Contents lists available at ScienceDirect





Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

The effects of anthropogenic noise on feeding behaviour in black-capped chickadees (*Poecile atricapillus*)



Kimberley A. Campbell^a, Darren S. Proppe^b, Jenna V. Congdon^a, Erin N. Scully^a, Shannon K. Miscler^a, Christopher B. Sturdy^{a,c,*}

^a Department of Psychology, University of Alberta, Canada

^b Department of Biology, Calvin College, United States

^c Neuroscience and Mental Health Institute, University of Alberta, Canada

ARTICLE INFO	A B S T R A C T
Keywords: Anthropogenic noise Black-capped chickadees Songbirds	Anthropogenic noise has been shown to impact animal behaviour. Most studies investigating anthropogenic noise, and the detrimental effect it has on behaviour, have been conducted in the field, where a myriad of covariates can make interpretation challenging. In this experiment, we studied the effects of an approximation of anthropogenic noise, simulated with brown noise, on the feeding behaviour of wild-caught black-capped chickadees in a laboratory setting. We measured the amount of time spent eating while subjects heard either conspecific calls, brown noise, or a combination of calls and brown noise. We found that subjects fed more in the silence following playback than during the playback itself for all types of stimuli, suggesting that chickadees may shift their feeding behaviour to avoid feeding during periods of noise. The ability to adapt to changing environments (e.g., varying noise levels) may allow species to thrive in the presence of anthropogenic noise. Our findings outline a laboratory-based method that could be adopted and adapted to examine a variety avian

species and of types anthropogenic noise.

1. Introduction

As the global population and level of urbanization increase, so too do the levels of noise associated with human activity. This humanproduced noise, or 'anthropogenic noise', has extensively changed environmental soundscapes world wide. Background noise exists in all habitats, but the sounds of urban environments and other areas of human activity exceed natural levels and include novel sounds not heard in a natural habitat. Anthropogenic noise tends to be composed of low frequency sounds from sources such as road vehicles, airplanes, industrial machinery, and air movement machinery (Tempest, 1985; Leventhall, 1988). Transportation networks (including rail, air, and road) are a widespread source of anthropogenic noise outside of urban areas. For example, 83% of the land in the continental U.S. is within 1 km of a road, highlighting the pervasiveness of noise pollution to our natural environments (Ritters and Wickham, 2003). High amplitude, low frequency noise is particularly damaging as it can be propagated at much longer distances, and therefore have farther reaching effects (Buxton et al., 2017).

Anthropogenic noise levels in the range of 40–100 dB have been shown to cause disturbances in both humans and non-human animals depending on the source and its proximity (Shannon et al., 2016). In humans, chronic noise exposure has been shown to cause a reduction in cognitive function (Szalma and Hancock, 2011) and sleep quality (Fyhri and Aasvang, 2010), as well as an increased risk of cardiovascular disease (Babisch et al., 2005; Hansell et al., 2013). In non-human animals, the impairments associated with chronic noise exposure include physical or physiological damage, masking of communication signals, and/or reduced available attention (Shannon et al., 2016; Slabbekoorn and Ripmeester, 2008).

While much is known about how noise impacts habitat selection (Slabbekoorn and Ripmeester, 2008), vocal behaviour (Francis and Barber, 2013), and population dynamics (Shannon et al., 2016), less is known about how it impacts daily foraging patterns in songbirds. Because songbirds often retain only enough fat to survive each night, reduced foraging - whether due to fear or to novelty - might have catastrophic impacts on individual survivorship. One recent study by Ware et al. (2015) found that migratory birds were less capable of gaining weight throughout the day when artificial noise was added to the habitat. However, Van Donselaar and colleagues (2018) found that urban black-chickadees were less likely than rural chickadees to avoid a feeder when noise was added. This suggests that some birds may

https://doi.org/10.1016/j.beproc.2018.10.015

Received 15 August 2018; Received in revised form 22 October 2018; Accepted 22 October 2018 Available online 12 November 2018 0376-6357/ © 2018 Elsevier B.V. All rights reserved.

^{*} Corresponding author. *E-mail address:* csturdy@ualberta.ca (C.B. Sturdy).

become accustomed to noise, and resume normal foraging behaviour.

Making adjustments that reduce the impacts of noise has been well documented in other songbird behaviours. For example, individuals can shift their spatial patterns of behaviour (e.g., avoid areas with increased noise levels), shift their temporal pattern of behaviour (e.g., sing earlier in the day to avoid noises associated with rush hour traffic; Fuller et al., 2007), alter the quality of their vocalizations (e.g., change frequency or amplitude; Brumm, 2004; change frequency and duration; Gentry et al., 2017), or change their behaviour entirely (e.g., singing a different song type; Quinn et al., 2006; Fuller et al., 2007; Nemeth and Brumm, 2010; Rios-Chelen et al., 2015).

Although many bird species alter their behaviour in response to noise, some do not. The effectiveness of intentional mitigation strategies, other than noise reduction, has not been well studied. The most common means of reducing intensity of anthropogenic noise is the use of physical barriers and while there are other, more effective, means of reducing anthropogenic noise (such as restricting road traffic and reducing speeds) there is evidence that these barriers reduce noise in both urban and rural environments (Murphy and King, 2011; Slabbekoorn and Ripmeester, 2008). The downside of these barriers are that their benefits only extend short distances and their presence can cause habitat fragmentation, making them better used near especially sensitive roadside habitats or surrounding localized noise sources (Summers et al., 2011). Costs for constructing barriers can also be prohibitive. Recently, Proppe et al. (2017) suggested that perhaps behaviour could be manipulated to increase songbird productivity in moderately noisy areas where aversion might be due to novelty rather than fitness costs. They demonstrated that playing conspecific calls (a known acoustic attractant) near low-use roads increased the density of birds in noisy habitats (Schepers and Proppe, 2017); however, density does not necessarily correlate with survivorship. For example, if foraging is less efficient in noisy habitats, birds drawn to these habitats may be less likely to survive and reproduce.

While a number of well-designed field experiments have tested the effects of noise on bird behaviour (e.g., Templeton et al., 2016; Bayne et al., 2008), it can be difficult to determine how particular behaviours are affected in isolation. For example, in a 20-year review of noise research Shannon and colleagues (2016) found that, while 88% of the 242 studies showed a significant biological response to noise, few studies took into account that the activities that cause anthropogenic noise are themselves a kind of disturbance (e.g., traffic, construction, agriculture, etc.). Although field studies are excellent at assessing behaviour within the myriad of signals and cues found in the natural environment, laboratory-based studies provide a more controlled environment, allowing the effects of anthropogenic noise on individuals to be studied without some of the confounding factors that must be accounted for in the field. For example, conspecific and heterospecific interactions, climactic events, and variations in natural and anthropogenic noise can all be tightly controlled in laboratory studies (e.g., Lohr et al., 2003; Potvin et al., 2016).

In the present study, we sought to investigate the effects of anthropogenic noise (as approximated by brown noise, a noise spectrum with more energy at lower frequencies) on the feeding behaviour of black-capped chickadees (Poecile atricapillus). Living primarily in forested areas, black-capped chickadees communicate mainly through acoustic signals (e.g., not visual or olfactory). Black-capped chickadees' ability to thrive in both urban and rural locations means that they inhabit environments with varying levels of anthropogenic noise. In addition to synthetic noise, we embedded chick-a-dee calls within noise tracks to determine if this potential mitigation strategy, as suggested by Proppe et al. (2017), altered foraging behaviour. We exposed 12 blackcapped chickadees to either brown noise, chick-a-dee calls, or a combination of brown noise and chick-a-dee calls, and evaluated how this affected their feeding behaviour. We predicted that the presence of lowfrequency noise would have a negative impact on feeding behaviour and that the presence of conspecific chick-a-dee calls may mitigate those negative effects.

2. Methods

2.1. Subjects

Twelve wild-caught black-capped chickadees (six males, six females) were used in this experiment. Subjects were caught in January 2016 in Edmonton, AB (North Saskatchewan River Valley, 53°53 N, 113°53 W) or Stony Plain, AB (53°46 N, 114°01 W) and determined to be at least one year of age at time of capture by referencing the shape and colour of their outer tail retrices (Pyle, 1997). Sex was determined using DNA analysis (Griffiths et al., 1998). All subjects had experience with the experimental apparatus for auditory GO/NOGO operant conditioning tasks (e.g., Hahn et al., 2017), but had no experience with the acoustic stimuli used (i.e., *chick-a-dee* calls, brown noise). Testing occurred between August 1 and September 17, 2017.

2.2. Housing

Prior to the experiment, individual chickadees lived in Jupiter Parakeet cages ($30 \times 40 \times 40$ cm, Rolf C. Hagen, Inc., Montreal, QB, Canada) in a communal colony room having visual and auditory contact with other chickadees, but no physical contact. Birds had free access to food (Mazuri Small Bird Maintenance Diet; Mazuri, St Louis, MO, USA), water (supplemented with vitamins three days a week; Prime vitamin supplement; Hagen, Inc.), grit, and cuttlebone. They also received three to five sunflower seeds each day, one superworm (*Zophobas morio*) three days a week and a mixture of hard-boiled egg and spinach or parsley two days a week. Subjects were kept on a light/ dark cycle that approximated the natural light cycle for Edmonton, AB.

During the experiment, chickadees were individually housed in the experimental apparatus (see Apparatus below). They had free access to water (vitamins added three days a week), grit, and cuttlebone and received a superworm twice a day. Mazuri food was provided following visits to the feeder. While in the experimental apparatus, subjects were kept on a 15:9 h light:dark cycle to match the average natural summer day:night cycle for Edmonton, AB, Canada.

2.3. Apparatus

Chickadees were housed in modified Jupiter Parakeet cages $(30 \times 40 \times 40 \text{ cm})$ that were singly enclosed in ventilated sound-attenuating chambers. Each chamber was lit with a full spectrum LED bulb (3 W, 250 lm E26, Not-Dim, 5000 K; Lohas LED, Chicago, IL, USA). The modified cages had an 11×16 cm opening that allowed access to a motorized feeder (described in Njegovan et al., 1994). The feeder contained infrared beams that signalled feeder visits. A personal computer connected to a single-board computer (Palya and Walter, 2001) recorded feeder visits and triggered the food cup to rise upon each visit, allowing the bird access to food. Acoustic stimuli played from a full-range speaker (Fostex FE108 R or FE108E R; Fostex Corp., Japan; frequency response range 80–18,000 Hz) located next to the feeder after passing through an integrated amplifier (Cambridge A300, Azur 640 A or Azur 351 A; Cambridge Audio, London, England). See Sturdy and Weisman (2006) for a detailed description of the apparatus.

2.4. Procedure

On the first day of the experiment, birds were moved to the apparatus and provided with free access to food from both a food cup and from the raised feeder cup. This allowed birds to acclimatize to the apparatus. This acclimatization period was followed by three days of silence, which served as the baseline for establishing normal feeding behaviour in each bird. Following baseline, birds received three days of each of the three conditions (Call Stimulus, Noise Stimulus, Call and



Fig. 1. A flowchart showing order and number of days for each stage of treatment.

Noise Stimulus) separated by one day of silence, which allowed the bird's feeding behaviour to return to baseline (see Fig. 1). Order of stimulus presentation was randomly assigned such that two individuals were assigned to each of the six possible stimulus presentation orders. Three subjects had an extra day of silence added between treatments to account for the loss of the data from the planned day of silence due to an error. This extra silence did not affect their performance.

Chamber houselights turned on each morning at 09:00. Stimulus playback started at 09:30 (average 09:29 \pm 00:12) once the previous days' data was saved and the recording program was restarted. Seven hours of stimulus presentation was followed by silence until lights out at 24:00. Birds could access food by visiting the feeder at any time between lights on and lights out.

2.5. Stimuli

This experiment used three types of stimuli: (1) black-capped chickadee *chick-a-dee* calls, (2) brown noise, and (3) a combination of *chick-a-dee* calls and brown noise (see Fig. 2). All stimuli consisted of 30 min of sound followed by 30 min of silence repeated for seven hours. After this seven-hour stimulus, no sounds played for the rest of the day. Background sound levels in experimental chambers were approximately 60 dB and the stimuli were presented at approximately 75 dB (measured approximately 20 cm from the speaker by a Brüel & Kjær Type 2239 decibel meter; Brüel & Kjær Sound and Vibration Measurement A/S, Nærum, Denmark; A weighting, slow response).

2.5.1. Chick-a-dee calls

Twenty adult black-capped chickadees (10 males, 10 females) captured in Edmonton, Alberta (North Saskatchewan River Valley, 53°53 N, 113°53 W; Mill Creek Ravine, 53°52 N, 113°47 W) and at Barrier Lake Field Station (51°02 N, 115°03 W) provided a total of 60 chick-a-dee calls (three calls per bird) for stimuli. Calls were randomly selected using a random number generator (i.e., random.org) from available recordings of those birds, however only calls that fell within the average number of notes per call plus or minus two standard deviations were used (4-9 notes; avg = 6.93, s.d. = 1.23; from previous acoustic study, Campbell et al., 2016). Birds that provided calls for stimuli were housed in a separate colony room from birds that were subjects so that subjects were not familiar with the stimuli. The calls were recorded in 2014 in individual sound-attenuating chambers (Industrial Acoustics Corporation, Bronx, NY, USA) using Marantz PMD670 digital recorders (Marantz America, Mahwah, NJ, USA). Calls were then bandpass filtered in GoldWave (version 6.30; GoldWave, Inc., St. John's, NL, Canada) to remove frequencies outside the range of the calls (500 – 13,000 Hz) and both ends of the stimulus were tapered at 5 ms to remove transients. Five ms of silence was added before and after each call in SIGNAL software (version 5.05.02, Engineering Design, Belmont, MA, USA).

Prepared calls from different individuals were randomly paired. Each pair was combined in SIGNAL software with three seconds of silence between the first and second calls, then silence was added following the second call to bring the total file length to 60 s. Two calls per minute is comparable to rates observed in the wild (15 calls/hour during summer days; Avey et al., 2008) and used in other playback experiments (2 calls/minute: Scully et al., 2018; 4 partial calls/minute: Avey et al., 2014). The 30 files created from the paired calls were concatenated in a randomly determined order to create a 30-minute file; silence was added at the end to bring the total file length to 60 min. This hour-long stimulus played seven times to make up the Call

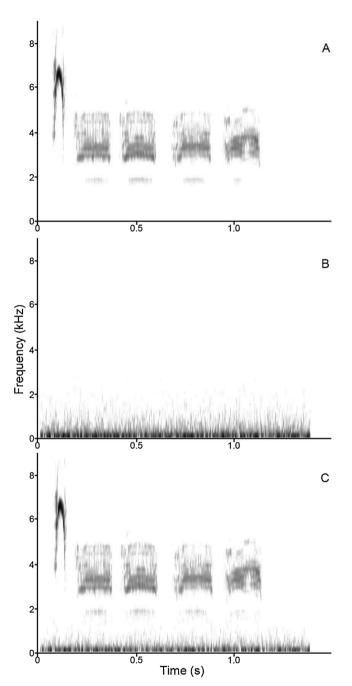


Fig. 2. A sound spectrogram (window size = 256 points, time resolution = 5.8 ms) showing the three stimulus types used for playback: (A) black-capped chickadee *chick-a-dee* calls, (B) brown noise, and (C) a combination of *chick-a-dee* calls and noise.

Stimulus.

2.5.2. Brown noise

Patange and colleagues (2013) conducted a spectral analysis of samples of traffic noise, concluding that it tends to behave as low frequency pink noise (1/f noise) with random fluctuations. Brown noise (also called red noise or Brownian noise) refers to a broadband spectrum of noise that has more energy at longer wavelengths than at

shorter wavelengths and whose sounds randomly change from one moment to the next. Audacity (version 2.1.3; Audacity Team) was used to create a 30-minute noise file using the generate function to make amplitude 0.8 Brownian noise. Silence was added to the end of the stimulus in SIGNAL to bring the total length to 30 min. As with the Call Stimulus, this file was played seven times to make up the seven-hour Noise Stimulus.

2.5.3. Chick-a-dee calls and brown noise

To make a seven-hour Call and Noise Stimulus, the Call Stimulus and Noise Stimulus were combined in GoldWave by moving each stimulus into one of two channels in a stereo file.

2.6. Statistical analyses

The time of each visit to the feeder was recorded and matched with the time of stimulus playback start. Visits were summed per 30-minute period for each bird for each day; lined up with 30 min playback and 30 min silence between. For analysis, the feeds from the seven 30minute playback periods were summed and treated as a single time period called Stimulus Playback. Similarly, the feeds from the seven 30minute periods of silence immediately following playback were summed and the time period was called Silence between Playback. The feeds from the remaining silence at the end of the day were also summed, with the time period called Late Silence.

To allow for comparison of feeding between different individuals with varying feeding patterns (total feeds ranged from 413 to 1359 per day with average of 1026), the first three days of silence were used to establish baseline feeding behaviour in the absence of playback. The feeds for silent baseline days were summed in the same manner as the treatment days, with the Stimulus Playback time period starting at the beginning of the day, even though no stimulus was used in the Silence condition. Using the same pattern of 30 min "Playback" followed by 30 min of Silence between Playback as during the stimulus playback conditions, the average feeds for each of the three time periods (Stimulus Playback, Silence between Playback, and Late Silence) were calculated. These baseline measures were subtracted from the number of feeds for the corresponding time period in each treatment day to scale each individual's performance.

Differences in feeding behaviour, as measured by baseline-scaled feeds, were analyzed using a repeated measures analysis of variance (rmANOVA) with Time (Stimulus Playback, Silence between Playback, and Late Silence) and Condition (Silence, Calls, Noise, Calls and Noise) as the between-subject factors. Sex of the individual and Order of stimulus presentation were included as within-subject factors. Tukey's post hoc tests were conducted to evaluate the nature of interactions between variables.

2.7. Ethical note

Studies were conducted with approval from the Animal Care and Use Committee for Biosciences for the University of Alberta (AUP 108) and all procedures were in accordance with the Canadian Council on Animal Care (CCAC) Guidelines and Policies and the ARRIVE (Animal Research: Reporting of in vivo Experiments) guidelines. Chickadees were captured under an Environment Canada Canadian Wildlife Service Scientific permit, Alberta Fish and Wildlife Capture and Research permits, and City of Edmonton Parks Permit.

3. Results

We conducted a rmANOVA on the baseline-scaled feeds to determine the relationship between the type of playback heard (Silence, Calls, Noise, or Calls and Noise) and the time relative to the playback (during Playback, Silence between Playback, or Late Silence) while accounting for both the sex of the subject and the order in which the

Behavioural Processes 158 (2019) 53-58

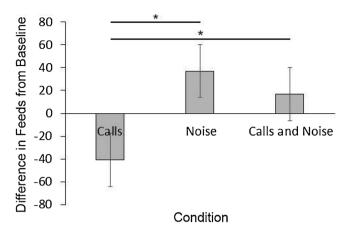


Fig. 3. Mean \pm SE of difference in total feeding across all subjects between each playback Condition (Calls, Noise, Calls and Noise) and Baseline. Here, a negative number means birds fed less during a treatment condition than during the baseline (silent) condition.* indicates a significant difference ($p \le 0.05$) between group means.

subject heard the types of playback. There was a significant effect of Condition on feeding behaviour (F₂, $_{24} = 11.62$, p < 0.001) such that birds visited the feeder fewer times on days when Calls were played than they did on days when Noise or Calls and Noise were played (p = 0.025; p < 0.001; see Fig. 3). Time also had a significant effect on feeding behaviour (F₃, $_{23} = 22.59$, p < 0.001), where birds fed less during Playback than they did during Silence between Playback (p < 0.001; see Fig. 4).

There was a significant Time × Condition interaction ($F_{6,20} = 11.89$, p < 0.001). When looking at the Silence between Playback, birds fed less on days when Calls were played than on days when Noise, or Calls and Noise, were played (p = 0.001; p = 0.001). There was no significant difference in feeding between Noise, and Calls and Noise, conditions ($p \ge 0.454$). Birds also fed less during Late Silence than would be expected if they fed at a constant rate (expected: 53.33%; observed: 46.78%).

There was no overall significant main effect of Sex (F_{1, 25} = 0.28, p = 0.599), meaning that the proportion of feeds was similar between males and females. Similarly, there was no significant main effect of presentation Order (F_{5, 25} = 0.74, p = 0.599). However, the three-way effects Condition × Time × Order (F_{30, 120} = 1.71, p < 0.001), Condition × Sex × Order (F_{8, 50} = 2.47, p = 0.024), and Time × Sex

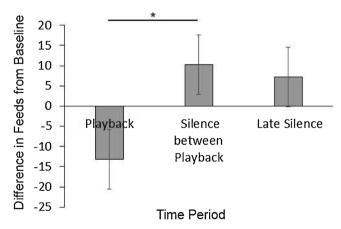


Fig. 4. Mean \pm SE of difference in total feeding across all subjects between each time period (Playback, Silence between Playback, Late Silence) and Baseline. Here, a negative number means birds fed less during a time period during treatment condition than at the equivalent time period during the baseline (silent) condition.* indicates a significant difference (p \leq 0.05) between group means.

× Order (F_{12, 75} = 4.40, p < 0.001) were significant. Neither the three-way Condition × Time × Sex interaction (F_{6, 20} = 2.66, p = 0.133046) nor the four-way Condition × Time × Sex × Order interaction were significant (F_{24, 92} = 1.68, p = 0.091).

4. Discussion

In this experiment, we looked at the effects of brown noise on the feeding behaviour of captive black-capped chickadees in the absence of other factors associated with the production of anthropogenic noise. We predicted that the presence of anthropogenic noise, approximated by brown noise, would have a negative impact on feeding behaviour in black-capped chickadees and that the presence of conspecific chick-adee calls may mitigate those negative effects. Instead, we observed that individuals fed significantly less on days when chick-a-dee calls were played than on days when either brown noise or the combination of chick-a-dee calls and brown noise were played. Though we did not predict higher feeding during playback of noise than during call playback, there is some evidence that songbirds experiencing stress and variable feeding (both of which may here be caused by the pattern of playback and silence) increase feeding and associated activity to compensate for increased metabolism (Fokidis et al., 2012). The increase observed in this experiment, therefore, could indicate that noise is elevating stress hormones or other internal processes that are not immediately observable.

We also observed that birds fed significantly less during stimulus playback than during the periods of silence between the playback. When considering the type of stimulus being played, we found that birds who had heard playback of conspecific *chick-a-dee* calls fed less during the subsequent period of silence than did birds who heard either brown noise or a combination of calls and brown noise. Quinn and colleagues (2006) found that chaffinches (*Fringilla coelebs*) decrease feeding behaviour in favour of vigilance behaviours in the presence of anthropogenic noise. While we did not monitor what behaviours chickadees were engaging in when not feeding, this may provide evidence that black-capped chickadees prefer to feed when anthropogenic and other sources of noise are not present to mask important auditory cues from their surroundings (e.g., sound of an approaching predator).

Our results show that black-capped chickadees are capable of altering their foraging behaviour in response to noise cues, preferring to feed when noise is not present. This ability could be part of what allows these and other species to thrive in environments with variable noise levels, like cities. This feeding behaviour could be adaptive, akin to birds shifting singing behaviour to avoid rush hour noise. Bergen and Abs (1997) found that urban songbird species sing earlier in the day than those in the forest. Similarly, Brumm (2004) found that nightingales (*Luscinia megarhynchos*) sing louder when traffic noise is present, increasing song amplitude during the week but not on weekends. Proppe and colleagues also found that black-capped chickadees sing at higher frequencies (2012) and sing shorter songs as levels of anthropogenic noise increase (2011). Overall, Barber and colleagues (2010) suggest that the ability to adapt may determine which species thrive in urban environments and which are forced to find new habitats.

We had predicted that the presence of conspecific calls would mitigate the effects of anthropogenic noise on feeding behaviour, however, our results did not support this. Schepers and Proppe (2017) found that playback of conspecific vocalizations in a wooded roadside environment increased the population density of a number of bird species in that habitat, suggesting that song playback could provide a means of fortifying species density and diversity near roads. In looking at feeding behaviour, we found that black-capped chickadees behaved similarly to both noise and noise with calls, altering their behaviour after the playback rather than during. Damsky and Gall (2016) found that both black-capped chickadees and the tufted titmouse (*Baeolophus bicolor*), another small North American songbird, did not attend to tufted titmouse mobbing calls (calls used to recruit both con- and heterospecifics to ward off predators) when the calls were played in combination with anthropogenic noise. They suggest that anthropogenic noise may mask vocalizations, limiting their effectiveness. These results, taken together with our own, suggest that playback of conspecific calls embedded within noise may not enhance feeding behaviour by simulating safety through the presence of conspecifics.

We observed that birds fed significantly less during the silent period at the end of the day (i.e., Late Silence) than during either stimulus playback or the silence between stimulus playback, regardless of playback condition, order of playback exposure, or sex. We believe this to be due to natural feeding tendencies in black-capped chickadees as during baseline birds were observed to feed primarily between 9:00 and 16:00 with feeder visits steadily declining until lights out. In nature, midday hours would be optimal for feeding to ensure appropriate caloric intake before nightfall.

Here, we have demonstrated the importance of conducting research in both the field and in a controlled laboratory. Having conducted research with species as diverse as pigeons (e.g., Columbia livia), chickadees (e.g., Poecile atricapillus and P. gambeli; Batty et al., 2009), ants (e.g., Melophorous bagoti and Veromessor pergandei), and humans (i.e., Homo sapiens), Dr. Marcia Spetch seeks the best model for each research question. This results in a spectrum of research methods, ranging from field studies investigating natural behaviours with controlled manipulations (e.g., navigational abilities in both humans and desert ants; Spetch et al., 1997; Legge et al., 2014, respectively), to lab studies investigating specific biological capacity for a behaviour (e.g., risky decision making in pigeons and humans, or timing in pigeons and chickadees; Ludvig et al., 2014; McMillan et al., 2016, 2017, respectively), and anywhere in between. Marcia Spetch's extensive body of work clearly demonstrates the value of studying human and non-human animals in both the wild and the laboratory in an attempt to investigate perception and cognition. For example, Spetch and colleagues (1997) conducted several experiments comparing pigeons and humans on a searching task. When searching for a hidden goal, as the square array increased, pigeons searched according to the distance and direction from a landmark. However, humans instead searched the middle of the table top as the array increased (i.e., a location that was similar to the goal in comparison to the original landmark array). To determine how human participants would respond on a larger scale, a comparative task was designed in an outdoor grassy field. Responding in the different settings was similar even though the participants had to physically move through space to find the goal (i.e., unlike the laboratory setting). This provided further evidence of the differences between pigeon and human search behaviour, confirming that humans' search strategy was not confined by size or a lack of physical movement. In this case, a laboratory research question was taken from the laboratory to the field, but there are many reasons to bring field research questions into the laboratory.

In conclusion, we found that black-capped chickadees fed significantly less when presented with conspecific calls than when presented with brown noise (with or without calls). Chickadees also fed significantly more during the periods of silence between stimulus playback than during the playback itself, regardless of playback type. Our experiment helps demonstrate the value of conducting research under the correct conditions for the research question. Our results provide evidence supporting research (e.g., in chaffinches Quinn et al., 2006) that has demonstrated songbirds are capable of adjusting their behaviour in response to anthropogenic noise and that some of these observed behaviours may be due to stress-driven changes in metabolism. The ability to adapt both feeding and communication behaviours allows species to exist in the presence of anthropogenic noise and thrive in the ever-growing urban landscapes.

Acknowledgements

We thank Isaac Lank and Al Denington for their technical assistance

in the chickadee operant chambers. This research was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant and Discovery Accelerator Supplement, an Alberta Ingenuity Fund (AIF) New Faculty Grant, a Canada Foundation for Innovation (CFI)New Opportunities Fund (NOF) and Infrastructure Operating Fund (IOF) grants along with start-up funding and CFI partner funding from the University of Alberta (UofA) to CBS. KAC was supported by an Alexander Graham Bell Canada Graduate Scholarship-Doctoral (NSERC CGS D).

References

- Avey, M.T., Bloomfield, L.L., Elie, J.E., Freeberg, T.M., Guillette, L.M., Hoeschele, M., et al., 2014. ZENK Activation in the Nidopallium of black-capped chickadees in response to both conspecific and heterospecific calls. PLoS ONE 9, e100927. https:// doi.org/10.1371/journal.pone.0100927.
- Avey, M.T., Quince, A.F., Sturdy, C.B., 2008. Seasonal and diurnal patterns of blackcapped chickadee (*Poecile atricapillus*) vocal production. Behav. Processes 77, 149–155. https://doi.org/10.1016/j.beproc.2007.12.004.
- Babisch, W., Beule, B., Schust, M., Kersten, N., Ising, H., 2005. Traffic noise and risk of myocardial infarction. Epidemiology 16, 33–40. https://doi.org/10.1097/01.ede. 0000147104.84424.24.
- Barber, J.R., Crooks, K.R., Fristrup, K.M., 2010. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. 25, 180–189. https://doi.org/10.1016/j. tree.2009.08.002.
- Batty, E.R., Bloomfield, L.L., Spetch, M.L., Sturdy, C.B., 2009. Black-capped (*Poecile at-ricapillus*) and mountain chickadees' (*Poecile gambeli*) use of geometric and featural information in a spatial orientation task. Anim. Cogn. 12, 633–641. https://doi.org/10.1007/s10071-009-0222-3.
- Bayne, E.M., Habib, L., Boutin, S., 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conserv. Biol. 22, 1186–1193. https://doi.org/10.1111/1-1523-1739.2008.00973-x.
- Bergen, F., Abs, M., 1997. Etho-ecological study of the singing activity of the Blue Tit (*Parus caeruleus*), Great Tit (*Parus major*) and Chaffinch (*Fringilla coelebs*). Journal fur Ornithologie 138, 451–467.
- Brumm, H., 2004. The impact of environmental noise on song amplitude in a territorial bird. J. Anim. Ecol. 73, 434–440. https://doi.org/10.1111/j.0021-8790.2004. 00814.x.
- Buxton, R.T., McKenna, M.F., Mennitt, D., Fristrup, K., Crooks, K., Angeloni, L., Wittemyer, G., 2017. Noise pollution is pervasive in U.S. protected areas. Science 356, 531–533.
- Campbell, K.A., Hahn, A.H., Congdon, J.V., Sturdy, C.B., 2016. An investigation of sex differences in acoustic features in black-capped chickadee (*Poecile atricapillus*) chicka-dee calls. J. Acoust. Soc. Am. 140, 1598–1608. https://doi.org/10.1121/1. 4962281.
- Damsky, J., Gall, M.D., 2016. Anthropogenic noise reduces approach of Black-capped Chickadee (*Poecile atricapillus*) and Tufted Titmouse (*Baeolophus bicolor*) to Tufted Titmouse mobbing calls. Condor 119, 26–33. https://doi.org/10.1650/CONDOR-16-146.1.
- Griffiths, R., Double, M.C., Orr, K., Dawson, R.J.G., 1998. A DNA test to sex most birds. Mol. Ecol. 7, 1071–1075. https://doi.org/10.1046/j.1365- 294x.1998.00389.x.
- Fokidis, H.B., Burin des Roziers, M., Sparr, R., Rogowski, C., Sweazea, K., Deviche, P., 2012. Unpredictable food availability induces metabolic and hormonal changes independent of food intake in a sedentary songbird. J. Exp. Biol. 215, 2920–2930. https://doi.org/10.1242/jeb.071043.
- Francis, C.D., Barber, J.R., 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. Front. Ecol. Environ. 11, 305–313.
- Fuller, R.A., Warren, P.H., Gaston, K.J., 2007. Daytime noise predicts nocturnal singing in urban robins. Biol. Lett. 3, 368–370. https://doi.org/10.1098/rsbl.2007.0134.
- Fyhri, A., Aasvang, G.M., 2010. Noise, sleep and poor health: modeling the relationship between road traffic noise and cardiovascular problems. Sci. Total Environ. 408, 4935–4942. https://doi.org/10.1016/j.scitotenv.2010.06.057.
- Gentry, K.E., Derryberry, E.P., Danner, R.M., Danner, J.E., Luther, D.A., 2017. Immediate signaling flexibility in response to experimental noise in urban, but not rural, white-crowned sparrows. Ecosphere 8, e01916. https://doi.org/10.1002/ecs2.1916.
- Hahn, A.H., Campbell, K.A., Congdon, J.V., Hoang, J., McMillan, N., Scully, E.N., Yong, J.J.H., Elie, J.E., Sturdy, C.B., 2017. Discrimination of acoustically similar conspecific and heterospecific vocalizations by black-capped chickadees (*Poecile atricapillus*). Anim. Cogn. 20, 639–654. https://doi.org/10.1007/s10071-017-1087-5.
- Hansell, A.L., Blangiardo, M., Fortunato, L., Floud, S., de Hoogh, K., Fecht, D., Ghosh, R.E., Laszlo, H.E., Pearson, C., Beale, L., Beevers, S., Gulliver, J., Best, N., Richardson, S., Elliott, P., 2013. Aircraft noise and cardiovascular disease near Heathrow airport in London: small area study. Br. Med. J. 347, 1–10. https://doi.org/10.1136/bmj. f5432.
- Legge, E.L.G., Wystrach, A., Spetch, M.L., Cheng, K., 2014. Combining sky and earth: desert ants (*Melophorus bagoti*) show weighted integration of celestial and terrestrial cues. J. Exp. Biol. https://doi.org/10.1242/jeb.107862. jeb-107862.

- Leventhall, H.G., 1988. Low frequency noise in buildings-internal and external sources. J. Low Freq. Noise Vib. 7, 74–85.
- Lohr, B., Wright, T.F., Dooling, R.J., 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. Anim. Behav. 65, 763–777.
- Ludvig, E.A., Madan, C.R., Pisklak, J.M., Spetch, M.L., 2014. Reward context determines risky choice in pigeons and humans. Biol. Lett. 10, 1–5. https://doi.org/10.1098/rsbl. 2014.0451.
- McMillan, N., Sturdy, C.B., Pisklak, J.M., Spetch, M.L., 2016. Pigeons perform poorly on a midsession reversal task without rigid temporal regularity. Anim. Cogn. 19, 855–859. https://doi.org/10.1007/s10071-016-0962-9.
- McMillan, N., Hahn, A.H., Congdon, J.V., Campbell, K.A., Hoang, J., Scully, E.N., Spetch, M.L., Sturdy, C.B., 2017. Chickadees discriminate contingency reversals presented consistently, but not frequently. Anim. Cogn. 20, 655–663. https://doi.org/10.1007/ s10071-017-1088-4.
- Murphy, E., King, E.A., 2011. Scenario analysis and noise action planning: modelling the impact of mitigation measures on population exposure. Appl. Acoust. 72, 487–494. https://doi.org/10.1016/j.apacoust.2010.10.006.
- Nemeth, E., Brumm, H., 2010. Birds and anthropogenic noise: Are urban songs adaptive? Am. Nat. 176, 465–475. https://doi.org/10.1086/656275.
- Njegovan, M., Hilhorst, B., Ferguson, S., Weisman, R., 1994. A motor-driven feeder for operant training in songbirds. Behav. Res. Methods Instrum. Comput. 26, 26–27. https://doi.org/10.3758/BF03204558.
- Palya, W.L., Walter, D.E., 2001. Document Set for the High-performance Experiment Controller. Retrieved 25 October 2014 from. http://www.jsu.edu/depart/ psychology/sebac/Exp-Ctl.html.
- Patange, K.B., Khan, A.R., Behere, S.H., Shaikh, Y.H., 2013. Traffic noise: 1/f characteristics. In: Magoulas, G. (Ed.), Investigations Into Living Systems, Artificial Life, and Real-World Solutions. IGI Global, Hershey, PA, pp. 44–53. https://doi.org/10. 4018/978-1-4666-3890-7.ch006.
- Potvin, D.A., Curcio, M.T., Swaddle, J.P., MacDougall-Shackleton, S.A., 2016. Experimental exposure to urban and pink noise affects brain development and song learning in zebra finches (*Taeniopygia guttata*). PeerJ 4, e2287. https://doi.org/10. 7717/peerj.2287.
- Proppe, D.S., McMillan, N., Congdon, J.V., Sturdy, C.B., 2017. Mitigating road impacts on animals through learning principles. Anim. Cogn. 20, 19–31. https://doi.org/10. 1007/s10071-016-0989-y.

Pyle, P., 1997. Identification Guide to North American Birds. Slate Creek Press, Bolinas.

Quinn, J.L., Whittingham, M.J., Butler, S.J., Cresswell, W., 2006. Noise, predation risk compensation and vigilance in the Chaffinch *Fringilla coelebs*. J. Avian Biol. 37, 601–608. https://doi.org/10.1111/j.2006.0908-8857.03781.x.

- Rios-Chelen, A.A., Lee, G.C., Patricelli, G.L., 2015. Anthropogenic noise is associated with changes in acoustic but not visual changes in Red-winged Blackbirds. Behav. Ecol. Sociobiol. 7, 1139–1151. https://doi.org/10.1007/s00265-015-1928-7.
- Ritters, K.H., Wickham, J.D., 2003. How far to the nearest road? Front. Ecol. Environ. 1, 125–129. https://doi.org/10.1890/1540-9295(2003)001[0125:HFITNR]2.0.CO;2.
- Schepers, M.J., Proppe, D.S., 2017. Song playback increases songbird density near low to moderate use roads. Behav. Ecol. 28, 123–130. https://doi.org/10.1093/beheco/ arw139.
- Scully, E.N., Schuldhaus, B.C., Congdon, J.V., Hahn, A.H., Campbell, K.A., Wilson, D.R., Sturdy, C.B., 2018. ZENK expression in the auditory pathway of black-capped chickadees (*Poecile atricapillus*) as a function of D note number and duty cycle of *chick-a-dee* calls. Behav. Brain Res. 356, 490–494. https://doi.org/10.1016/J.BBR. 2018.06.006.
- Shannon, G., McKenna, M.F., Angeloni, L.M., Crooks, K.R., Fristrup, K.M., Brown, E., Warner, K.A., Nelson, M.D., White, C., Briggs, J., McFarland, S., Wittemyer, G., 2016. A synthesis of two decades of research documenting the effects of noise on wildlife. Biol. Rev. 91, 982–1005. https://doi.org/10.1111/brv.12207. 982.
- Slabbekoorn, H., Ripmeester, E.A.P., 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Mol. Ecol. 17, 72–83. https://doi.org/10. 1111/j.1365-294X.2007.03487.x.
- Spetch, M.L., Cheng, K., MacDonald, S.E., Linkenhoker, B.A., Kelly, D.M., Doerkson, S.R., 1997. Use of landmark configuration in pigeons and humans: II. Generality across search tasks. J. Comp. Psychol. 111, 14–24.
- Sturdy, C.B., Weisman, R.G., 2006. Rationale and methodology for testing auditory cognition in songbirds. Behav. Processes 72, 265–272. https://doi.org/10.1016/j. beproc.2006.03.007.
- Summers, P.D., Cunnington, G.M., Fahrig, L., 2011. Are the negative effects of roads on breeding birds caused by traffic noise? J. Appl. Ecol. 48, 1527–1534. https://doi.org/ 10.1111/j.1365-2664.2011.02041.x.
- Szalma, J.L., Hancock, P.A., 2011. Noise effects on human performance: a meta-analytic synthesis. Psychol. Bull. 137, 682–707. https://doi.org/10.1037/a0023987.
- Tempest, W. (Ed.), 1985. The Noise Handbook. Academic Press, London, UK. Templeton, C.N., Zollinger, S.A., Brumm, H., 2016. Traffic noise drowns out great tit
- alarm calls. Curr. Biol. 26, 1173–1174. https://doi.org/10.1016/j.cub.2016.09.058. Van Donselaar, J.L., Atma, J.L., Kruyf, Z.A., LaCroix, H.N., Proppe, D.S., 2018.
- Urbanization alters fear behavior in black-capped chickadees. Urban Ecosyst. 21, 1–9. Ware, H.E., McClure, C.J., Carlisle, J.D., Barber, J.R., 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. Proc. Nat. Acad. Sci. 112, 12105–12109.