



RESEARCH ARTICLE

Anthropogenic noise reduces approach of Black-capped Chickadee (*Poecile atricapillus*) and Tufted Titmouse (*Baeolophus bicolor*) to Tufted Titmouse mobbing calls

Jacob Damsky and Megan D. Gall*

Department of Biology, Vassar College, Poughkeepsie, New York, USA

* Corresponding author: megall@vassar.edu

Submitted August 11, 2016; Accepted October 18, 2016; Published December 28, 2016

ABSTRACT

Successful communication between a sender and a receiver is critical for coordinating behaviors between organisms. This coordination can be disturbed by anthropogenic noise, which has been shown to alter vocal signal production in many species of birds. In addition to affecting senders, noise may also alter reception and behavioral response. Here we investigated the effects of anthropogenic noise on behavioral response to acoustic signals in mixed-species flocks of songbirds. We used playbacks of Tufted Titmouse (*Baeolophus bicolor*) *chick-a-dee* calls and local anthropogenic noise to determine how receivers respond to calls with and without added noise. We found that the addition of noise caused a significant decrease of ~80% in the number of birds that approached the speaker during a *chick-a-dee* call playback; however, we saw no effect of noise on feeding behavior. Our data support the hypothesis that anthropogenic noise can alter behavioral responses to *chick-a-dee* calls. This finding is of particular concern because *chick-a-dee* calls are given in response to a threatening stimulus. If receivers are slow to respond to these warnings, they may be unable to take advantage of the warning.

Keywords: masking, predators, noise pollution, urbanization

El ruido antropogénico reduce el acercamiento de *Poecile atricapillus* y *Baeolophus bicolor* a las llamadas de acoso de *B. bicolor*

RESUMEN

La comunicación exitosa entre un emisor y un receptor es fundamental para coordinar comportamientos entre los organismos. Esta coordinación puede verse afectada negativamente por ruido antropogénico, el cual se ha demostrado que altera la producción de señales vocales en muchas especies de aves. Además de afectar a los emisores, el ruido también puede alterar la recepción y la respuesta comportamental. En este trabajo investigamos los efectos del ruido antropogénico sobre la respuesta comportamental a las señales acústicas en bandadas mixtas de especies de aves canoras. Empleamos la reproducción de llamados previamente grabados de tipo *chick-a-dee* de *Baeolophus bicolor* y de ruido antropogénico local para determinar cómo los receptores responden a las llamadas con y sin la adición de ruido. Encontramos que la adición de ruido causó una disminución significativa de aproximadamente 80% en el número de aves que se acercaron al parlante durante la reproducción de la llamada *chick-a-dee*. Sin embargo, no vimos un efecto del ruido en el comportamiento de alimentación. Nuestros datos apoyan la hipótesis de que el ruido antropogénico puede alterar las respuestas comportamentales a las llamadas de tipo *chick-a-dee*. Esto es preocupante, ya que las llamadas de tipo *chick-a-dee* son emitidas como respuesta a una amenaza. Si los receptores son lentos en responder a estas advertencias, pueden ser incapaces de aprovechar el hecho de que se emita una advertencia.

Palabras clave: depredadores, enmascaramiento, polución sonora, urbanización

INTRODUCTION

Anthropogenic noise is a common form of pollution that has a detrimental impact on many species (reviewed in Barber et al. 2010). Anthropogenic noise can reduce foraging efficiency, predator detection, and social communication (Fuller et al. 2007, Blickley and Patricelli 2012, Leonard and Horn 2012, Luther and Magnotti 2014,

McMullen et al. 2014) by masking cues or signals, causing distractions that reduce attention, or evoking stress-related changes in physiology (Blas et al. 2007, Slabbekoorn and Ripmeester 2008, Hanna et al. 2011, Dowling et al. 2012, McMullen et al. 2014). To minimize the effects of anthropogenic noise, animals can alter the temporal or spatial patterns of behavior, alter the intensity of behaviors, or use alternative behaviors (Quinn et al. 2006, Fuller et al.

2007, Nemeth and Brumm 2010, Rios-Chelen et al. 2015). For instance, when animals perceive an increase in predation risk (e.g., when detection is compromised) they may compensate by avoiding areas with higher perceived levels of predation risk, scanning more frequently, joining larger groups, or increasing reliance on public information (Owens et al. 2012, Meillère et al. 2015, Klett-Mingo et al. 2016). Similarly, animals may compensate for reduced signaling efficiency by changing the spatial arrangement of signalers, changing the timing of communication, changing vocal frequency (i.e. pitch), increasing song amplitude, switching song types, or changing the rate of song production (Slabbekoorn and Peet 2003, Wood and Yezerinac 2006, Fuller et al. 2007, Slabbekoorn et al. 2007, Francis et al. 2009, Diaz et al. 2010, Nemeth and Brumm 2010, Cardoso and Atwell 2011).

Despite a large body of work focused on song production, relatively less work has focused on the effects of anthropogenic noise on the reception and behavioral response to acoustic signals, particularly when these signals lie outside a mating context (but see Pohl et al. 2009, Meillère et al. 2015). We investigated how animals respond to anti-predator vocalizations with and without the presence of anthropogenic noise maskers. We hypothesized that anthropogenic noise could influence receiver behavior either because noise (1) masked calls or (2) was generally aversive. These hypotheses are not mutually exclusive nor comprehensive. For example, distraction or other mechanisms may be involved.

To investigate masking and aversion, we examined the response of Tufted Titmouse (*Baeolophus bicolor*) to playback of *chick-a-dee* calls. These calls are used in a variety of contexts, including as a type of anti-predator vocalization known as a mobbing call (Ritchison et al. 2015). In most of these contexts, and particularly in a mobbing context, *chick-a-dee* calls attract conspecifics to the signaler's location. We chose titmice as our study species for several reasons. First, at our study site the Tufted Titmouse formed mixed-species flocks with Black-capped Chickadee (*Poecile atricapillus*) and White-breasted Nuthatch (*Sitta carolinensis*). These species forage in mixed-species groups, engage in mixed-species mobbing behavior, and respond to both conspecific and hetero-specific anti-predator vocalizations. Thus, this model system allowed us to investigate the behavioral responses of both conspecifics and heterospecifics to an anti-predator vocalization. Second, anthropogenic noise has previously been shown to affect risk-taking and social behavior in titmice (Owens et al. 2012).

We played *chick-a-dee* calls alone, *chick-a-dee* calls with anthropogenic noise, and noise alone. We then measured 3 behaviors in response to the playbacks: (1) the number of unique birds approaching the speaker; (2) the number of unique birds feeding at a feeder located 20 m from the

playback before, during, and after playback; and (3) the latency of each species to resume foraging following the playback. We predicted that if anthropogenic noise primarily affects communication through masking, we would see approaches to the speaker only during *chick-a-dee* call playbacks and little change in feeding behavior across all playbacks. We predicted that if anthropogenic noise affects communication because it is aversive (or is causing both masking and is aversive), animals would avoid the speaker and reduce their feeding rate during all playbacks containing noise.

METHODS

Study Site

We performed our experiments at the Vassar Ecological Preserve, a 527-acre ecological preserve located in Poughkeepsie, New York, USA. All experiments took place between 0800 and 1000 hours from October through December 2014 and February through April 2015. We used a repeated-measure design to assess behavioral responses to Titmouse *chick-a-dee* calls, anthropogenic noise, and a combination of noise and calls at 10 locations on the Vassar Ecological Preserve. All work was approved by the Vassar College institutional animal care and use committee (IACUC protocol # 14-11B).

We first erected ten 1.22 m-tall feeding platforms averaging 0.5 km apart. We baited each platform with sunflower seed 3 times a week for 2 weeks before any trials began to establish consistent places where the birds had access to food (Desrochers et al. 2002). Individuals foraging at these platforms were captured in potter traps and color-banded before the experiment. We encountered unbanded individuals during our playback experiments, but with multiple observers we were able to follow these individuals during trials. Once the trials began, we baited each platform on the day before the playback experiment.

Audio

We created 3 different types of playback stimuli in Raven Pro (1.4 beta) from recordings made at the Vassar Ecological Preserve and on the Vassar College campus: one set of *chick-a-dee* calls alone, one set of anthropogenic noise, and one set including both *chick-a-dee* calls and anthropogenic noise. The anthropogenic noise was composed primarily of traffic noise, with occasional airplane and lawnmower noise. We removed background noise from the calls using the noise reduction function in Audacity 2.0.4.0. We then used PRAAT 5.4.08 to adjust the voltage so the peak amplitude of all our playbacks was equivalent. This corresponded to an RMS amplitude of 82.3 ± 3.2 dB for the *chick-a-dee* call playback (including silent periods) and an RMS amplitude of 90.0 ± 3.1 dB for the noise playback at 1 m from the speaker. The *chick-a-*

dee calls were presented at a rate of ~22 calls per minute, although the interval between calls was not fixed. Each call contained between 4 and 12 D-notes because calls used in mobbing contexts typically contain 4 or more D-notes (Courter and Ritchison 2010). Additionally, each of the calls we used were recorded from titmice that were actively mobbing, thus representing the natural variation in calls of our study population. For each type of playback, we had 10 exemplars, one unique recording for each experimental location.

To ensure the call could theoretically be detected when combined with the anthropogenic noise recording, we calculated the signal to noise ratio (SNR) for the noise–call combination using the intensities of the respective elements in PRAAT 5.4.08. Previous work on several model species found that when combining a call with noise, the call needs to be no more than 13–19 dB lower (i.e. quieter) than the noise level to be detectable, due primarily to the concentration of spectral energy at lower frequencies in anthropogenic noise (Lohr et al. 2002). Within all of our combined calls, the difference in average overall dB level was never >15 dB between call and noise, meaning that the calls should have been detectable to the birds in each playback. Spectral masking by traffic noise was greatest below 2.5 kHz. The temporal patterning of the noise and an upward spread of excitation (a phenomenon in which loud low frequency noise can activate areas of the inner ear that respond to higher frequencies) could lead to masking of important higher frequency components, including most of the energy in the D-notes of the *chick-a-dee* call, despite positive average SNR in these frequency regions (Figure 1). Calls mixed with anthropogenic noise were detectable to the human ear at a distance of 10 m.

Experimental Methods

We used a counterbalanced repeated measure design. We conducted 3 trials (calls alone, anthropogenic noise alone, or calls and noise together) at each of 10 feeding platforms. Each trial was split into 3 observational periods of 5 min each. The pre-trial period was the 5 min before the playback started, the trial period was the 5 min during the playback, and the post-trial period was the 5 min after the playback stopped. Trials at a given platform were separated by at least a week. We had 27 trials because we excluded 3 trials in which no birds fed at the platform or came within 10 m of the speaker.

In each trial we had a feeding platform 20 m from the playback source (a Pignose portable speaker, Model #7-100, connected to a SanDisk portable WAV player on a tripod). This distance allowed us to set up the playback equipment without initiating a mobbing response from birds foraging at the platform. Before the experiment, the playback level of the speaker was calibrated using a 1 kHz calibration tone and a Pyle sound level meter (PSPL05R)

with a C-weighting at 1 m from the speaker. After setting up our equipment we waited 10 min before starting our observations.

In each trial we were interested in 3 dependent variables: the number of unique birds approaching the speaker, the number of birds foraging on the feeding platform, and the latency to resume foraging once a playback began. Two observers 30 m from the playback speaker determined the number of unique Black-capped Chickadee, Tufted Titmouse, and White-breasted Nuthatch that approached within 10 m of the speaker. Colored flags were placed 10 m from the speaker in each cardinal direction to provide reliable landmarks for our approach data. Visits to the foraging platforms were recorded using a Kodak Pixpro SP1 digital action camera placed on a tripod 1 m from the feeding platform. Following the playback experiments, we used JWatcher 1.5.0 (Blumstein and Daniel 2007) to determine the number of unique individuals of each species of bird that fed during each 5-min period of the playbacks and latency to resume foraging following a playback.

Data Analysis

We used SPSS 19 and SAS 9.2 for our statistics. We had 3 statistical models, one each for the number of birds that approached the speaker, the number of birds that fed at the platform, and the latency to resume foraging after the playback began. The number of birds that approached the speaker and the number that approached the platform were count data that best fit a negative binomial distribution, so we analyzed the data with a generalized linear model with a log link function. We used a repeated measures mixed model to analyze feeding latency because we used the platforms repeatedly (each of 3 stimuli at each platform, 3 trial periods within each playback). Latency was log-transformed to meet normality and homogeneity of variance assumptions. In the speaker approach and foraging latency models, we did not include data from White-breasted Nuthatch because they infrequently approached the speaker, instead remaining to feed at the platform.

The independent variables in our speaker approach model were playback type (*chick-a-dee* call, anthropogenic noise, or mixed calls and noise), trial time (before, during, after), responding species (Tufted Titmouse, Black-capped Chickadee), and their interactions. The independent variables in our feeding platform approach model were playback type (*chick-a-dee* call, anthropogenic noise, or mixed calls and noise), trial time (before, during, after), responding species (Tufted Titmouse, Black-capped Chickadee, White-breasted Nuthatch), and their interactions. The independent variables in the foraging latency mixed model were playback type (*chick-a-dee* call, anthropogenic noise, or mixed calls and noise), trial time (before, during,

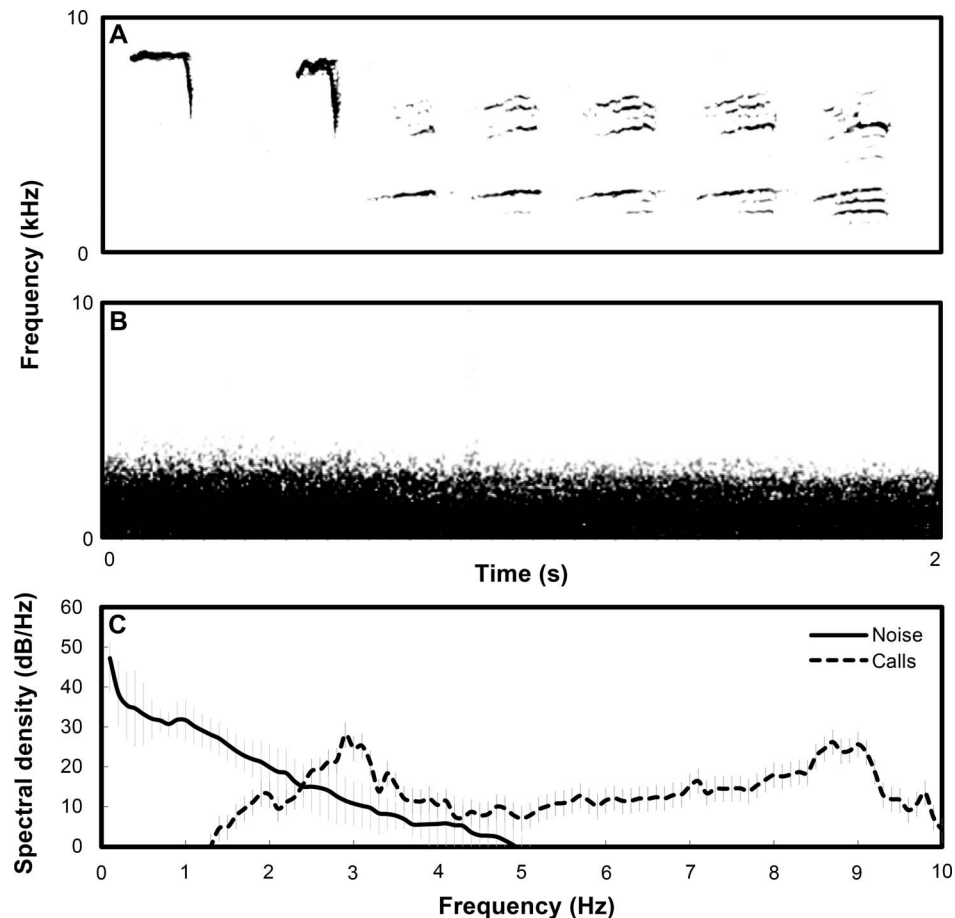


FIGURE 1. (A) Spectrogram of a titmouse mobbing call. (B) Spectrogram of anthropogenic noise generated by vehicle and air traffic. (C) Average spectral density in dB/kHz of all exemplars. All recordings were made at the Vassar Farm and on the Vassar College campus in Poughkeepsie, New York. The power spectrum was generated in PRAAT using 100 Hz frequency bins. The vertical lines show the 95% confidence interval. Note that noise contains more energy than the calls below 2.2 kHz, whereas the calls have greater energy than the noise near 3 kHz and above 5 kHz.

after), responding species (Tufted Titmouse, Black-capped Chickadee), and their interactions. In each model we included location as a subject factor and the number of birds in the area as a random factor to control for differences among the platforms in the likelihood of an individual randomly approaching the speaker or foraging platform. We initially included all interaction effects in our analyses and removed nonsignificant interaction terms based on P value. Significant effects were explored post hoc with least significant differences, and P values were adjusted using the Bonferroni method.

RESULTS

Speaker Approach

We found that the number of birds approaching the speaker was not significantly influenced by species ($\chi^2 = 0.466$, $df = 1$, $P = 0.495$), trial time ($\chi^2 = 0.546$, $df = 2$, $P = 0.761$), or playback type ($\chi^2 = 3.306$, $df = 2$, $P = 0.192$).

Approaches to the speaker were also not affected by the species * trial time, ($\chi^2 = 0.627$, $df = 2$, $P = 0.731$), species * playback type, ($\chi^2 = 2.124$, $df = 2$, $P = 0.346$), or species * trial time * playback type interactions (Figure 2; $\chi^2 = 6.478$, $df = 4$, $P = 0.166$).

We did find, however, a significant influence of the trial time * playback type interaction ($\chi^2 = 52.817$, $df = 4$, $P = 0.001$) on the number of birds approaching the speaker (Figure 2). This interaction was driven by an increase in the number of birds approaching the speaker during the playback of the mobbing calls compared to before (mean difference [MD] = 0.83, $P = 0.001$) or after (MD = 0.82, $P = 0.001$) the call was played. Comparatively, no change was detected in the number of approaches to the speaker across trial times with the playback of noise alone or noise and calls combined (MD = -0.18, $P = 0.234$). Thus, for all species combined, there were ~5 times as many speaker approaches during the playback of the call alone compared to noise alone or the call presented with noise.

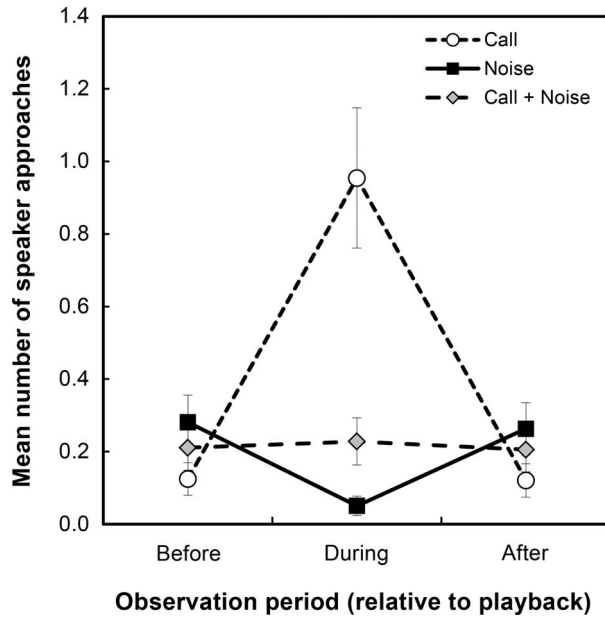


FIGURE 2. Black-capped Chickadee and Tufted Titmouse speaker approaches (means \pm SEM) for each of the trial periods (before, during, after) within the 3 playback types (mobbing call, noise, mixed).

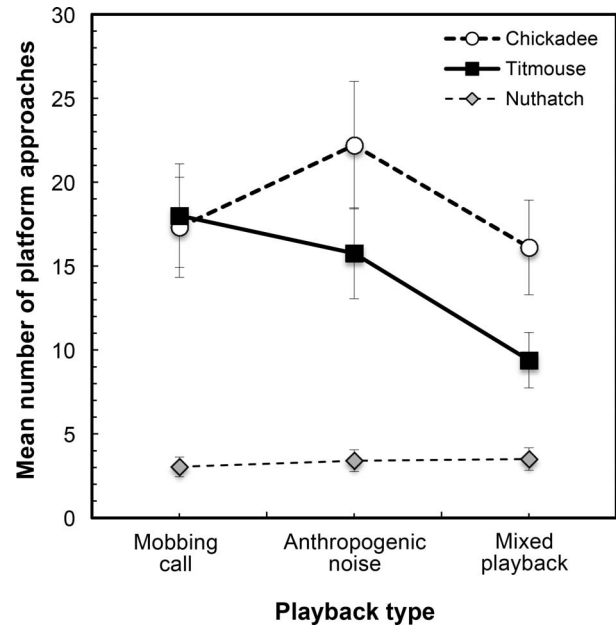


FIGURE 3. Feeding platform visits (means \pm SEM) for the 3 species (Tufted Titmouse, Black-capped Chickadee, and White-breasted Nuthatch) across the 3 playback types (mobbing call, noise, mixed).

Platform Approach

We found that the number of birds feeding from the platform was not significantly influenced by trial time ($\chi^2 = 0.362$, $df = 2$, $P = 0.834$) or playback type ($\chi^2 = 2.7$, $df = 2$, $P = 0.259$). Nor were approaches to the platform affected by the time * species ($\chi^2 = 0.68$, $df = 4$, $P = 0.954$), trial time * playback type ($\chi^2 = 0.885$, $df = 4$, $P = 0.927$), species * playback type ($\chi^2 = 4.518$, $df = 4$, $P = 0.34$), or trial time * species * playback type interactions (Figure 3; $\chi^2 = 3.547$, $df = 8$, $P = 0.896$).

We did find, however, a significant influence of the species ($\chi^2 = 113.056$, $df = 2$, $P = 0.001$) on the number of birds approaching the platform (Figure 4). This interaction was driven by the number of nuthatches that approached the platform; significantly fewer nuthatches approached the feeding platform than did chickadees ($MD = -15.09$, $P = 0.001$) or titmice ($MD = -10.56$, $P = 0.001$). This finding was not unexpected because there are typically many fewer nuthatches in a given location than chickadees or titmice. The chickadees and titmice did not differ significantly in the number of feeding platform approaches ($MD = 4.53$, $P = 0.286$).

Approach Latency

Feeding latency following initiation of the playback was not significantly influenced by any factor. The main effects of species ($F = 1.183$, $df = 2$ and 67 , $P = 0.323$), playback type ($F = 2.47$, $df = 2$ and 67 , $P = 0.092$), and the playback

type * species interaction (Figure 4; $F = 0.754$, $df = 6$ and 67 , $P = 0.608$) were not significant. Nuthatches infrequently approached the platform and were therefore not included in the analysis.

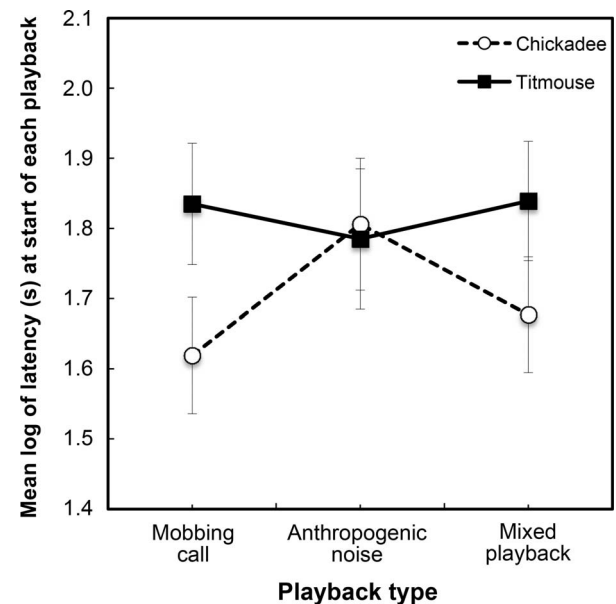


FIGURE 4. Mean log-transformed feeding latency (marginal means \pm SEM) in seconds for Black-capped Chickadee and Tufted Titmouse following the start of each each playback type (mobbing call, noise, mixed).

DISCUSSION

Our results suggest that anthropogenic noise can affect the behavior of songbirds receiving a signal from a sender. We hypothesized that receiver behavior could be affected by noise through (at least) 2 different mechanisms: (1) anthropogenic noise masking signals and/or (2) anthropogenic noise causing an aversive response in the receivers, irrespective of whether or not the signal was present. If noise was masking signals, we expected that individuals would approach the mobbing call at a reduced rate when both noise and call were present; however, we did not expect that noise (both with and without calls) would affect their foraging behavior at a location remote from our playback. If, however, there was a general aversion to noise (or both masking and aversion to noise), we expected that approaches to the speaker would decrease (as with masking) but that foraging behavior would be decreased during all playbacks that contained noise.

We found a significant increase in the number of birds approaching the speaker during the playbacks when the mobbing call was played alone compared to the 5 min preceding or following the playbacks. When anthropogenic noise or a combination of the noise and call were played, however, there was no significant change in bird approaches to the speaker across trial periods. We also found that the number of foraging attempts on the platform was not affected by playback type, trial time, or their interactions. Noise affected behavioral response to a communication signal but not foraging at a more remote location, which supports the masking hypothesis rather than the general aversion hypothesis. Our results add to the growing body of literature that suggests anthropogenic noise masks signals and therefore can have a detrimental effect on both the sender and receiver end of communication (Quinn et al. 2006, Cardoso and Atwell 2011, Hanna et al. 2011, Dowling et al. 2012, McMullen et al. 2014, Meillère et al. 2015). Additionally, other factors we have not addressed may be at play, including an increase in perceived predation risk in noisy environments, distraction caused by noise, or an increase in time required for perceptual processing. Future work should investigate the role of these factors in behavioral responses to anti-predator vocalizations in noise.

Noise, Predation, and Communication

A relatively large body of work suggests that noise alone can increase perceived or actual predation risk in both invertebrates and vertebrates (Quinn et al. 2006, Chan et al. 2010a, 2010b, Meillère et al. 2015, Klett-Mingo et al. 2016). An increase in perceived predation risk can lead to an increase in time spent vigilant and thus decrease time available for foraging (Quinn et al. 2006, Owens et al. 2012, Klett-Mingo et al. 2016). Additionally, noise can also mask

the approach of predators or cause distractions that increase the risk of predation because the latency to detect and flee from a predator increases. Thus, increased noise in the environment can make many prey species more vulnerable to both lethal and sub-lethal predation effects (Chan et al. 2010a, 2010b).

Animals that rely on communication and personal information about predation threats may be particularly vulnerable to anthropogenic noise. In addition to noise increasing perceived predation risk, the ability to detect and/or localize anti-predator communication signals is expected to decrease in anthropogenic noise. For instance, anthropogenic noise can reduce the responses of Tree Swallow (*Tachycineta bicolor*) nestlings to parental alarm calls (Leonard and Horn 2012). Similarly, we found that 2 songbird species that engage in mixed-species mobbing reduced their response to anti-predator vocalizations in the presence of anthropogenic noise. This reduction in response could be due to masking decreasing the ability to detect mobbing calls, the ability to localize the source of the sender, or the sense of urgency in the receiver. The number of D-notes per call or per unit time are important in conveying the relative threat of the mobbing target (Courter and Ritchison 2010). Thus, if individual calls or call elements are masked, the level of response from the receivers may decrease because of a decreased risk perception.

Are there ways that animals can mitigate the effects of anthropogenic noise on their anti-predator communication? Although little work has been done on noise and anti-predator vocalizations, we know animals can employ several strategies on both the production and reception ends to combat the effects of noise on mate attraction signals. For instance, songbirds singing in noise have been shown to change the temporal patterns of their song, increase the frequency or amplitude of their songs, or increase the number of songs produced (Fuller et al. 2007, Slabbekoorn and Ripmeester 2008, Diaz et al. 2010, Luther and Baptista 2010, Nemeth and Brumm 2010, Francis et al. 2011, Dowling et al. 2012).

For animals producing anti-predator signals, however, there are greater constraints on signal production, in particular, animals are constrained in their ability to alter the timing of signal production because anti-predator signals, such as mobbing calls, are evoked by predator stimuli and thus are only of value over a short period (Desrochers et al. 2002). Similarly, the structure of these calls is often closely linked to their function (e.g., localization for mobbing calls); thus, altering the structure of the calls may reduce their effectiveness (Ficken and Popp 1996) or shift the balance of costs and benefits of signal production. For instance, alarm calls, which are given in response to high risk predators, are typically high in frequency, which is thought to reduce their localizability

by predators at the cost of making detection by target individuals more difficult.

Noise-related changes in alarm call frequency can improve detection by conspecifics but may also increase the risk of detection by predators. Interestingly, Potvis et al. (2014) found that urban Silvereye (*Zosterops lateralis*) produced lower frequency calls than those in rural areas. Moreover, the frequency of alarm vocalizations decreased with increasing noise level, resulting in a larger active signal space. This shift could increase risk of localization by predators, a risk likely offset by the improved signal detection by conspecifics. Furthermore, for chickadees and titmice, the degree of predation risk is coded in the number of D-notes per vocalizations or the number of D-notes per unit time (Courter and Ritchison 2010). Thus, altering the number of vocalizations produced may only be valuable if the sender can accurately predict how the current noise environment is likely to influence the detection of individual calls or call elements.

Plasticity in production of anti-predator vocalizations is likely more constrained than in production of song; thus, plasticity in receiver physiology or behavior is more likely to be successful in mitigating some of the negative effects of anthropogenic noise on signal detection. Work on receiver responses to signals in anthropogenic noise is limited; however, a rich history exists examining how animals can improve detection of signals masked by natural abiotic (e.g., rivers, waterfalls) or biotic (e.g., insects, other animal vocalizations) noise. In these circumstances, animals can benefit from auditory systems adept at filtering out noise. For instance, frogs that live near waterfalls tend to have narrower auditory filters than frogs in quieter locations (Witte et al. 2005). These narrow auditory filters lead to a smaller frequency bandwidth of noise being processed with the signal, improving the ability to detect the signal in noise. This type of response requires either physiological plasticity or adaptation to the acoustic environment.

Animals can also employ behavioral strategies to combat noise, such as orienting the body in a way that spatially separates the noise from the signal, again, improving detection (Schwartz and Gerhardt 1989). This behavior could be employed in situations where anthropogenic noise is directional (for instance on a preserve flanked on one side by a road). Finally, animals may employ a strategy called dip listening, in which animals catch “glimpses” of the signal of interest in periodic low levels of noise. This strategy is employed by frogs listening for individual male signals in chorus background noise (Vélez and Bee 2011). Taking a receiver-oriented approach in addition to a producer-oriented approach may allow us to more accurately predict which animals are likely to fare well in areas with high levels of noise. Future work investigating the fine-scale changes in behavior to anti-predator communication signals in anthro-

pogenic noise could improve our understanding of how noise affects anti-predator behavior and the perception of predation risk.

Conclusions

Despite a wealth of studies on how anthropogenic noise affects the production of communication signals, we still know relatively little about how noise affects the reception of communication signals, particularly non-song signals. Our data suggest that anthropogenic noise masking can have a detrimental effect on the ability to respond to conspecific anti-predator signals. Anti-predator communication may be particularly vulnerable to the effects of anthropogenic noise because the timing of vocalizations is relatively inflexible and the consequences of inappropriate responses are high. Although our results suggest that masking is the most likely source of reduced anti-predator vocalization detection, other mechanisms may also produce a reduced response to communication signals. Mobbing calls of many species, including that of the Tufted Titmouse studied here, may be particularly susceptible to masking because mobbing calls generally contain acoustic energy at lower frequencies; however, alarm calls in many species tend to be higher in frequency and may be less likely inhibited by anthropogenic noise masking. If future work found that anthropogenic noise diminishes responses to alarm calls and mobbing calls, it would suggest that additional and non-mutually exclusive factors, such as divided attention or distraction, may affect the detection and response to anti-predator vocalizations in anthropogenic noise.

ACKNOWLEDGMENTS

Thanks to Tim Boycott and Carly Barbara for helping with data collection in the field and data analysis in the lab. Thanks to Dr. Christenson for reading and commenting on the paper. **Funding statement:** Funding for this project came from Vassar College.

Ethics statement: All work was approved by the Vassar institutional animal care and use committee (IACUC protocol # 14-11B).

Author contributions: M.D.G. designed the experiment, developed methods, and analyzed data. J.D. developed the methods and performed the experiments. M.D.G. and J.D. co-wrote the manuscript.

LITERATURE CITED

- Barber, J. R., K. R. Crooks, and K. M. Fristrup (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution* 25:180–189.
- Blas, J., G. R. Bortolotti, J. L. Tella, R. Baos, and T. A. Marchant (2007). Stress response during development predicts fitness in a wild, long lived vertebrate. *Proceedings of the National Academy of Sciences USA* 104:8880–8884.

- Blickley, J. L., and G. L. Patricelli (2012). Potential acoustic masking of Greater Sage-Grouse display components by chronic industrial noise. In *The Influence of Anthropogenic Noise on Birds and Bird Studies* (C. D. Francis and J. L. Blickley, Editors). Ornithological Monographs 74:23–35.
- Blumstein, D. T., and J. C. Daniel (2007). *Quantifying Behavior the JWatcher Way*. Sinauer Associates, Sunderland, MA, USA.
- Chan, A. A., P. Giraldo-Perez, S. Smith, and D. T. Blumstein (2010a). Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biology Letters* 6: 458–461.
- Chan, A. A. Y. H., W. D. Stahlman, D. Garlick, C. D. Fast, D. T. Blumstein, and A. P. Blaisdell (2010b). Increased amplitude and duration of acoustic stimuli enhance distraction. *Animal Behaviour* 80:1075–1079.
- Cardoso, G. C., and J. W. Atwell (2011). On the relation between loudness and the increased song frequency of urban birds. *Animal Behaviour* 82:831–836.
- Courter, J. R., and G. Ritchison (2010). Alarm calls of Tufted Titmice convey information about predator size and threat. *Behavioral Ecology* 21:936–942.
- Desrochers, A., M. Belisle, and J. Bourque (2002). Do mobbing calls affect the perception of predation risk by forest birds? *Animal Behaviour* 64:709–714.
- Diaz, M., A. Parra, and C. Gallardo (2010). Serins respond to anthropogenic noise by increasing vocal activity. *Behavioral Ecology* 22:332–336.
- Dowling, J. L., D. A. Luther, and P. P. Marra (2012). Comparative effects of urban development and anthropogenic noise on bird songs. *Behavioral Ecology* 23:201–209.
- Ficken, M. S., and J. W. Popp (1996). A comparative analysis of passerine mobbing calls. *The Auk* 113:370–380.
- Francis, C. D., C. P. Ortega, and A. Cruz (2009). Noise pollution changes avian communities and species interactions. *Current Biology* 19:1415–1419.
- Francis, C. D., C. P. Ortega, and A. Cruz (2011). Different behavioural responses to anthropogenic noise in closely related passerine birds. *Biology Letters* 7:850–852.
- Fuller, R. A., P. H. Warren, and K. J. Gaston (2007). Daytime noise predicts nocturnal singing in urban robins. *Biology Letters* 3: 368–370.
- Hanna, D., G. Blouin-Demers, D. R. Wilson, and D. J. Mennill (2011). Anthropogenic noise affects song structure in Red-winged Blackbirds (*Agelaius phoeniceus*). *Journal of Experimental Biology* 214:3549–3556.
- Klett-Mingo, J. I., I. Pavon, and D. Gil (2016). Great Tits, *Parus major*, increase vigilance time and reduce feeding effort during peaks of aircraft noise. *Animal Behaviour* 115:29–34.
- Leonard, M. L., and A. G. Horn (2012). Ambient noise increases missed detections in nestling birds. *Biology Letters* 8:530–532.
- Lohr, B., T. F. Wright, and R. J. Dooling (2002). Detection and discrimination of natural calls in masking noise by birds: Estimating the active space of the signal. *Animal Behaviour* 65:763–777.
- Luther, D., and L. Baptista (2010). Urban noise and the cultural evolution of bird songs. *Proceedings of the Royal Society of London, Series B* 277:469–473.
- Luther, D., and J. Magnotti (2014). Can animals detect differences in vocalizations adjusted for anthropogenic noise? *Animal Behaviour* 92:111–116.
- McMullen, H., R. Schmidt, and K. P. Hansjoerg (2014). Anthropogenic noise affects vocal interactions. *Behavioural Processes* 103:125–128.
- Meillère, A., F. Brischoux, and F. Angelier (2015). Impact of chronic noise exposure on antipredator behavior: An experiment in breeding House Sparrows. *Behavioral Ecology* 26:569–577.
- Nemeth, E., and H. Brumm (2010). Birds and anthropogenic noise: Are urban songs adaptive? *The American Naturalist* 176:465–475.
- Owens, J. L., C. L. Stec, and A. O'Hatnick (2012). The effects of extended exposure to traffic noise on parid social and risk-taking behavior. *Behavioural Processes* 91:61–69.
- Pohl, N. U., H. Slabbekoorn, G. M. Klump, and U. Langemann (2009). Effects of signal features and environmental noise on signal detection in the Great Tit, *Parus major*. *Animal Behaviour* 78:1293–1300.
- Potvis, D. A., R. A. Mulder, and K. M. Parris (2014). Silvereyes decrease acoustic frequency to increase efficacy of alarm calls in urban noise. *Animal Behaviour* 98:27–33.
- Quinn, J. L., M. J. Whittingham, S. J. Butler, and W. Cresswell (2006). Noise, predation risk compensation and vigilance in the Chaffinch *Fringilla coelebs*. *Journal of Avian Biology* 37: 601–608.
- Rios-Chelen, A. A., G. C. Lee, and G. L. Patricelli (2015). Anthropogenic noise is associated with changes in acoustic but not visual changes in Red-winged Blackbirds. *Behavioral Ecology and Sociobiology* 7:1139–1151.
- Ritchison, G., T. C. Grubb, and V. V. Pravasudov (2015). Tufted Titmouse (*Baeolophus bicolor*). In *Birds of North America Online* (A. Poole, Editor) Cornell Laboratory of Ornithology, Ithaca, NY, USA. <http://bna.birds.cornell.edu/bna/species/086>
- Schwartz, J. J., and H. C. Gerhardt (1989). Spatially mediated release from auditory masking in an anuran amphibian. *Journal of Comparative Physiology* 166:37–41.
- Slabbekoorn, H., and M. Peet (2003). Birds sing at a higher pitch in urban noise—Great Tits hit the high notes to ensure that their mating calls are heard above the city's din. *Nature* 424: 267.
- Slabbekoorn, H., and E. Ripmeester (2008). Birdsong and anthropogenic noise: Implications and applications for conservation. *Molecular Ecology* 17:72–83.
- Slabbekoorn, H., P. Yeh, and K. Hunt. (2007). Sound transmission and song divergence: A comparison of urban and forest acoustics. *The Condor* 109:67–78.
- Vélez A., and M. A. Bee (2011). Dip listening and the cocktail party problem in grey treefrogs: Signal recognition in temporally fluctuating noise. *Animal Behaviour* 82:1319–1327.
- Witte, K., H. E. Farris, M. J. Ryan, and W. Wilczynski (2005). How cricket frog females deal with a noisy world: Habitat-related differences in auditory tuning. *Behavioral Ecology* 16:571–579.
- Wood, W. E., and S. M. Yezerinac (2006). Song Sparrow (*Melospiza melodia*) song varies with urban noise. *The Auk* 123:650–659.