing call as mynas may have taken the same amount of time to resume relaxed behavior (foraging and preening) regardless of the type of treatment during the playback experiment. This highlights how animals temporally assess predation risk; mobbing vocalizations may only affect risk assessment when being heard and no longer alter risk assessment when not emitted.

Interestingly, some of the variation in our model was explained by the residuals for rates of looking and locomotion. Mynas with higher baseline rates of looking or locomotion tended to flee at greater distances. Thus, the propensity for individuals to look or engage in locomotion could explain some of the variation in FID among individuals. Individual differences affect how individuals process information (Kurvers et al. 2010; Krippel et al. 2013) and including direct measurements of consistent individual differences into future studies could enhance our understanding of behavior (Wolf and Weissing 2012).

Individual differences, such as boldness and shyness have been shown to determine whether an individual is more likely to make use of social information (Webster et al. 2009; Kurvers et al. 2010). While we did not formally quantify boldness or shyness, bolder individuals may be more likely to move in response to playback, and this may account for some of the unexplained variation.

Additionally, individual differences in physical conditions (e.g., pectoral muscle volume and mass) may explain some variation in response. For instance, low body condition male dark-eyed juncos (*Junco hyemalis*) were more likely to actively mob a simulated predator (Abolins-Abols and Ketterson 2017). Future studies that document how conspecific mobbing calls affect risk perception and subsequent decisions may benefit from testing whether there are consistent individual differences that explain variation in escape behaviors.

Our results suggest that while mynas respond to being primed with conspecific mobbing call playbacks, these effects do not carry over into their subsequent decisions to flee. Given that previous studies show that the time between a vocalization can affect response intensity and that animals may only perceive a threat when continuously receiving information and may assume the threat is gone when broadcast of calls is stopped (Lind et al. 2005; Griffin 2009), it is important to determine whether animals change their escape behavior over time. Future work is needed to investigate if FID differs when approached at different times during and after a playback. Pending future insights, we now conclude that mynas do not change their subsequent escape behavior after being primed with 5 s of conspecific mobbing calls 30 s before a simulated predatory approach.

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Compliance with ethical standards

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

Ethical approval Research was conducted under permits issued by the Government of French Polynesia (permit approved on 21 November 2019). Common mynas were studied under University of California Los Angeles (UCLA) IACUC Protocol 2001-147-62B (4 November 2019).

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