



Bioacoustics The International Journal of Animal Sound and its Recording

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tbio20

Hard of hearing: the effect of distance and experimental noise on mountain chickadee song transmission

C. L. Snell, M. W. Reudink & K. A. Otter

To cite this article: C. L. Snell, M. W. Reudink & K. A. Otter (2023): Hard of hearing: the effect of distance and experimental noise on mountain chickadee song transmission, Bioacoustics, DOI: 10.1080/09524622.2023.2172080

To link to this article: https://doi.org/10.1080/09524622.2023.2172080



Published online: 09 Feb 2023.



🖉 Submit your article to this journal 🗹



💽 View related articles 🗹



View Crossmark data 🗹



Check for updates

Hard of hearing: the effect of distance and experimental noise on mountain chickadee song transmission

C. L. Snell^a, M. W. Reudink^b and K. A. Otter^a

^aNatural Resources and Environmental Studies, University of Northern British Columbia, Prince George, BC, Canada; ^bDepartment of Biological Sciences, Thompson Rivers University, Kamloops, BC, Canada

ABSTRACT

Urban noise can disrupt avian communication networks, resulting in reduced communication among individuals. Mountain chickadees alter their vocalisations in areas of high ambient noise; however, it is unknown how audible their signals are within the nest cavity, where the female remains during dawn signalling. To test the relative audibility of songs within the nest box of urban and rural chickadees, we conducted a playback experiment directed at empty nest boxes using an autonomous recording unit above the box with external microphones and an internal microphone inside the nest box. We placed a speaker 25-75 m from the nest box and played two playback files of mountain chickadee songs - one with added noise and one without. Songs had a higher signal-to-noise ratio (SNR) in rural habitats and in 'Without Added Noise' treatments, however, SNR decreased with increasing distance from the nest box. The lower frequency song notes had a lower SNR inside the nest in both treatment types. As expected, noise and distance resulted in decreased SNR of chickadee songs within the nest cavity. These findings suggest a possible constraint in urban birds requiring them to reduce their distance from the nest to ensure audibility to the female while in noise.

ARTICLE HISTORY

Received 22 February 2022 Accepted 13 January 2023

KEYWORDS

Birdsong; female perception; mountain chickadee; nest box; signal-to-noise ratio; urbanisation

Introduction

Many temperate and tropical species of songbirds engage in intense bouts of singing in the period prior to, and extending through, sunrise. Known as the dawn chorus, singing during this period is hypothesised to function for territorial defence, mate attraction, and facilitating social dynamics (Staicer et al. 1996; Collins 2004; Burt and Vehrencamp 2005). Early research on great tits (*Parus major*) suggested that one of the primary intended receivers of these vocal signals are female listeners (Krebs et al. 1981; Mace 1986, 1987; McGregor 1991). In several species of cavity-nesting birds, males end their dawn singing when their mate leaves the nest (Mace 1986; Pårt 1991; Otter and Ratcliffe 1993; Gammon 2004; McCallum et al. 2020), and peaks of dawn song output coincide with female fertility and/or commencement of egg-laying (Welling et al. 1995). In black-capped chickadees (*Poecile atricapillus*), male chorus behaviour such as movement

patterns, distance from the nest, and song rates, were associated with the fertility of their mate (Foote et al. 2008).

Differences in song output during dawn singing also correlate with male dominance/ rank, extra-pair mating success, and age (Welling et al. 1995; Kempenaers et al. 1997; Otter et al. 1997; Poesel et al. 2001; Ballentine et al. 2003), suggesting that dawn singing may be a means of honestly advertising the fitness or quality of a male (Otter and Ratcliffe 1993; Welling et al. 1995; Kempenaers et al. 1997; Otter et al. 1997). Females are thought to use dawn signalling as a means of assessing suitable mates, whether by eavesdropping to assess the relative quality of interacting males (Otter et al. 1999; Mennill et al. 2003; Peake 2005; Mennill and Otter 2007), or by directly evaluating song traits that may indicate overall fitness, such as age, dominance, or stamina (Otter et al. 1997; Burt and Vehrencamp 2005). Females can simultaneously sample and assess multiple territorial males by strategically positioning themselves within a communication network, or by cautiously sampling males from a distance while remaining undetected (Murphy and Gerhardt 2002; Otter and Ratcliffe 2005), especially if signal transmission is long-range (Otter and Ratcliffe 2005).

These vital communication networks can, though, be masked and disrupted by urban ambient noise (Patricelli and Blickley 2006; Naguib 2013; Slabbekoorn 2013), leading to a reduction in efficacy of intra- and interspecific signals, delayed responses, reduced information received, or increased risk of predation (Kern and Radford 2016; Grabarczyk and Gill 2019b). Anthropogenic noise is predominately low-frequency and can, for example, extend >300 m from either side of roads (Forman and Deblinger 2000). This anthropogenic noise can decrease the area and distance that acoustic signals can be detected by animals (Barber et al. 2010), while differentially disrupting or overlapping low-frequency bird song or call notes (Halfwerk et al. 2011). Some animals adjust their behaviours/vocalisations in response to persistent noise pollution by shifting songs upwards in pitch to avoid overlap with noise (Slabbekoorn and Peet 2003; Wood and Yezerinac 2006; Nemeth and Brumm 2009; Francis et al. 2011; Nemeth et al. 2013; Redondo et al. 2013; LaZerte et al. 2016, 2017), increasing song output (Grabarczyk and Gill 2019a), increasing song amplitude (Nemeth and Brumm 2010), singing atypical songs which may have higher transmission properties (LaZerte et al. 2019) or altering temporal patterning of singing to avoid peak periods of anthropogenic noise (Fuller et al. 2007; Nordt and Klenke 2013; Dominoni et al. 2016). However, not all vocal adjustments have proven successful and may even be less effective if the signal receiver is in an environment that may impede sound transmission, such as a nest cavity or amidst loud ambient noise.

Female chickadees typically roost within their nest cavity, and the acoustic properties of the cavity may determine their ability to discern songs of their mates and prospective neighbouring males without having to leave the nest (Otter and Ratcliffe 2005). In black-capped chickadees, females have been shown to excavate nest entrance holes to orient towards neighbouring males (Mennill and Ratcliffe 2004), and nest cavities themselves were often chosen in trees located close to territory boundaries, especially if neighbouring males were higher-ranked than their social partner (Ramsay et al. 1999). These choices may improve audibility for the roosting female to assess multiple males during the dawn chorus, but noise pollution could impede female assessment (Huet des Aunay et al. 2014; Grabarczyk and Gill 2019b). Previous studies showed the signal-to-noise ratio (the level

of the observed signal compared to the level of the background noise) of great tit and house wren (*Troglodytes aedon*) songs were reduced inside the nest box compared to outside (Blumenrath et al. 2012; Grabarczyk and Gill 2019b), and pied flycatcher (*Ficedula hypoleuca*) songs were found to have higher song degradation within the box than outside (Lampe et al. 2004).

To a female chickadee roosting in the nest, the signal-to-noise-ratio of songs is expected to decrease with increasing distance of the male from the nest (Lampe et al. 2004; Blumenrath et al. 2012) but this may be exacerbated with increasing noise around the nest (Halfwerk et al. 2012; Grabarczyk and Gill 2019b). Therefore, information gained from honest advertising of males during the dawn signalling period may be reduced for females in noisy environments (Halfwerk et al. 2012; Grabarczyk and Gill 2019b).

The objective of this study was to test the effect of distance and noise on signal-tonoise ratios of mountain chickadee (*Poecile gambeli*) songs by broadcasting songs from 25 to 75 m distances to previously used nest boxes in both urban and rural habitats. We placed a microphone outside and inside the nest box, and at each distance, we broadcasted mountain chickadee songs with and without added noise. We predicted that noise and distance would decrease the signal-to-noise ratio of chickadee songs and may differentially affect the audibility of songs within the nest cavity within the nest cavity, especially in urban habitats.

Methods

Study species

Mountain chickadees are small, non-migratory songbirds that inhabit high elevation, montane coniferous forests of western North America (McCallum et al. 2020). This species has a life history that is somewhat atypical of most urban-adapting birds; rather than being habitat generalists like most successful urban-adapting species (Blair 1996; Kozlovsky et al. 2017), they are considered habitat specialists (McCallum et al. 2020). Mountain chickadees are secondary cavity nesters largely reliant on cavities created by other species (McCallum et al. 2020), which means they can be attracted to artificial nest boxes placed in urban landscapes.

Field site and nest box locations

We conducted this study in Kamloops, BC, Canada, during the 2019 breeding season. We made use of a network of approximately 65 nest boxes in rural and 40 in urban locations in the South Kamloops region (Marini et al. 2017) which have been part of ongoing research on urban nesting in mountain chickadees since 2013. Nest boxes were located in Kenna Cartwright Nature Park and several tracks of urban greenbelts containing native vegetation (Rural sites), and several neighbourhoods in the upper urban areas of South Kamloops, including the Thompson Rivers University campus (Figure 1). Kenna Cartwright Nature Park and isolated greenbelts primarily consist of native ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) mixed conifer forests, with grassland and sagebrush (*Artemisia* sp.) open areas and ground covering, with little



Figure 1. Mountain chickadee (*Poecile gambeli*) nest boxes were located throughout the southern area of Kamloops, BC, Canada. The Rural sites were mostly in Kenna Cartwright Nature Park, while the Urban sites were at Thompson Rivers University and throughout several high elevation urban neighbourhoods. Photo credit Google Earth Pro.

anthropogenic disturbance within a 75 m radius of the nest. Urban sites contain significant urban structures around the nest locations, including roads, buildings, mown lawns, and non-native tree species, resulting in a much higher deciduous component and larger open-canopy space than native forests (Marini 2016). However, despite this dichotomy in habitat characteristics between rural and urban sites, we have intentionally selected placement of boxes in both habitat types at varying distances from major motorways and industrial sites in the region such that nests in either habitat experience the full spectrum of noise pollution from quiet to loud ambient noise. This has allowed us to disentangle the effects of noise pollution vs habitat on other aspects of chickadee nesting success. For the purpose of the current study, we selected nests in both habitat types to conduct experimental playback of songs/noise; because of the intentional placement noted above, this should not create discrepancies in the relative ambient noise levels between sites, but include habitat type (rural vs urban) to account for any influence this might have exerted on outcomes.

Field protocol

Nest boxes consisted of multiple design variants due to the gradual addition of boxes to the study site over time. This led to five slightly different box types in the population with similar internal dimensions, but different construction materials, which could potentially affect acoustics (Swaddle et al. 2012). To account for these differences, we added box type as a random variable in statistical models.

We chose nest boxes in the long-term mountain chickadee study population that were actively occupied during the 2019 field season (when the study was conducted) or had been occupied at least one time in the previous 5 years (indicating their potential suitability; N = 23) across both urban and rural habitats. Once active nests had fledged and/or boxes were vacant, we mounted a Wildlife Acoustic SM4 Autonomous Recording Unit (ARU; Wildlife Acoustics, Inc) above the nest box. The ARU unit recorded in stereo channels, with one channel having a microphone recording outside the box (external) and the other channel recording from a microphone attached to a 3 m cord placed inside the nest box (internal). A small square piece of the nest box (~1.9 cm \times 1.9 cm) was removed from the upper edge of a side wall, where we then affixed the internal microphone, so the microphone was above the entrance hole by ~7.6 cm and facing into the nest cavity. The ARU was set to record continuously until the speaker trials were completed (recordings were set at 16-bit digitisation with 44.1kHz sampling rate in WAV format). We used a retractable measuring tape to mark 25 m, 50 m, and 75 m from the nest box, in the direction directly in front of the box entrance hole, as previous work has shown sounds from directly in front of the cavity entrance to be most audible (Mennill and Ratcliffe 2004). By conducting trials directly in front of the nest entrance, we created optimal conditions for signals without broadcast noise to be detected (bestcase scenario) to compare with a signal that is broadcast with noise from a similar direction (worst-case scenario).

Using the files created by LaZerte et al. (2019), we used 40 different playback files; this consisted of 20 files without added noise and 20 matching files with added noise. Each of the 20 distinct files randomly contained the songs of one of 13 different male mountain chickadees recorded during the dawn chorus in central British Columbia (LaZerte et al. 2019). Where the same male was used in different files, it was paired with a different noise file (see below). Each stimulus consisted of two audio signals split to the left and right audio channels of a stereo output. On one channel were 28 evenly spaced songs (14 songs/min for a total of 28 over 2 min) of a male mountain chickadee, broadcast at a typical singing volume of 75 ± 2 dB (Z; mean \pm standard deviation, measured at 5 m using a Pulsar 30 (Pulsar Instruments plc., Filey, North Yorkshire, UK)). The second channel contained either a blank signal (without added noise) or a synthetic noise file simulating typical highway traffic noise broadcast at 68 dB \pm 2 dB (Z). This synthetic white noise was derived to imitate an average traffic frequencyspectrum (LaZerte et al. 2017, 2019), and a different noise file was created for each playback. The noise spectrum contained enough high-frequency noise to partially mask chickadee vocalisations and similar synthetic sound clips have been used on other Parid species (cf. Halfwerk and Slabbekoorn 2009; Halfwerk et al. 2011). These sound files were created for a previous study (LaZerte et al. 2016) and derived based on spectral analysis of continuous-traffic highway noise recorded at several locations. Synthetic experimental noise was used instead of actual traffic noise as traffic recordings could contain other sounds that may influence chickadee responses, such as biological signals, and add a confounding factor that could lead to pseudoreplication issues (Slabbekoorn and Bouton 2008).

We broadcast the playbacks through a 5W Roland Mobile Cube amplifier, which has two built-in loudspeakers (Roland Corporation, Los Angeles, USA; full range audio frequency response ~ 100 Hz-20 kHz). The two speakers are side-by-side, with 10 cm

6 🕒 C. L. SNELL ET AL.

between their centres, and each speaker being 8.75 cm in diameter and are independently controlled by separate left vs right audio channels; this allowed us to simultaneously broadcast the song files from one speaker, and noise files from an independent speaker (LaZerte et al. 2017, 2019). At each distance interval, we broadcast two paired playback stimuli in succession: one stimulus consisted of mountain chickadee songs broadcast from the left speaker with a blank signal in the right speaker (signal without added noise); the second stimulus consisted of the same male vocalisations from the same speaker as above, but with synthetic white noise broadcast from the second speaker. Each 'With Added Noise' stimulus sound file consisted of gradual fading in of the background noise over 20 s until at full volume, followed by 40 s at full volume for acclimation. We then initiated the 28 sequential mountain chickadee songs (14 songs/min for a total of 28 over 2 min) and ended with fading out the background noise over 20 s (LaZerte et al. 2019). The 'Without Added Noise' stimulus files were structurally the same but with no added synthetic background noise (LaZerte et al. 2017, 2019). The speaker system was attached to a Slik Able 300 DX tripod to raise the speaker (1.6 m above the ground) and to ensure the playback songs were not impeded by any low shrub vegetation.

We conducted this experiment on 23 nest boxes distributed across the Kamloops, BC, study sites between June 10 - July 2, 2019. This period falls well past the typical peak in mountain chickadee chorusing and was chosen to avoid acoustic overlap between our playbacks and resident males. Experiments were conducted early in the morning between 06:00 and 08:00, scheduled just after standard dawn chorus timing to avoid acoustic interference with other species that may still be actively chorusing at this point of the season. Start times were cut off at 08:00 as signal transmission is more consistent in early morning (Henwood and Fabrick 1979; Brown and Handford 2003). Each box was tested several days after the nest had fledged. This approach allowed us to retain similar weather and climate characteristics of when the nests were active, to prevent the previous pair from being stressed, and to reduce the potential of interference or countersinging from the resident male during playbacks. We also made note of the status of neighbouring nests and whether they were still active, or in range of the speaker trial and would adjust our speaker trial date so that no known nests within audibility range were active during trials. Two trials were removed from analysis due to incomplete recordings or excess wind, leaving a total of 21 nest box trials for analysis.

Data analysis

Mountain chickadee songs typically contain two note types, '*fee*' and '*bee*' (McCallum et al. 2020), with a typical song structure in the population of two '*fee*' notes followed by two lower frequency '*bee*' notes. However, songs can often vary in frequency and number of notes based on the individual, or habitat. Below, the '*fee*' notes are labelled as note one (N1) and '*bee*' notes are note two (N2).

Audio files from each speaker trial were viewed in Audacity v2.4.2 software (Audacity Team 2020). To visualise and identify the start of the signal, each audio file was viewed in stereo tracks; one track was the microphone inside the nest box while the other track was the external microphone. The audio track was then 'fit to height' and zoomed into approximately 10 s frames in the Hann window set at 1024 Hz bandwidth. Audio files were unaltered; no noise reduction was used. For each distance category (25 m, 50 m, and

75 m) a blind observer scanned the entire recording and selected the three clearest songs from each audio file using selection criteria that the time immediately before and during the stimulus song was not overlapped by other bird vocalisations, noises or heavy wind that would influence the measure of SNR of the song notes. If it proved difficult to find three clear songs per distance category, we used a minimum of at least one song. Each song was then clipped into individual files and labelled, with the start of each note (N1 and N2) labelled (Figure 2; N = 466). In addition, we ensured that each song clipping had at least 0.5 s of space prior to the start of the first note for background noise analysis (Figure 2; Figure 3).



Figure 2. An example Audacity software (v2.4.2; Audacity Team 2020) spectrogram representing a typical mountain chickadee (*Poecile gambeli*) song clip from a playback trial, with labels at the start of each note type, N1 and N2. This example song playback clip is from an urban nest box in Kamloops, BC, Canada, using a without added noise playback file. The speaker was 25 m from the box and this song clip was recorded by the microphone placed inside the nest box.



Figure 3. Example root-mean-square (RMS) spectrograms of one mountain chickadee (Poecile gambeli) playback file song. All images are from one song broadcast from 25 m away from the nest in the same Urban nest box in Kamloops, BC, Canada. The left column spectrograms were during a With Added Noise playback trial, while the right column spectrograms were from Without Added Noise trials. The two images on the top row were from the inside microphone and the two on the bottom row are from the outside microphone.

8 🕒 C. L. SNELL ET AL.

All analyses were conducted with R statistical software (v4.0.3, 2020, R Core Team 2021) through RStudio IDE (v1.3.1093, RStudio Team 2022). R packages 'tuneR' (Ligges et al. 2018), 'glue' (Hester 2020), 'kableExtra' (Zhu et al. 2021), 'tidyverse' (Wickham et al. 2019), and 'assertr' (Fischetti 2021) were used for general song data manipulation. First, we filtered by a frequency range of 3000–5000 Hz to approximate the entire song and ensured no notes were out of this range. Using the R package 'seewave' (v2.1.6, Sueur et al. 2008), we extracted 0.5 s of background noise before the first note ('noise') and 0.5 s of each note type ('note' - based on the minimum length of N2 being approximately 0.5 s) to use for conducting root-mean-square (RMS) analysis (Figure 3). RMS spectrograms were created in RStudio using 1024 window length, frequency limits of 0 Hz and 6kHz, and in Hann window. Any song clips that resulted in an RMS value lower than the background noise were checked and removed if the noise or overlap was too disruptive (N = 4). These RMS values were used to calculate signal-to-noise ratios (the level of the observed signal compared to the level of the background noise; SNR) in decibels using the following equation:

$$(SNR = RMS \frac{note}{noise})$$

Then convert the signal-to-noise ratios to decibels using the following equation:

$$(SNR(dB) = 10 * log10(SNR))$$

We then took the mean of the song clips to obtain one mean value per distance category (25 m, 50 m, 75 m), nest box, treatment type (With Added Noise or Without Added Noise), and microphone location (inside or outside). Next, we compared the signal-to-noise ratio of the songs between the inside and the outside of the nest box using RStudio.

We ran our analysis on each note type as chickadees have been known to adjust their songs, particularly the last few notes, in urban environments (LaZerte et al. 2017). A generalised linear mixed effects model was performed using the 'lme4' (Bates et al. 2015) package for R, to assess associations between the signal-to-noise ratio of both note types and microphone position (inside or outside the nest box), distance from the box, treatment type (Without Added Noise and With Added Noise), and habitat type (Urban or Rural) and any interaction between treatment type and distance of the playback from the nest. Each model incorporated box design type as a random effect to account for the different box designs used in the trials. Figures were created using 'ggplot2' (Wickham 2016) and 'patchwork' (Pedersen 2020).

Results

Songs were broken into both note types, note 1 (N1) and note 2 (N2) for analysis. The signal-to-noise ratio (SNR) of N1 declined with increasing distance from the box, was lower in the With Added Noise treatment than the Without Added Noise treatment, and was slightly lower in Urban than Rural habitats (Table 1; Figure 4(b)). Microphone location (outside vs inside) did not significantly affect the SNR of the N1 note (Table 1; Figure 5(a)). However, there was also an interaction effect between treatment type (Without Added Noise and With Added Noise) and distance of the playback from the nest (25 m, 50 m, 75 m; Table 1; Figure 4(a)); this indicated that the decline in SNR with

Table 1. Results from a general linear mixed effects model, assessing the relationship between the signal-to-noise ratios of mountain chickadee (*Poecile gambeli*) playback song note 1 (N1) and treatment type (Without Added Noise, With Added Noise), distance of the playback from the nest (25 m, 50 m, 75 m), microphone location (outside, inside), and habitat type (urban or rural), with an interaction effect between treatment type and distance from the nest.

	<i>,</i> .					
	Estimate	Std. Error	df	t-value	Pr(> t)	
Treatment Type	8.11	1.50	251.34	5.40	<0.00001***	
Distance	-0.082	0.020	251.46	-4.05	<0.00001***	
Microphone Location	-0.34	0.57	251.40	-0.59	0.55	
Habitat Type	1.77	0.82	167.55	2.15	0.033*	
Treatment:Distance	-0.090	0.028	251.41	-3.16	0.0018**	

increasing distance was greater in the Without Added Noise treatment than the With Added Noise treatment. This effect was largely due to the SNR already being fairly low at short distances (25 m) once noise was added, and so had less room to decline much further with increasing distance. By comparison, SNR was high at short distances in Without Added Noise treatments and only reach low levels at 75 m in these trials (Figure 4(a)).

The SNR of N2 was lower in With Added Noise vs Without Added Noise treatments, declined with increasing distance of the playback from the nest, and was lower on the internal microphone than the external (Table 2; Figure 4(b); Figure 5(b)). There was no effect of habitat on SNR of the N2 note. There was, though, an interaction effect between treatment type (Without Added Noise and With Added Noise) and distance of the playback from the nest (25 m, 50 m, 75 m; Table 2). This interaction between treatment type and distance of the playback parallels the effect seen on the N1 note: SNR of the N2 note is high at 25 m but declines rapidly to 75 m in the Without Added Noise treatment, but in the With Added Noise treatment the SNR of the N2 note is already quite low even at short playback distances (25 m), and only declines marginally with increasing playback distance (Figure 4(b)).

In contrast to N1 results above, N2 was also affected by microphone location (Table 2); overall, the SNR ratio of songs was lower from recordings made inside the nest box compared to songs recorded on the external microphone (Figure 5(b)).

Discussion

Distance was a major factor affecting the audibility of songs within the nest, particularly when playbacks were conducted without added noise. There was also a slight impact of

Table 2. Results from a general linear mixed effects model, assessing the relationship between the signal-to-noise ratios of mountain chickadee (*Poecile gambeli*) playback song note 2 (N2) and treatment type (Without Added Noise, With Added Noise), distance of the playback from the nest (25 m, 50 m, 75 m), microphone location (outside, inside), and habitat type (urban or rural), with an interaction effect between treatment type and distance from the nest.

	Estimate	Std. Error	df	t-value	Pr(> t)
Treatment Type	7.04	1.41	249.27	4.99	<0.00001***
Distance	-0.080	0.019	249.29	-4.14	0.000047***
Microphone Location	1.89	0.54	249.27	3.48	0.00058***
Habitat Type	-1.19	0.79	230.38	-1.50	0.13
Treatment:Distance	-0.065	0.027	249.27	-2.45	0.015*

Figure 4. Signal-to-noise ratio (dB) of note one (N1; A) and note two (N2; B) of mountain chickadee (*Poecile gambeli*) playback songs at each distance interval (25 m, 50 m, 75 m) for both With Added Noise and Without Added Noise treatments, while comparing the signal-to-noise ratio of notes at each habitat type (R = rural and U = urban) in Kamloops, BC, Canada. Without Added Noise trials exhibited a steeper decline in the signal-to-noise ratio of both note types as distance increased from the nest, regardless of habitat type. Whereas With Added Noise trials exhibited similar signal-to-noise ratios regardless of distance from the nest, habitat type or note type.

habitat, with rural settings having better signal-to-noise ratios than urban sites but only notable at the farthest transmission distance. However, once noise was added to the playbacks, the difference between habitat classes was lost; rather the signal-to-noise ratio of songs was heavily diminished in both habitats even at short distances and increasing

Figure 5. Signal-to-noise ratio (dB) of note one (N1; A) and note two (N2; B) of mountain chickadee (Poecile gambeli) playback songs in Kamloops, BC, Canada at each distance interval (25 m, 50 m, 75 m) for both With Added Noise and Without Added Noise treatments, while comparing the signal-to-noise ratio of notes at the two microphone positions (i = inside the nest and o = outside the nest). As distance from the nest increased, both note types exhibited a steeper decline in signal-to-noise ratio in without added noise trials compared to with added noise trials, regardless of microphone location.

distance had a lesser effect on further degrading the songs. This finding could negatively impact the ability of females nesting in noisy habitats to assess males in a network-like fashion during the dawn chorus.

We also found that the two note-type elements of songs showed differential degradation, particularly in how the signal was affected by noise and by acoustics of the nest box. The lower-pitched N2 note of the song had a decreased signal-to-noise ratio inside versus

11

12 👄 C. L. SNELL ET AL.

outside of the nest in both treatment types, whereas the higher-pitched N1 note of the start of songs was not affected by the position of the recording microphone. This finding is consistent with studies on other cavity-nesting species that suggests cavities alter signal transmission (Lampe et al. 2004; Kight et al. 2012) and vocalisations are marginally degraded within the nest box (Lampe et al. 2004; Blumenrath et al. 2012; Grabarczyk and Gill 2019b). There was an interaction between distance and treatment type for the signalto-noise ratios of both note types, suggesting that the signal-to-noise ratio decreased as distance of the speaker increased from the nest box, but that this decline was far more pronounced in songs broadcast without added noise. At greater distances (75 m), the lower-pitched N2 notes also showed a sharp drop in signal-to-noise ratio on recordings inside the box relative to outside, particularly in the With Added Noise treatment. These effects were evident despite playbacks being conducted in circumstances that would normally provide optimal sound transmission parameters (i.e. optimal time of day, directly in line with nest entrance, and using previously successful nest cavities). This impact of noise and the acoustic dampening of the nest box differentially impacted the lower-pitched N2 elements of the song, which may explain a previous study (LaZerte et al. 2016) that found male mountain chickadees singing in noisy environments reduce their use of this note type. LaZerte et al. (2016) showed individual males would often repeat the high note (N1) more and reduce the number of low notes (N2) when singing in areas of high ambient noise. Our results confirm LaZerte et al. (2016) suggestion that shifting songs to greater repetition of higher-pitched notes in the song would increase audibility, particular in urban-noise situations.

In this study, the signal-to-noise ratio was used as an indicator of relative audibility of songs. We assumed that vocalisations picked up by the microphone placed inside the nest box would mimic how the signals during the chorus may be perceived by a female roosting within the nest. Our work does indicate that in low-noise conditions, the signals are still audible within the cavity even at long distances (75 m – the greatest distance tested). This finding is further supported by field recordings during actual dawn choruses, in which mountain chickadees have been observed singing from distances greater than 75 m from the nest box, yet these songs have continued to elicit vocal responses from the female within the nest (Snell 2021). However, the addition of noise has a high potential to disrupt the ability of females to assess distant males, such as those counter-singing against the female's mate from neighbouring territories. Signal-to-noise ratios during treatments with added noise were so diminished that playbacks at 25 m mimicked the signal loss of songs at 75 m in treatments without added noise.

Our results confirm that noise and distance interact to decrease signal audibility, so we would predict that males occupying noisier environments (whether urban or rural) may be more constrained to chorus close to the cavity than males on quieter territories. Such a constraint on movement during dawn singing may have two impacts on communication networking: it may constrain the male's signal being heard by neighbouring females, and thus limit his potential for extra-pair mating opportunities (cf. Kempenaers et al. 1997; Otter et al. 2022); and it could impede his ability to signal to neighbouring males in defence of his territory. By understanding how signal transmission among cavity-nesting species is affected by noise pollution, we may better understand the broad ecological impacts of urban noise, so can better prioritise mitigation of these pressures on surrounding biodiversity.

Acknowledgements

We wish to acknowledge our work was conducted on the unceded territories of the Tk'emlúps te Secwépemc and Skeetchestn First Nations, and Lheidli T'enneh, part of the Dakelh (Carrier), First Nations. We thank field assistants B. Smith, M. Oud, A. Lamberton, and numerous volunteers provided by Thompson Rivers University, as well as K. Legeard for assisting with initial data preparations and Dr. S. LaZerte for assisting with preliminary data organisation and coding script preparations. R. Dawson and J. Foote kindly provided feedback on previous drafts of this manuscript. We also acknowledge the City of Kamloops for permitting us to conduct our studies in parks and urban areas.

Disclosure statement

All authors declare that they have no established conflicting financial interests or personal relationships that may have influenced the research presented in this paper.

Funding

This work was supported by Project Learning Tree Canada under Project ID [80482]; Natural Sciences of Engineering Research Council of Canada Discovery Grant under grant [RGPIN-2019-07045 and 4603-2018]; the University of Northern British Columbia through a British Columbia Graduate Scholarship; the University of Northern British Columbia Research Project Award under grant [29232] and an Indspire Almina Pokrant Award.

Data availability statement

Data can be requested from the Corresponding Author.

Ethical statement

Our study followed the institutional and national ethical guidelines for scientific research in Canada, the home country of our institutions. All work was approved by the University of Northern British Columbia Animal Care and Use Committee (UNBC-2017-01 and UNBC-2020-01) and was conducted under a Canadian Federal Master Banding Permit and Scientific Collection Permit no. 10940.

References

- Audacity Team. 2020. Audacity: free audio editor and recorder [Computer application]. Version 2.4.2.
- Ballentine B, Badyaev A, Hill GE. 2003. Changes in song complexity correspond to periods of female fertility in blue grosbeaks (*Guiraca caerulea*). J Ethol. 109(1):55–66. doi:10.1046/j.1439-0310.2003.00852.x.
- Barber JR, Crooks KR, Fristrup KM. 2010. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol Evol. 25(3):180–189. doi:10.1016/j.tree.2009.08.002.
- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw. 67(1):1–48. doi:10.18637/jss.v067.i01.
- Blair RB. 1996. Land use and avian species diversity along an urban gradient. Ecol Appl. 6 (2):506-519. doi:10.2307/2269387.

14 👄 C. L. SNELL ET AL.

- Blumenrath SH, Dabelsteen T, Pedersen SB. 2012. Being inside nest boxes: does it complicate the receiving conditions for great tit (*Parus major*) females? Bioacoustics. 14(3):209–223. doi:10. 1080/09524622.2004.9753526.
- Brown TJ, Handford P. 2003. Why birds sing at dawn: the role of consistent song transmission. Ibis. 145(1):120–129. doi:10.1046/j.1474-919X.2003.00130.x.
- Burt JM, Vehrencamp SL. 2005. Dawn chorus as an interactive communication network. In: McGregor P, editor. Animal communication networks. Cambridge (UK): Cambridge University Press; p. 320–343.
- Collins S. 2004. Vocal fighting and flirting: the functions of birdsong. In: McGregor P Slabbekoorn H, editors. Nature's music: the science of birdsong. California (USA): Elsevier Academic Press; p. 39–79.
- Dominoni DM, Greif S, Nemeth E, Brumm H. 2016. Airport noise predicts song timing of european birds. Ecol Evol. 6(17):6151-6159. doi:10.1002/ece3.2357.
- Fischetti T. 2021. 3D printing and bioprinting to model bone cancer: the role of materials and nanoscale cues in directing cell behavior. Cancers. 13(16). doi:10.3390/cancers13164065.
- Foote JR, Fitzsimmons LP, Mennill DJ, Ratcliffe LM. 2008. Tied to the nest: male black-capped chickadees decrease dawn chorus movement behaviour when their mate is fertile. Anim Behav. 76(4):1227–1233. doi:10.1016/j.anbehav.2008.06.007.
- Forman RTT, Deblinger RD. 2000. The ecological road-effect zone of a massachusetts (U.S.A.) suburban highway. Conserv Biol. 14(1):36–46. doi:10.1046/j.1523-1739.2000.99088.x.
- Francis CD, Ortega CP, Cruz A. 2011. Different behavioural responses to anthropogenic noise by two closely related passerine birds. Biol Lett. 7(6):850–852. doi:10.1098/rsbl.2011.0359.
- Fuller RA, Warren PH, Gaston KJ. 2007. Daytime noise predicts nocturnal singing in urban robins. Biol Lett. 3(4):368–370. doi:10.1098/rsbl.2007.0134.
- Gammon DE. 2004. Black-capped chickadee dawn chorus and subsequent sexual activity. Wilson Bull. 116(3):252–256. doi:10.1676/04-009.
- Grabarczyk EE, Gill SA. 2019a. Anthropogenic noise affects male house wren response to but not detection of territorial intruders. PLoS One. 14(7):e0220576. doi:10.1371/journal.pone.0220576.
- Grabarczyk EE, Gill SA. 2019b. A female perspective: testing the effects of noise masking on signal transmission patterns inside the nest box. Behaviour. 157(1):59–76. doi:10.1163/1568539X-00003581.
- Halfwerk W, Bot S, Buikx S, van der Velde M, Komdeur J, ten Cate C, Slabbekoorn H. 2011. Lowfrequency songs lose their potency in added noise urban conditions. Proc Natl Acad Sci. 108 (35):14549–14554. doi:10.1073/pnas.1109091108.
- Halfwerk W, Bot S, Slabbekoorn H. 2012. Male great tit song perch selection in response to noise-dependent female feedback. Funct Ecol. 26(6):1339–1347. doi:10.1111/j.1365-2435.2012. 02018.x.
- Halfwerk W, Slabbekoorn H. 2009. A behavioural mechanism explaining nose-dependent frequency use in urban birdsong. Anim Behav. 78(6):1301–1307. doi:10.1016/j.anbehav.2009.09. 015.
- Henwood K, Fabrick A. 1979. A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. Am Nat. 114(2):260–274. doi:10.1086/283473.
- Hester J. 2020. Glue: interpreted string literals. R package version 1.4.2.
- Huet des Aunay G, Slabbekoorn H, Nagle L, Passas F, Nicolas P, Draganoiu TI. 2014. Urban noise undermines female sexual preferences for low-frequency songs in domestic canaries. Anim Behav. 87(January):67–75. doi:10.1016/j.anbehav.2013.10.010.
- Kempenaers B, Verheyen GR, Dhondt AA. 1997. Extrapair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. Behav Ecol. 8 (5):481-492. doi:10.1093/beheco/8.5.481.
- Kern JM, Radford AN. 2016. Anthropogenic noise disrupts use of vocal information about predation risk. Environ Pollut. 218(November):988–995. doi:10.1016/j.envpol.2016.08.049.
- Kight CR, Saha MS, Swaddle JP. 2012. Anthropogenic noise is associated with reductions in the productivity of breeding eastern bluebirds (*Sialia sialis*). Ecol Appl. 22(7):1989–1996. doi:10. 1890/12-0133.1.

- Kozlovsky DY, Weissgerber EA, Pravosudov VV. 2017. What makes specialized food-caching mountain chickadees successful city slickers? Proc Royal Soc B. 284(1855):20162613. doi:10. 1098/rspb.2016.2613.
- Krebs JR, Avery M, Cowie RJ. 1981. Effect of removal of mate on the singing behavior of great tits. Anim Behav. 29(2):635–637. doi:10.1016/S0003-3472(81)80134-0.
- Lampe HM, Dabelsteen T, Larsen ON, Pedersen SB. 2004. Degradation of song in a species using nesting holes: the pied flycatcher *Ficedula hypoleuca*. An Acad Bras Cienc. 76(2):264–266. doi:10.1590/S0001-37652004000200012.
- LaZerte SE, Marini KLD, Slabbekoorn H, Reudink MW, Otter KA. 2019. More mountain chickadees (*poecile gambeli*) sing atypical songs in urban than in rural areas. Can Field-Nat. 133 (1):28–33. doi:10.22621/cfn.v133i1.1994.
- LaZerte S, Otter KA, Slabbekoorn H. 2017. Mountain chickadees adjust songs, calls and chorus composition with increasing ambient and experimental noise. Urban Ecosyst. 20(5):989–1000. doi:10.1007/s11252-017-0652-7.
- LaZerte SE, Slabbekoorn H, Otter KA. 2016. Learning to cope: vocal adjustment to urban noise is correlated with prior experience in black-capped chickadees. Proc Royal Soc B. 283 (1833):20161058. doi:10.1098/rspb.2016.1058.
- LaZerte SE, Slabbekoorn H, Otter KA. 2017. Territorial black-capped chickadee males respond faster to high- than to low-frequency songs in experimentally elevated noise conditions. PeerJ. 5: e3257. doi:10.7717/peerj.3257.
- LaZerte SE, Slabbekoorn H, Otter KA. 2019. A field test of the audibility of urban versus rural songs in mountain chickadees. Ethol Eth. 12876. doi:10.1111/eth.12876.
- Ligges U, Krey S, Mersmann O, Schnackenberg S. 2018. TuneR: analysis of music and speech.
- Mace R. 1986. Importance of female behavior in the dawn chorus. Anim Behav. 34(2):621-622. doi:10.1016/S0003-3472(86)80139-7.
- Mace R. 1987. The dawn chorus of the great tit *Parus major* is directly related to female fertility. Nature. 330(6150):745–746. doi:10.1038/330745a0.
- Marini KLD. 2016. City life and chickadees: effects of urbanization on vocal output and reproductive success of the mountain chickadee (*Poecile gambeli*) [master's thesis]. Kamloops (BC): Thompson Rivers University.
- Marini KLD, Otter KA, LaZerte SE, Reudink MW. 2017. Urban environments are associated with earlier clutches and faster nestling feather growth compared to natural habitats. Urban Ecosyst. 20(6):1291–1300. doi:10.1007/s11252-017-0681-2.
- McCallum DA, Grundel R, Dahlsten DL. 2020. Mountain chickadee (*Poecile gambeli*), version 1.0. In: Poole AF, and Gill FB, editors. Birds of the world. Ithaca, NY, USA: Cornell Lab of Ornithology. [updated 1 Jan 1999; cited Sept 2019]. https://birdsoftheworld.org/bow/species/ mouchi/cur/introduction.
- McGregor PK. 1991. The singer and the song: on the receiving end of bird song. Biol Rev. 66 (1):57–81. doi:10.1111/j.1469-185X.1991.tb01135.x.
- Mennill DJ, Boag PT, Ratcliffe LM. 2003. The reproductive choices of eavesdropping female black-capped chickadees, *Poecile atricapillus*. Sci Nat. 90(12):577–582. doi:10.1007/s00114-003-0479-3.
- Mennill D, Otter KA. 2007. Status signalling and communication networks in chickadees: complex communication with a simple song. In: Otter K, editor. Ecology and behavior of chickadees and titmice: an integrated approach. Oxford: Oxford University Press; p. 215–233.
- Mennill DJ, Ratcliffe LM. 2004. Nest cavity orientation in black-capped chickadees *Poecile atricapillus*: do the acoustic properties of cavities influence sound reception in the nest and extra-pair matings? null. 35(6):477–482. doi:10.1111/j.0908-8857.2004.03351.x.
- Murphy CG, Gerhardt HC. 2002. Mate sampling by female barking treefrogs (*Hyla gratiosa*). Behav Ecol. 13(4):472–480. doi:10.1093/beheco/13.4.472.
- Naguib M. 2013. Living in a noisy world: indirect effects of noise on animal communication. Behaviour. 150(2013):1069–1084. doi:10.1163/1568539X-00003058.

16 🛭 🖌 C. L. SNELL ET AL.

- Nemeth E, Brumm H. 2009. Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? Anim Behav. 78(3):637–641. doi:10.1016/j.anbehav. 2009.06.016.
- Nemeth E, Brumm H. 2010. Birds and anthropogenic noise: are urban songs adaptive? Am Nat. 176(4):465-475. doi:10.1086/656275.
- Nemeth E, Pieretti N, Zollinger SA, Geberzahn N, Partecke J, Miranda AC, Brumm H. 2013. Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. Proc Royal Soc B. 280(1754):20122798. doi:10.1098/rspb.2012.2798.
- Nordt A, Klenke R. 2013. Sleepless in town drivers of the temporal shift in dawn song in urban European blackbirds. PLoS One. 8(8):e71476. doi:10.1371/journal.pone.0071476.
- Otter K, Chruszcz B, Ratcliffe LM. 1997. Honest advertisement and song output during the dawn chorus of black-capped chickadees. Behav Ecol. 8(2):167–173. doi:10.1093/beheco/8.2.167.
- Otter K, McGregor PK, Terry AMR, Burford FRL, Peake TM, Dabelsteen T. 1999. Do female great tits (*Parus major*) assess males by eavesdropping? A field study using interactive song playback. Proc Royal Soc B. 266(1426):1305–1309. doi:10.1098/rspb.1999.0779.
- Otter K, Ratcliffe LM. 1993. Changes in singing behavior of male black-capped chickadees (*Parus atricapillus*) following mate removal. Behav. 33(6):409–414. doi:10.1007/BF00170256.
- Otter K, Ratcliffe L. 2005. Enlightened decisions: female assessment and communication networks. In: McGregor P, editor. Animal communication networks. Cambridge (UK): Cambridge University Press; p. 133–151.
- Otter K, Reudink M, Foote J, McKellar A, Flood N. 2022. Sexual selection and mating systems under Anthoprogenic disturbance. In: Proppe D, editor. Songbird behavior and conservation in the Anthropocene. Boca Raton, FL, USA: CRC Press; p. 105–126.
- Pårt T. 1991. Is dawn singing related to paternity insurance? The case of the collared flycatcher. Anim Behav. 41(3):451–456. doi:10.1016/S0003-3472(05)80847-4.
- Patricelli GL, Blickley JL. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. Auk. 123(3):639–649. doi:10.1093/auk/123.3.639.
- Peake T. 2005. Eavesdropping in communication networks. In: McGregor P, editor. Animal communication networks. Cambridge (UK): Cambridge University Press; p. 13–37.
- Pedersen TL. 2020. Patchwork: the composer of plots. R package version 1.1.1.
- Poesel A, Foerster K, Kempenaers B. 2001. The dawn song of the blue tit *Parus caeruleus* and its role in sexual selection. Ethol. 107(6):521–531. doi:10.1046/j.1439-0310.2001.00680.x.
- Ramsay SM, Otter K, Ratcliffe LM. 1999. Nest-site selection by female black-capped chickadees: settlement based on conspecific attraction? Auk. 116(3):604–617. doi:10.2307/4089322.
- R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Redondo P, Barrantes G, Sandoval L. 2013. Urban noise influences vocalization structure in the house wren *Troglodytes aedon*. Ibis (Lond 1859). 155(3):621–625. doi:10.1111/ibi.12053.
- RStudio Team. 2022. Rstudio: integrated development environment for R. RStudio, PBC, Boston, MA.
- Slabbekoorn H. 2013. Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. Anim Behav. 85(5):1089–1099. doi:10.1016/j.anbehav.2013.01.021.
- Slabbekoorn H, Bouton N. 2008. Soundscape orientation: a new field in need of sound investigation. Anim Behav. 76(4):e5-8. doi:10.1016/j.anbehav.2008.06.010.
- Slabbekoorn H, Peet M. 2003. Birds sing at a higher pitch in urban noise. Nature. 424(6946):267. doi:10.1038/424267a.
- Snell CL. 2021. Avian communication networks: how audible are mountain chickadee males during dawn signalling? [master's thesis]. Prince George (BC): University of Northern British Columbia.
- Staicer CA, Spector DA, Horn AG. 1996. The dawn chorus and other diel patterns in acoustic signaling. In: Kroodsma D, and Miller E, editors. Ecology and evolution of acoustic communication in birds. Ithaca NY, USA.: Cornell University Press; p. 426–453.
- Sueur J, Aubin T, Simonis C. 2008. Seewave: a free modular tool for sound analysis and synthesis. Bioacoustics. 18(2):213–226. doi:10.1080/09524622.2008.9753600.

- Swaddle JP, Kight CR, Perera S, Davila-Reyes E, Sikora S. 2012. Constraints on acoustic signaling among birds breeding in secondary cavities: the effects of weather, cavity material, and noise on sound propagation. Ornithol Monogr. 74:63–77.
- Welling P, Koivula K, Lahti K. 1995. The dawn chorus is linked with female fertility in the willow tit *Parus montanus*. null. 26(3):241–246. doi:10.2307/3677325.
- Wickham H. 2016. Ggplot2: elegant graphics for data analysis. New York: Springer-Verlag.
- Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, et al. 2019. Welcome to the tidyverse. J Open Source Softw. 4(43):1686. doi:10.21105/joss.01686.
- Wood WE, Yezerinac SM. 2006. Song sparrow (*Melospiza melodia*) song varies with urban noise. Auk. 123(3):650-659. doi:10.1093/auk/123.3.650.
- Zhu H, Travison T, Tsai T, Beasley W, Xie Y, Yu G, Laurent S, Shepherd R, Sidi Y, Salzer B, et al. 2021. kableExtra: construct complex table with 'kable' and pipe syntax.