Behavioral Ecology

The official journal of the ISBE International Society for Behavioral Ecology

Behavioral Ecology (2015), 26(2), 632–638. doi:10.1093/beheco/arv002

Original Article

Heterospecific nonalarm vocalizations enhance risk assessment in common mynas

Lilah Hubbard, William King, Anmy Vu, and Daniel T. Blumstein
Department of Ecology and Evolutionary Biology, University of California, 621 Charles E. Young Drive South, Los Angeles, CA 90095-1606, USA

Received 22 August 2014; revised 29 December 2014; accepted 30 December 2014; Advance Access publication 10 February 2015.

Animals rely on their acoustic environments to gain information regarding predator threats and social opportunities. However, because individuals have limited attention, focusing on a particular aspect of their acoustic environment may affect their ability to allocate attention elsewhere. Some previous studies support the distracted prey hypothesis, which suggests that animals may be distracted by any stimuli, inhibiting their ability to detect approaching predators. In this study, we further tested the distracted prey hypothesis by employing playback experiments to simultaneously examine the relative effects of 3 types of noises—anthropogenic sounds, conspecific nonalarm sounds, and heterospecific nonalarm sounds—as distractors for common mynas (*Acridotheres tristis*). We used 3 different stimuli: motorcycle noise, social common myna calls, and social red-vented bulbul (*Pycnonotus cafer*) calls. We first examined myna response to each stimulus by measuring time allocation to various behaviors immediately before and during broadcasting the 3 playbacks. We then studied how these stimuli affected their antipredator behavior by measuring the distance at which they fled from an approaching predator (flight initiation distance). We found that mynas responded to all 3 stimuli by delaying their return to relaxed behavior following the playbacks compared with a silent treatment. In contrast to the distracted prey hypothesis, we found that mynas fled at greater distances when hearing red-vented bulbul social vocalizations than during our silent treatment. This suggests that rather than distracting, some social vocalizations may enhance prey vigilance and lead to earlier flight.

Key words: **antipredator behavior, carryover effects, common mynas, distraction, flight initiation distance, heterospecific vocalizations.**

INTRODUCTION

Attention is a selective process in which an organism processes only a small subset of the surrounding stimuli at a given moment (Bushnell 1998; Dukas 2004). Because attention is limited (Dukas 2004), organisms must divide the time to which they allocate attention among different behaviors. Here, we define a distraction as any stimulus that causes an organism to reallocate attention away from fitness-related activities (Chan and Blumstein 2011). Distractions can indirectly affect fitness, including lowering foraging efficiency by reallocating attention away from foraging (Purser and Radford 2011). Distractions can also have direct impact on fitness by changing antipredator behavior and rendering organisms more susceptible to predation (Dukas 2004).

Social animals must allocate attention to both monitoring conspecifics (Roberts 1988) and detecting predators (Blumstein 2006). Therefore, animals engaged in social activity with conspecifics may be less able to detect predatory threats. For instance, impalas (*Aepyceros melampus*) engaged in social grooming were distracted from monitoring predators (Mooring and Hart 1995), male willow warblers (*Phylloscopus trochilus*) engaged in fighting behavior responded later to predators (Jakobsson et al. 1995), golden marmots (*Marmota caudata aurea*) exhibiting play behavior responded more slowly to alarm calls (Blumstein 1998), and brown anoles (*Anolis sagrei*) exposed to moving conspecific visual models tolerated closer predator approaches (Yee et al. 2013).

But it is not just natural stimuli that have the potential to distract animals. As urbanization expands and alters ecosystems (Vitousek et al. 1997; Western 2001), anthropogenic noise becomes an increasingly important component of the acoustic environments in which organisms find themselves (Slabbekoorn and Peet 2003; Katti and Warren 2004). A growing body of literature shows that, aside from interfering with acoustic signals (Foote et al. 2004) and masking vocalizations (Slabbekoorn and Peet 2003; Warren et al. 2006; Wood and Yezerinac 2006; Bee and Swanson 2007), anthropogenic noises can also reallocate attention (e.g., Chan et al. 2010). For example, tourist conversation affects predator risk assessment in hoatzins (*Opisthocomus hoazin*), causing heightened disturbance responses (Karp and Root 2009). Similarly, terrestrial hermit crabs subjected to motorboat noise playbacks allowed a simulated predator to approach closer before hiding (Chan et al. 2010).

Address correspondence to D.T. Blumstein. E-mail: marmots@ucla.edu.

L. Hubbard and W. King contributed equally to this work.

The distracted prey hypothesis states that "any stimulus an animal can perceive is capable of distracting it by reallocating part of its finite attention and thus preventing it from responding to an approaching threat" (Chan et al. 2010, p. 459). Although previous studies provide general support for the distracted prey hypothesis (Chan et al. 2010; Yee et al. 2013), there is substantially less knowledge about how acoustic signals may affect attention and antipredator behavior (but see Adams et al. 2006). Furthermore, although previous studies have focused on the use of both conspecific alarm calls (e.g., Weary and Kramer 1995; Hanson and Coss 2001; Suzuki 2011; Cäsar et al. 2012; Gill and Bierema 2013; Nakano et al. 2013) and heterospecific alarm calls (review: Magrath et al. 2014), to gain information regarding predator risks, we are unaware of any studies that have examined the effect of conspecific or heterospecific *nonalarm* calls on antipredator behavior. Because they can also constitute a part of an animal's environment, it is certainly conceivable that conspecific and heterospecific nonalarm sounds may distract an animal and affect its antipredator behavior.

In this study, we further explored the distracted prey hypothesis by simultaneously examining the relative effects of 3 types of sounds—anthropogenic sounds, conspecific nonalarm sounds, and heterospecific nonalarm sounds—as distractors using a playback experiment on common mynas (*Acridotheres tristis*) in Mo'orea, French Polynesia. We ask the question: do anthropogenic noises, conspecific nonalarm vocalizations, or heterospecific nonalarm vocalizations distract mynas? To answer this question, we examined 1) how acoustic stimuli affect behavioral time allocation in common mynas and 2) how response to acoustic stimuli affects risk assessment.

To investigate the effects of these stimuli on risk assessment, we quantified flight initiation distance (FID)—the distance a prey flees an approaching predator. However, because the distance at which prey are alerted by a predator (alert distance [AD]) has a profound effect on FID (Blumstein 2003; Samia et al. 2013), AD must be incorporated into subsequent analyses that seek to identify how specific factors (acoustic treatments in our case) explain variation in FID. We hypothesized that all 3 types of stimuli would distract mynas from risk assessment and predator detection compared with silent control treatments. However, the relative distracting effect would be greatest with anthropogenic sounds (because they may be evolutionarily novel), medium with conspecific sounds (because they may be social cues), and least with heterospecific sounds (because they may provide less "useful" information). We also predicted that more distracted mynas would tolerate closer approaches by predators (i.e., lower FID).

METHODS

Study system

Common mynas (also known as Indian mynas) are native to south Asia (Kannan and James 2001). They were introduced to French Polynesia (Lowe et al. 2000) and are now abundant on the island of Mo'orea. Mynas are social, pairing up throughout the year (Siddique et al. 1993), and often forage and roosts in groups (Pell and Tidemann 1997). They are omnivorous (Pell and Tidemann 1997) and emit a variety of vocalizations (Kannan and James 2001). Mynas are known to be aggressive toward other bird species (Pell and Tidemann 1997; Fitzsimons 2006).

The common myna on Mo'orea provides an ideal opportunity to examine how anthropogenic and conspecific sounds influence predation risk assessment for 4 reasons. First, because mynas are both social and vocal, it is likely that conspecific vocalizations influence their attention. Second, because common mynas on Mo'orea are sympatric with humans, we can reasonably expect that anthropogenic noise may impact them. Third, although common mynas have become somewhat tolerant to human presence (McGiffin et al. 2013) and permit humans to approach them, they still ultimately flee from persistent approach, which was a precondition for our experiment. Finally, common mynas have easily identifiable antipredator responses (Griffin 2008).

Study site

We studied mynas in and around the Richard B. Gump Mo'orea Field Research Station (−17.49°S, −149.82°W) on Mo'orea, French Polynesia from 23 January to 5 February 2014. We conducted experiments along roads and in open areas at 11 locations: Gump Station, Teavaro Beach (−17.80°S, −149.75°W); Juice Factory (−17.49°S, −149.83°W); Agricultural School (−17.53°S, −149.83°W); Sailing School (−17.49°S, −149.85°W); Cultural Center (−17.49°S, −149.82°W); St. Joseph's Church (−17.50°S, −149.82°W); Gump Neighborhood (−17.49°S, −149.82°W); Farm Road (−17.50°S, −149.82°W); Shrimp Farm Road (−17.52°S, −149.83°W); and Main Road (−17.49°S, −149.82°W). Mynas usually only travel about 1–3 km from their roosting site (Pell and Tidemann 1997; Grarock et al. 2012). Our study sites were 0.5–9.0 km apart. We took care to conduct experiments on mynas in different areas within each site. Mynas were found primarily in rural areas at all sites. Experiments were conducted between 0630 and 1800 hours during dry periods between intermittent bouts of rain.

Stimulus selection

For the playback experiment, we broadcast anthropogenic, conspecific, and heterospecific sounds. We selected nonalarm vocalizations for both conspecific and heterospecific stimuli because mynas could associate alarms calls with an approaching predator, whereas we were mainly interested in the effects of those sounds as distractors. For heterospecific stimuli, we selected songs from red-vented bulbuls (*Pycnonotus cafer*), a tropical songbird sympatric with mynas on Mo'orea (Thibault et al. 2002). Red-vented bulbuls sing throughout the year (Kumar 2003), were ubiquitous at our study sites, and primarily feed on fruit and plant parts (Bhatt and Kumar 2001). They are known to act aggressively toward other bird species outside of Mo'orea (Thibault et al. 2002) despite being nonterritorial (Kumar 2004). Thus, bulbuls were a suitable choice for examining the effects of heterospecific social vocalizations on common myna behavior. Our anthropogenic playbacks were recordings of engine noise from motorcycles, a mode of transportation on Mo'orea. We were unaware of any cases where motorists on the island harassed or hunted mynas and thus presumed that mynas did not interpret motorcycle noise itself as a signal of predatory threat. Our control was silence. This silent control permitted us to determine natural patterns of vigilance and was essential to calculate an undistracted FID in response to our experimental approaches.

We obtained, from the Internet, 4 different exemplars of common myna vocalizations, red-vented bulbul vocalizations (macaulaylibrary.org and xeno-canto.org), and motorcycle engine sounds (soundjay.com) (Figure 1). Internet sources labeled bird vocalizations as social calls or songs but did not specify the purpose of each vocalization, but we regularly heard similar vocalizations while conducting fieldwork. Because we were interested in distraction due to sociality in general, we allowed for the possibility that our exemplars included different types of social calls or songs and focused on using the available, high-quality, nonalarm vocalizations. Because our vocalization exemplars were recorded outside of Mo'orea for both mynas (Madagascar, Mauritius, and South Africa) and bulbuls (American Samoa, Hawaii, and Pakistan), we eliminated any potential familiarity effects that would have arisen if some exemplars recorded on the island were familiar to some mynas but not others. Because we were interested in determining whether social sounds could act as distractors, we wanted to ensure that the songs used sounded similar to what we heard in Mo'orea. In addition to listening to the songs in the field and confirming that they sounded similar, we also compared the rates of natural myna and bulbul vocalizations that we recorded at our study site to those of the exemplars we used. Average calling rates did not differ significantly between natural recordings and our playbacks for either species' vocalizations (2-tailed, independent sample *t*-tests, $P > 0.05$ for both).

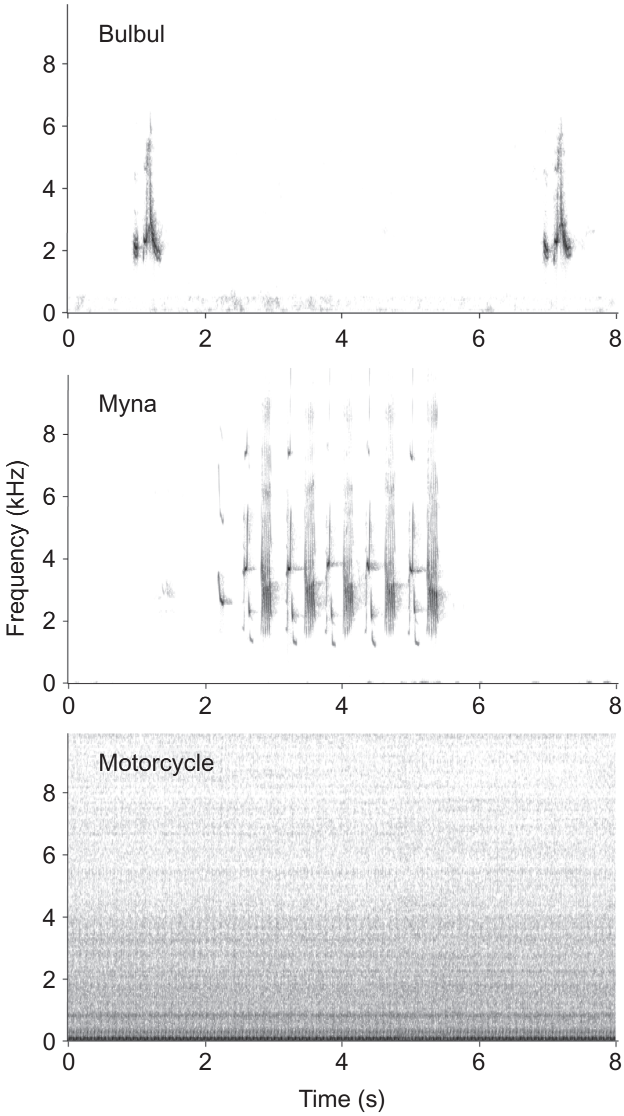

Figure 1
Example spectrograms of common myna (top), red-vented bulbul (middle), and motorcycle (bottom) playbacks. Spectrogram parameters: 1024 point, boxy spectrogram, Hamming filter, 87.5% overlap, 2.902 ms time resolution, 43.07 Hz frequency resolution. Spectrograms were created using Canary (version 1.2.4; Charif et al. 1998).

We removed background noise and created playback tracks using Audacity (version 2.0.5, Audacity Team 2013). After selecting suitable segments of vocalizations (10–45 s in duration), each exemplar was looped for 150 s. We then added 30 s of baseline silence to the beginning of each playback to create a 180-s audio file. In total, we had 4 different treatments: silence (no stimulus played back), bulbul nonalarm vocalization, myna nonalarm vocalization, and motorcycle noise.

Experimental setup

We walked through suitable habitat and conducted an experiment when we identified a subject that could be approached on foot. Most mynas (83%) were on the ground, but some playbacks were conducted on birds within 5 m of the ground. Once a subject was identified, we slowly and quietly approached it and then began a 30-s silent baseline observation period, followed by the initiation of 1 of the 4 treatments. Each focal myna was subjected to 1 treatment, and treatments and exemplars were delivered sequentially between trials to avoid carryover effects and to ensure that a variety of exemplars were used. Stimuli were broadcast at 85 dB SPL (measured 1 m from speaker using SPER Scientific digital sound level meter [#840029], weighting A, peak response). All playbacks were broadcasted through a battery-powered speaker (Pignose 7-100-R, Pignose Industries, Las Vegas, NV) about 1.5 m off the ground from sound files uploaded to a Generation 6 iPod nano (Apple Computer, Cupertino, CA). The speaker was set into place at the start of the silent baseline observation period and remained stationary for the duration of each experiment.

Quantifying behavioral time budgets

A single observer (A.V.) dictated the focal myna's behavioral transitions (ethogram in Table 1) onto a handheld digital recorder throughout 30 s of silent baseline and the subsequent 30 s of playback. Our ethogram was based on those used to study activity time budget of common mynas (Mahabal 1991) and antipredator behavior in other birds (e.g., Adams et al. 2006).

Table 1
Ethogram used for focal behavior observations

Behavior	Description
Pecking (aggressive)	Jabbing of beak toward another animal
Chasing (aggressive)	Pursuit toward an animal via either flight or foot
Biting (aggressive)	Closing beak on another animal
Flapping (aggressive)	One or more wing movements toward another animal
Fly	Utilizing wings to locomote in air
Hop	In air without utilizing wings
Walk	One or more slow-paced steps
Run	One or more fast-paced steps
Stand and forage	Feeding with head down
Preen	Contact of beak to any part of own body
Look	Standing in place, focused on one object scored each time head moves
Ruffle	Shaking body part while sitting or standing in place
Social vocalization	Emitting one of multiple nonalarm vocalizations
Alarm vocalization	Emitting one of multiple alarm vocalizations
Wing spread	Extending wings away from body without taking flight
Out of sight	Subject is no longer visible
Other	Any unlisted behavior

The distance between the focal subject and speaker varied (between 5 and 29 m), so to account for differences in perceived amplitude, we included distance to speaker in our analyses. In addition, noise due to passing traffic may have also affected perceived amplitude of our playbacks, and therefore, we scored each trial for the presence or absence of traffic and accounted for this binary variable in our analyses. We quantified the time mynas allocated to different activities during the focal observations using JWatcher (version 1.0; Blumstein and Daniel 2007). Behaviors were scored by a single observer (A.V.) in 2 separate parts: the 30-s baseline silence period and the 30-s playback period before FID. Using only the time that the mynas were in sight, we calculated the differences in proportion of time allocated to behavior between the 30-s baseline period and the first 15 s of the playback period. Our analysis focused on the first 15 s of the playback period to capture immediate behavioral responses. We analyzed the time allocated to the behaviors that were consistently observed: looking, relaxed behavior (preen and forage), and locomotion (run, walk, fly, and hop). All other behaviors (Table 1) were rare and could not be grouped into 1 of the 3 categories (looking, relaxed behavior, or locomotion).

Quantifying antipredator responses

Animals may perceive humans as predators (Frid and Dill 2002), so we simulated an approaching predator by walking toward the target animal to measure "FID", defined as the "distance between a prey and an approaching predator when the prey begins to flee" (i.e., physically move away from predator) (Cooper and Blumstein 2015). Related studies have used FID as a measure of perceived risk in prey (e.g., Yee et al. 2013). In addition to FID, we recorded "AD", defined as "the distance between a prey and an approaching predator when the prey responds overtly to the predator by change of posture or orientation to monitor the predator" without changing its location (Cooper and Blumstein 2015), and "starting distance" (SD), defined as "the distance between prey and predator when the predator begins to approach" (Cooper and Blumstein 2015). FID has been shown to be highly correlated with both SD (Blumstein 2003; Samia et al. 2013) and AD (Blumstein et al. 2005; Blumstein 2010). To measure FID, AD, and SD, following the 1-min observation period, and with the playback treatment still being broadcast, 1 person (L.H.) consistently approached the subject myna at 0.5 m/s starting from the same location as the speaker. Following Adams et al. (2006), the approacher dropped markers while approaching the prey to mark SD, AD, and FID. The same experimenter measured all 3 distances in paces and then converted them to meters. If the subject was already in motion (in a relaxed manner) on approach, rather than using the initiation of movement away from the predator, we considered FID to be the distance at which the focal myna changed behavior markedly (i.e., agitated locomotion; Blumstein et al. 2004). Thus, in these cases, FID may equal AD.

We did not conduct FID experiments on subjects that were inaccessible by foot (i.e., on subjects that flew far away or moved to a location that was blocked from direct approach). We also attempted to consistently have a SD of 15 m. However, many subjects flew to a farther location during the time between the start of the baseline observation period and the start of the FID approach. Therefore, we could not control our SD in the field and consequently accounted for it in our analyses. The bulk of our SDs were between 10 and 50 m; we excluded trials with a SD outside this range. For the subjects that were above ground when flushed, we calculated $\mathrm{FID}_{\mathrm{direct}}$, defined as the distance between the approacher and the focal animal when it fled, using the formula: $[\mathrm{FID}_{\mathrm{direct}} = \sqrt{(\mathrm{FID}^2_{\mathrm{horizontal}} + \text{perching height}^2)}]$ (Blumstein et al. 2004). $\mathrm{FID}_{\mathrm{horizontal}}$ was the distance measured at time of flight from the observer to the location directly under the focal animal (Blumstein et al. 2004). Using the same method, we also calculated $\mathrm{AD}_{\mathrm{direct}}$ and $\mathrm{SD}_{\mathrm{direct}}$. Perching height in tree was "estimated by visually rotating the location of the bird in the tree onto the ground, and then measuring the ground distance" (Blumstein et al. 2004, p. 275). Our designated FID approacher trained to estimate distance by pacing and had minimal error in their estimates (average proportion of error in their distance estimates was 0.06 (±0.06 SD, *n* = 10 estimates).

Analyses

Because transformations could not homogenize the variation in time allocation, we fitted generalized linear models with a Gaussian link function to compare the effects of the playback treatment (fixed effects) on the proportion of time allocated to each of the 3 behaviors. Each model incorporated 2 random effects: distance to speaker as a covariate and binary presence of traffic as a factor. We also tested for exemplar effects using these models, but with exemplar as the fixed factor. We used partial eta square to look at the effect size of various variables in the model and Cohen's *d* values to estimate the effect size of pairwise comparisons between treatments. Here and elsewhere, statistical models were fitted using SPSS Statistics 21.0 Software (IBM Corp. 2012); we interpreted *P*-values <0.05 as significant. Cohen's *d* values were calculated from marginal mean values and pooled variances using an online effect size calculator (www.uccs.edu/~lbecker/). Ninety-five percent confidence intervals (CIs) for Cohen's *d* values were calculated (Nakagawa and Cuthill 2007). To examine the differences in risk assessment among treatments using our FID results, we fitted a general linear model to test how the playback treatments influenced the relationship between $\mathrm{AD}_{\mathrm{direct}}$ and $\mathrm{FID}_{\mathrm{direct}}$. In our model, $\mathrm{FID}_{\mathrm{direct}}$ was the response variable, $\mathrm{AD}_{\mathrm{direct}}$ was a covariate, and treatment was the categorical factor. We examined the main effects of treatments and $\mathrm{AD}_{\mathrm{direct}}$ by conducting pairwise comparisons of marginal means between treatments. The effects of the interaction between treatment and $\mathrm{AD}_{\mathrm{direct}}$ were examined by conducting pairwise comparisons of the regression slopes of AD versus FID using the lmatrix custom hypothesis test subcommand in SPSS. Finally, we tested for the effect of the exemplar played by fitting a similar model for each treatment and using exemplar as the factor.

RESULTS

How do acoustic stimuli affect behavioral time allocation in common mynas?

We conducted focal observations on 95 individuals (*n* = 25 for silent control, *n* = 25 for bulbul treatment, *n* = 25 for myna treatment, and *n* = 20 for motorcycle treatment). Mynas varied the proportion of time engaged in relaxed behavior as a function of treatment (Omnibus test, likelihood ratio $\chi^2 = 11.947$; degrees of freedom [df] = 5; *P* = 0.036). They increased the proportion of time engaged in relaxed behavior during silent controls compared with myna (*P* = 0.036; Cohen's *d* = 0.590; 95% CI = 0.012–1.168), bulbul (*P* = 0.006; Cohen's *d* = 0.791; 95% CI = 0.203–1.379), and motorcycle playbacks (*P* = 0.003; Cohen's *d* = 0.884; 95% CI = 0.257–1.511) (Figure 2a). Proportion of time mynas engaged in relaxed behavior did not differ between myna, bulbul, and motorcycle playbacks (all *P*-values > 0.05; Supplementary Table S1). Mynas did not vary the proportion of time spent looking (Omnibus test, likelihood ratio $\chi^2 = 9.503$; df = 5; $P = 0.091$, Figure 2b) or engaged in locomotion (Omnibus test, likelihood ratio $\chi^2 = 3.510$; df = 5; $P = 0.622$, Figure 2c) as a function of treatment. Neither the distance to the speaker nor the presence of vehicles had an effect on the proportion of time engaged in behaviors (Wald chi-square tests, all $P > 0.05$; Supplementary Table S2).

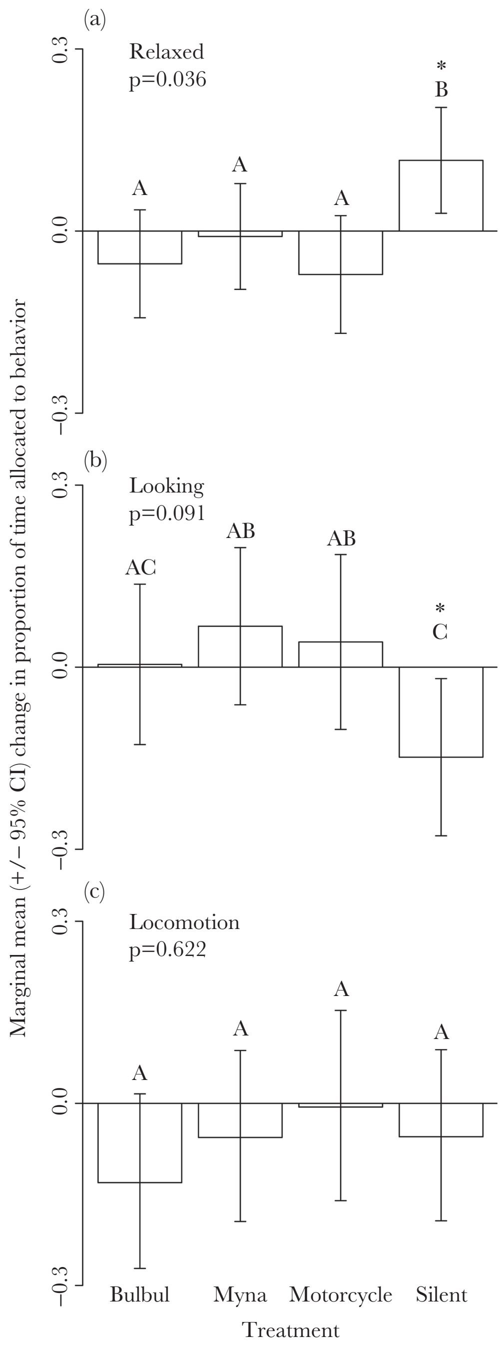

Figure 2

Marginal mean (±95% CI) change in proportion of time allocated to behavior, between the silent baseline period and during playback. Behavior calculated as the proportion time in sight spent relaxed (a), looking (b), or in locomotion (c) as a function of playback treatment (bulbul, myna, motorcycle, or silent control). Asterisk indicates that the mean is significantly different ($P < 0.05$) from silent baseline; shared uppercase letters indicate means are not significantly different across treatments.

How does response to acoustic stimuli affect risk assessment?

Of the 95 individuals we conducted playback experiments on, we were able to conduct a subsequent FID experiment on 60 individuals (n = 14 for silent treatment, n = 16 for bulbul treatment, n = 15 for myna treatment, and n = 15 for motorcycle treatment) (Figure 3). Our model significantly explained 62.7% of the variation in FID ($R^2 = 0.627$; $P < 0.001$). There was a significant effect of AD ($F = 39.176$; df = 1, 52; $P < 0.001$; partial $\eta^2 = 0.430$). The main effect of treatment in general did not significantly influence FID ($F = 2.485$; df = 3, 52; $P = 0.071$; partial $\eta^2 = 0.125$). However, we found a significant interaction between AD and treatment ($F = 4.271$; df = 3, 52; $P = 0.009$; partial $\eta^2 = 0.198$). The slope of AD versus FID was greater in response to bulbul playbacks compared with silent control ($F = 4.776$; df = 1, 52; $P = 0.033$; partial $\eta^2 = 0.084$) or to motorcycle sounds ($F = 10.093$; df = 1, 52; $P = 0.003$; partial $\eta^2 = 0.163$). The slope of the AD versus FID relationship for mynas hearing myna playbacks was also greater compared with motorcycle sounds ($F = 5.636$; df = 1, 52; $P = 0.021$; partial $\eta^2 = 0.098$) but was not different from the silent treatment ($F = 2.698$; df = 1, 52; $P = 0.107$; partial $\eta^2 = 0.049$). There were no significant exemplar effects in either of our models (all *P*-values > 0.05; Supplementary Tables S3 and S4).

DISCUSSION

Contrary to our hypothesis, we found that the acoustic stimuli used in this experiment—anthropogenic noise, conspecific nonalarm calls, and heterospecific nonalarm calls—did not distract mynas. Rather, playback of the sounds prevented the mynas from relaxing

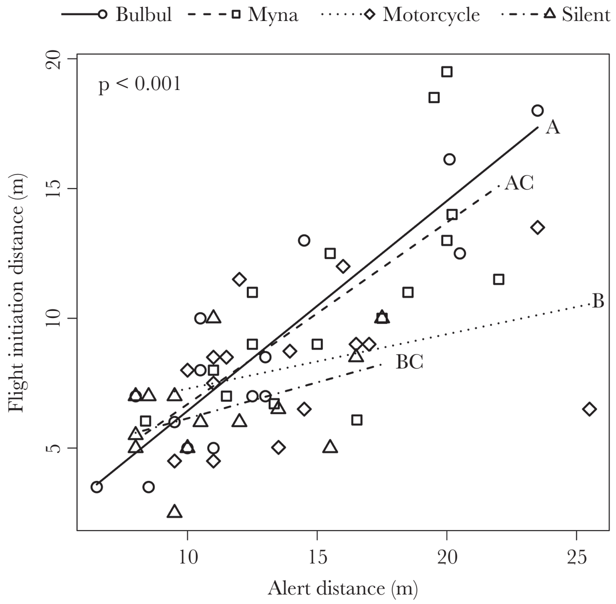

Figure 3

The relationship between AD and FID for mynas during bulbul playback (circle, solid line), myna playback (square, dashed line), motorcycle playback (diamond, dotted line), and silent control (triangle and dotted and dashed line). Shared uppercase letters indicate that slopes are not significantly different across treatments.

and, depending on the sound, enhanced their responsiveness to a simulated predatory approach. Evidence for this comes from the observation that only the silent treatment resulted in increased time allocated to relaxed behavior. Moreover, while hearing bird vocalizations, the slope of the AD × FID relationship was significantly steeper. Thus, rather than being distractions, nonalarm vocalizations seemingly facilitate antipredator behavior.

The increased relaxed behavior during the silent control treatment suggests that anthropogenic noise or bird nonalarm vocalizations may cause mynas to remain more sensitive to their surroundings and possible threats. This suggests that mynas may attend to other species' vocalizations to gain information regarding their surroundings. Although previous studies have shown that animals gain information by eavesdropping on heterospecific alarm calls (review: Magrath et al. 2014), our results suggest that animals may also eavesdrop on nonalarm calls. The effects from the presence of nonalarm vocalizations subsequently lead to quicker responses to an approaching human.

The flush early and avoid the rush hypothesis states that "animals will flee approaching predators soon after they detect and identify them as a threat to reduce or minimize ongoing attentional costs of monitoring the approaching predators" (Blumstein 2010, p. 440). The main effect of AD on FID supports the flush early and avoid the rush hypothesis (Blumstein 2010) by showing that FID increased with AD. Perhaps more interestingly, the AD and treatment interaction effect on FID suggests that this hypothesis is sensitive to context and may be contingent on external stimuli. Mynas conformed to the predictions of the flush early and avoid the rush hypothesis (Blumstein 2010) only when they heard bird vocalizations. During the silent and motorcycle playbacks, mynas did not flush much earlier when they alerted sooner. Indeed, in this context, their FID remained fairly consistent across a wide range of ADs. This suggests that their consistent decision to flee around a range of 6–10 m from the predator may be a baseline predator response behavior. In contrast, their decision to flee earlier in the presence of bird vocalizations suggests that the bird vocalizations may have caused the mynas to allocate more attention to the activity surrounding them, causing them to be more sensitive to the approaching predator. Focusing their attention on the surrounding bird vocalizations, as well as the approaching predator, may have added an attentional cost to mynas and, therefore, they fled soon after alerting to the approaching person to avoid the cost of monitoring both birds and a potential predator.

Although the motorcycle treatment and silent control had different effects on the ability of mynas to relax (only the silent control was associated with enhanced relaxation), mynas hearing either sound responded similarly when experimentally approached. It is possible that the similarity in FID responses between the motorcycle treatment and silent control was due to traffic frequently passing by field sites during our experiments, making the acoustic environments of silent control and motorcycle playbacks similar from the mynas' perspective. Furthermore, mynas may not monitor traffic noise the way that they monitor bird vocalizations. Thus, the contrast between the mynas antipredator response in the silent and motorcycle noise environments versus the bird vocalization environments provides new insight suggesting that the flush early and avoid the rush hypothesis might be context dependent.

Although it is well known that animals assess risk based on conspecific and heterospecific alarm vocalizations (e.g., Weary and Kramer 1995; Shriner 1998; Hanson and Coss 2001; Randler 2006; Vitousek et al. 2007; Goodale and Kotagama 2008; Ito and Mori 2010; Suzuki 2011; Cäsar et al. 2012; Gill and Bierema 2013; Nakano et al. 2013), we found that heterospecific nonalarm vocalizations also influence antipredator behavior and risk assessment. It is possible that the maintained vigilance mynas engaged in when responding to heterospecific vocalizations "carried over" to their subsequent risk assessment when experimentally approached. Carryover effects have been considered as the mechanism for various patterns observed in antipredator behavior (Sih et al. 2003; Blumstein 2006). This is because behavioral traits often serve multiple functions—predators selected to detect the movements of prey are also attuned to the movements of their predators (Blumstein 2006).

We suspect that the responsiveness of mynas to heterospecific vocalizations during our experimental FID approaches resulted from carryover effects of myna responsiveness toward other bird species. Mynas are known to be aggressive toward other bird species (Pell and Tidemann 1997; Fitzsimons 2006). It is possible that, rather than becoming distracted, mynas paid more attention to their surroundings during bulbul vocalizations in part because they were trying to locate the heterospecific. The altered risk assessment, as determined by FID, was thus possibly a carryover effect from a potentially aggressive response. Because red-vented bulbuls are also known for their aggressiveness toward other bird species (Thibault et al. 2002), it is possible that mynas interpreted even social bulbul vocalizations as signals of threat and consequently became more alert to potential predators. Increased vigilance during playbacks may have carried over to the FID portion and "primed" the mynas to flee. Such carryover effects may be an important component in priming animals for subsequent antipredator behavior. It is possible that acoustic stimuli tend to increase alertness in prey rather than distracting them when carryover effects occur. Our results provide evidence that even environmental stimuli not directly indicative of predators may be generally important to risk assessment and therefore affect alertness and response to predation and therefore possibly affect predator–prey dynamics.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

FUNDING

D.T.B. is supported by the U.S. National Science Foundation.

Research was conducted under University of California, Los Angeles (UCLA) ARC protocol 2000-147-42 and under permits issued by the Government of French Polynesia. We thank the UCLA Department of Ecology and Evolutionary Biology, the UCLA Office of Instructional Development, the Holmes O. Miller Endowment and the Joseph Epperson Memorial Field Biology Scholarship for partial support, F. Murphy and H. Murphy and the staff at the UC Berkeley's Gump South Pacific Research Station for their support, N. Munoz for advice and assistance, D.S.M. Samia for helpful comments, 2 anonymous reviewers for insightful feedback, and the UCLA Statistical Consulting Center for statistical help.

Handling editor: Shinichi Nakagawa

REFERENCES

Adams JL, Camelio KW, Orique MJ, Blumstein DT. 2006. Does information of predators influence general wariness? Behav Ecol Sociobiol. 60:742–747.

Audacity Team. 2013. Audacity version 2.0.5 [cited 2014 Jan 19]. Available from: http://audacity.sourceforge.net.

Bee MA, Swanson EM. 2007. Auditory masking of anuran advertisement calls by road traffic noise. Anim Behav. 74:1765–1776.

Bhatt D, Kumar A. 2001. Foraging ecology of red-vented bulbul *Pycnonotus cafer* in Haridwar, India. Forktail. 17:109–110.

Blumstein DT. 1998. Quantifying predation risk for refuging animals: a case study with golden marmots. Ethology. 104:501–516.

Blumstein DT. 2003. Flight-initiation distance in birds is dependent on intruder starting distance. J Wildlife Manage. 67:852–857.

Blumstein DT. 2006. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. Anim Behav. 71:389–399.

Blumstein DT. 2010. Flush early and avoid the rush: a general rule of antipredator behavior? Behav Ecol. 21:440–442.

Blumstein DT, Daniel JC. 2007. Quantifying behavior the JWatcher Way. Sunderland (MA): Sinauer Associates, Inc.

Blumstein DT, Fernández-Juricic E, LeDee O, Larsen E, Rodriguez-Prieto I, Zugmeyer C. 2004. Avian risk assessment: effects of perching height and detectability. Ethology. 110:273–285.

Blumstein DT, Fernández-Juricic E, Zollner, PA, Garity SC. 2005. Interspecific variation in avian responses to human disturbance. J Appl Ecol. 42:943–953.

Bushnell PJ. 1998. Behavioral approaches to the assessment of attention in animals. Psychopharmacology. 138:231–259.

Cäsar C, Byrne RW, Hoppitt W, Young RJ, Zuberbühler K. 2012. Evidence for semantic communication in titi monkey alarm calls. Anim Behav. 84:405–411.

Chan AAYH, Blumstein DT. 2011. Attention, noise, and implications for wildlife conservation and management. Appl Anim Behav Sci. 131:1–7.

Chan AAYH, Giraldo-Perez P, Smith S, Blumstein DT. 2010. Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biol Lett. 6:458–461.

Charif RA, Mitchell S, Clark WCC. 1998. Canary 1.2.4 user's manual. Ithaca (NY): Cornell Laboratory of Ornithology.

Cooper WE Jr, Blumstein DT. 2015. Escape behavior: importance, scope, and variables. In: Cooper WE Jr, Blumstein DT, editors. Escaping from predators: an integrative view of escape decisions and refuge use. Cambridge (UK): Cambridge University Press.

Dukas R. 2004. Causes and consequences of limited attention. Brain Behav Evol. 63:197–210.

Fitzsimons J. 2006. Anti-predator aggression in the common myna *Acridotheres tristis*. Aust Field Ornithol. 23:202–205.

Foote AD, Osborne RW, Hoelzel AR. 2004. Environment: whale-call response to masking boat noise. Nature. 428:910.

Frid A, Dill LM. 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv Ecol. 6:11.

Gill SA, Bierema AMK. 2013. On the meaning of alarm calls: a review of functional reference in avian alarm calling. Ethology. 119:449–461.

Goodale E, Kotagama SW. 2008. Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. Behav Ecol. 19:887–894.

Grarock K, Tidemann CR, Wood J, Lindenmayer DB. 2012. Is it benign or is it a pariah? Empirical evidence for the impact of the Common myna (*Acridotheres tristis*) on Australian birds. PLoS One. 7:e40622.

Griffin AS. 2008. Social learning in Indian mynahs, *Acridotheres tristis*: the role of distress calls. Anim Behav. 75:79–89.

Hanson MT, Coss RG. 2001. Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to conspecific alarm calls. Ethology. 107:259–275.

IBM Corp. 2012. IBM SPSS statistics for Windows, version 21.0. Armonk (NY): IBM Corp.

Ito R, Mori A. 2010. Vigilance against predators induced by eavesdropping on heterospecific alarm calls in a non-vocal lizard *Oplurus cuvieri* (Reptilia: Iguania). Proc R Soc B Biol Sci. 277:1275–1280.

Jakobsson S, Brick O, Kullberg C. 1995. Escalated fighting behaviour incurs increased predation risk. Anim Behav. 49:235–239.

Kannan R, James DA. 2001. Common myna (*Acridotheres tristis*). In: Poole A, editor. The birds of North America online. Ithaca (NY): Cornell Lab of Ornithology.

Karp DS, Root TL. 2009. Sound the stressor: how hoatzins (*Opisthocomus hoazin*) react to ecotourist conversation. Biodivers Conserv. 18:3733–3742.

Katti M, Warren PS. 2004. Tits, noise and urban bioacoustics. Trends Ecol Evol. 19:109–110.

Kumar A. 2003. Acoustic communication in birds. Resonance. 8:44–55.

Kumar A. 2004. Acoustic communication in the red-vented bulbul *Pycnonotus cafer*. An Acad Bras Ciências. 76:350–358.

Lowe S, Browne M, Boudjelas S, De Poorter M. 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Auckland (New Zealand): Invasive Species Specialist Group.

Magrath RD, Haff TM, Fallow PM, Radford AN. 2014. Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. Biol Rev. doi: http://dx.doi.org/10.1111/brv.12122.

Mahabal A. 1991. Activity-time budget of Indian Myna *Acridotheres tristis* (Linnaeus) during the breeding season. J Bombay Nat Hist Soc. 90:96–97.

McGiffin A, Lill A, Beckman J, Johnstone CP. 2013. Tolerance of human approaches by common mynas along an urban–rural gradient. Emu. 113:154–160.

Mooring MS, Hart BL. 1995. Costs of allogrooming in impala: distraction from vigilance. Anim Behav. 49:1414–1416.

Nakagawa S, Cuthill IC. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol Rev. 82:591–605.

Nakano R, Nakagawa R, Tokimoto N, Okanoya K. 2013. Alarm call discrimination in a social rodent: adult but not juvenile degu calls induce high vigilance. J Ethol. 31:115–121.

Pell AS, Tidemann CR. 1997. The ecology of the common myna in urban nature reserves in the Australian Capital Territory. Emu. 97:141–149.

Purser J, Radford AN. 2011. Acoustic noise induces attention shifts and reduces foraging performance in three-spined sticklebacks (*Gasterosteus aculeatus*). PLoS One. e17478.

Randler C. 2006. Red squirrels (*Sciurus vulgaris*) respond to alarm calls of Eurasian jays (*Garrulus glandarius*). Ethology. 112:411–416.

Roberts SC. 1988. Social influences on vigilance in rabbits. Anim Behav. 36:905–913.

Samia DSM, Nomura F, Blumstein DT. 2013. Do animals generally flush early and avoid the rush? A meta-analysis. Biol Lett. 9:20130016.

Shriner WM. 1998. Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. Anim Behav. 55:529–536.

Siddique M, Mushtaq-ul-Hassan M, Beg MA. 1993. Breeding behavior of common myna (*Acridotheres tristis*). Pakistan J Agr Sci. 30:337–342.

Sih A, Kats LB, Maurer EF. 2003. Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. Anim Behav. 65:29–44.

Slabbekoorn H, Peet M. 2003. Ecology: birds sing at a higher pitch in urban noise. Nature. 424:267.

Suzuki TN. 2011. Parental alarm calls warn nestlings about different predatory threats. Curr Biol. 21:R15–R16.

Thibault JC, Martin JL, Penloup A, Meyer JY. 2002. Understanding the decline and extinction of monarchs (Aves) in Polynesian Islands. Biol Conserv. 108:161–174.

Vitousek MN, Adelman JS, Gregory NC, St Clair JJ. 2007. Heterospecific alarm call recognition in a non-vocal reptile. Biol Lett. 3:632–634.

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human domination of Earth's ecosystems. Science. 277:494–499.

Warren PS, Katti M, Ermann M, Brazel A. 2006. Urban bioacoustics: it's not just noise. Anim Behav. 71:491–502.

Weary DM, Kramer DL. 1995. Response of eastern chipmunks to conspecific alarm calls. Anim Behav. 49:81–93.

Western D. 2001. Human-modified ecosystems and future evolution. Proc Natl Acad Sci USA. 98:5458–5465.

Wood WE, Yezerinac SM. 2006. Song sparrow (*Melospiza melodia*) song varies with urban noise. Auk. 123:650–659.

Yee J, Lee J, Desowitz, A, Blumstein DT. 2013. The costs of conspecifics: are social distractions or environmental distractions more salient? Ethology. 119:480–488.