Black-capped chickadees *Poecile atricapillus* sing at higher pitches with elevated anthropogenic noise, but not with decreasing canopy cover

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Several songbird species sing at higher frequencies (i.e. higher pitch) when anthropogenic noise levels are elevated. Such frequency shifting is thought to be an adaptation to prevent masking of bird song by anthropogenic noise. However, no study of this phenomenon has examined how vegetative differences between noisy and quiet sites influence frequency shifting. Variation in vegetative structure is important because the acoustic adaptation hypothesis predicts that birds in more open areas should also sing at higher frequencies. Thus, vegetative structure may partially explain the observation of higher frequency songs in areas with high levels of anthropogenic noise. To distinguish between frequency shifting due to noise or vegetative structure we recorded the songs of black-capped chickadees *Poecile atricapillus* vocalizing in high and low noise sites with open and closed canopy forests. Consistent with the noise-dependent frequency hypothesis, black-capped chickadees sang at higher frequencies in high noise sites than in low noise sites. In contrast, birds did not sing at higher frequencies in sites with more open canopies. These results suggest that frequency shifting in chickadees is more strongly related to ambient noise levels than to vegetative structure. A second frequency measure, inter-note ratio, was reduced at higher levels of canopy cover. We speculate that this may be due to a non-random distribution of dominant males. In sum, our results support the hypothesis that some birds sing at higher frequencies to avoid overlap with anthropogenic noise, but suggest that vegetative structure may play a role in the modification of other song traits.

High levels of anthropogenic noise are related to changes in the diversity (Rheindt 2003, Francis et al. 2009), density (Reijnen and Poppen 1995, Reijnen et al. 1996, Bayne et al. 2008), dispersal, and age structure (Habib et al. 2007) of songbird communities. Because many birds depend upon acoustic communication (Slabbekoorn and Ripmeester 2008, Parris and Schneider 2009), anthropogenic noise may interfere with acoustically mediated processes such as territorial defence, mate selection, nest provisioning, and predator alarm (Catchpole and Slater 2008). The behavior and abundance of some bird species seem unaffected by high levels of anthropogenic noise and variation among species may be related to song frequencies. Specifically, species whose song frequencies are overlapped by anthropogenic noise (generally between 0 and 4 KHz; Skiba 2000) are less likely to inhabit noisy areas, while the densities of species using non-overlapped frequencies appear to be less affected by anthropogenic noise (Rheindt 2003, Hu and Cardoso 2009).

Species whose song frequencies overlap with anthropogenic noise may improve the efficacy of their vocal signals by shifting to higher song frequencies (Rabin and Greene 2002). A pioneering study by Slabbekoorn and Peet (2003) found that urban great tits *Parus major* inhabiting noisy locations sang at higher frequencies than their counterparts in quieter locales. This initial observation has now been confirmed in a handful of other species (Fernandez-Juricic et al. 2005, Slabbekoorn and den Boer-Visser 2006, Wood and Yezerinac 2006, Mockford and Marshall 2009, Nemeth and Brumm 2009, Parris and Schneider 2009) leading to the noise-dependent frequency hypothesis (Halfwerk and Slabbekoorn 2009), which suggests that variation in anthropogenic noise may be partially responsible for variation in the song frequencies of many songbird species (reviewed by Patricelli and Blickley 2006, Barber et al. 2010).

Despite its emerging prevalence, the association between anthropogenic noise and bird song frequencies has rarely been studied with concomitant attention to variation in habitat. Areas with high levels of anthropogenic noise are typically closer to roads, human infrastructure, and areas of higher human habitation, all of which can dramatically alter vegetative structure (Bowles and McBride 1998, Chace and Walsh 2006, McEwan and McCarthy 2008, Flory and Clay 2009). Depending on the history of settlement and land use patterns in an area, forest patches in more
Vegetative structure is particularly relevant to the frequency of bird song because it creates selective pressures that generate both inter- and intra-specific variation in bird song frequencies. Morton (1975) discovered that bird species inhabiting different habitat types (e.g. forest, edge, grassland) exhibited different song characteristics. Subsequent work showed that in obstructed environments (such as forests) birds typically sing at relatively low frequencies (Marten and Marler 1977, Padgham 2004) whereas in more open environments (such as grasslands) birds sing higher frequency songs and use more trill-like vocalizations (Brown and Handford 1996, Naguib 2003). Similar intra-specific differences in song structure have been demonstrated in populations that inhabit different forest types (Hunter and Krebs 1979, Nicholls and Goldizen 2006, Dingle et al. 2008). Lower frequency sound waves generally travel further then higher frequencies, but high frequencies are particularly susceptible to scattering and degradation by obstructing objects such as trees (Wiley and Richards 1978, 1982). Thus, selection against higher frequencies in dense forests may be stronger than in more open habitats. The finding that bird songs correlate with the ideal transmission characteristics for the habitat in which they dwell is known as the acoustic adaptation hypothesis (AAH; Morton 1975, Rothstein and Fleischer 1987).

Because habitat changes typically accompany anthropogenic noise, the increases in song frequency associated with noise may actually be caused (or at least affected) by concurrent changes in vegetation structure. Previous studies of noise effects have typically either standardized or ignored variation in vegetation. Here, we explicitly test whether differences in vegetative structure can account for the higher frequencies observed in the songs of birds exposed to high levels of anthropogenic noise. We tested this hypothesis by recording the fee-bee songs of male black-capped chickadees *Poecile atricapillus* inhabiting forest with open and closed canopies, in areas with high and low levels of anthropogenic noise. Previous work has shown that chickadees flexibly alter song frequency (Weisman et al. 1990, Horn et al. 1992), but whether overall frequency changes correlate with changes in noise or canopy cover has not been previously examined. If vegetative structure is a primary factor driving changes in black-capped chickadee song frequency, we predicted that chickadees in more open canopies would sing at higher song frequencies. Conversely, if anthropogenic noise is a primary factor driving changes in song frequency, we predicted that chickadees in areas with higher noise levels would sing at higher frequencies.

To further understand how the fee-bee song is affected by noise and vegetative structure, we examined three additional song characteristics. We measured the frequency ratio (inter-note ratio) and the amplitude ratio between the fee and bee note. Both can be modified, with higher quality males maintaining more consistent ratios (Christie et al. 2004, Hoeschele et al. 2010). The ideal despotic distribution suggests that dominance may vary with territory quality (Fretwell and Lucas 1970) and both noise level and canopy cover may affect territory quality. Finally, we examine song duration because it has been shown to decrease with increasing noise in great tits, a species closely related to the black-capped chickadee (Slabbekoorn and den Boer-Visser 2006).

**Methods**

**Site selection**

Twenty-six sites were selected for song recording. To encompass all potential canopy/noise scenarios, each site was defined as 1) noisy – closed canopy, 2) noisy – open canopy, 3) quiet – closed canopy, or 4) quiet – open canopy, with 6–7 sites in each category. Sites were selected from within the City of Edmonton and Elk Island National Park, all located within a 23 km radius; a range unlikely to be affected by different vocal dialects (Kroodsma et al. 1999). Urban sites provided the opportunity to record chickadee songs within high levels of anthropogenic noise while sites in Elk Island allowed for recording in more natural soundscapes. Both areas also contained forests patches with open and closed canopies. Forest density estimates produced by Mandryk and Wein (2006) for the City of Edmonton and the Alberta Vegetative Inventory (AVI) for Elk Island National Park were used for the initial assessment of canopy cover.

Each site was separated by >300 m with a mean pairwise distance between sites of 6.71 ± 1.06 km (standard error; SE) in Edmonton and 5.82 ± 0.98 km (SE) in Elk Island, making it unlikely that a single black-capped chickadee was recorded at more than one site (territories <175 m in diameter; Stefanski 1967). All recordings were made in areas within at least 1 ha of forest with similar canopy cover. Deciduous tree cover was dominant in all sites and edge habitat was minimized by selecting continuous forest tracks with similar within-stand structural characteristics (i.e. stand age, species composition, density, and tree height; based on data from Mandryk and Wein (2006) and the Alberta Vegetative Inventory (AVI)). To avoid confounding effects of anthropogenic disturbance and to minimize variation in noise within a site, no site was closer than 400 m to a highly or moderately used paved road (>5000 cars d<sup>-1</sup>, 2007 Traffic Flow Map, City of Edmonton).

To assess predicted differences in density between our forest categories, overhead canopy cover was measured in four locations at every point where a chickadee was recorded. Since canopy cover correlates with basal area (Dawkins 1963, Philip 1994), and thus forest density, agreement between our measurement and previous data was considered to be a realistic assessment of the differences in the density of forest objects obstructing a bird’s path of communication in each site. To assess overhead canopy cover a photo was taken directly upward with a digital camera (Canon PowerShot S50, Canon Canada, Mississauga, ON, Canada) at 1.5 m above the ground within 20 m of the bird’s location. Three additional photos were taken at the remaining corners of a 10 × 10 m square which encompassed or approached the location of the recorded individual.
bird. Using this method, habitat characteristics were quantified along the transmission lines of our recorded chickadee songs.

Vocal recording

Each site was visited twice between 23 April and 11 May, 2007. Black-capped chickadees were recorded from 30 min before sunrise (~05:00 h) until 13:00 h. Multiple sites were recorded simultaneously so that birds were recorded at similar dates and times in all categories. All recordings were conducted using a Marantz PMD670 solid state recorder and a Sennheiser ME67 directional microphone (Saul Mineroff Electronics, Elmont, New York, USA). All chickadees were recorded within 25 m of the microphone. Once a chickadee was located, recording continued until singing ceased or the recording time reached 5 min. We recorded up to six birds at each site. In some cases multiple birds were recorded simultaneously. We pooled these individuals for the analyses because it was not always possible to positively distinguish among individuals.

Analysis

Twenty black-capped chickadee songs, consisting of 2 tonal notes (fee-bee song with fee and lower-pitched bee notes) were selected from each recording site for analysis. Song selections were spread evenly among all recording sessions made from each site, and randomly selected within recording sessions. Once selected, four song characteristics were analyzed for each song using SIGNAL 5.0 sound analysis software (Engineering Design 2008, Berkeley, CA, USA). Peak frequency (i.e. frequency at maximum amplitude) of the fee and the bee note were measured using a power spectrum (i.e. fast Fourier transform; FFT) with a window size of 32,768 points for a frequency resolution of 1.3 Hz. Fee and bee note measures were highly correlated (Pearson's $r = 0.94$; $p < 0.001$). Other studies have also noted that the fee and bee note frequency in chickadee songs are highly correlated (Weisman et al. 1990, Horn et al. 1992). Thus, we used the frequency of the bee note as a reliable predictor of the overall song frequency.

Inter-note ratio was calculated by recording the peak frequency (same power spectrum settings as above) of the last 100 ms of the fee note and dividing it by the peak frequency of the first 100 ms of the bee note. To calculate amplitude ratio for each song we divided the amplitude at the peak frequency of the fee note by the same measure in the bee note. Finally, duration of the entire song, the fee note, and the bee note were measured on a sound spectrograph (Hanning window) with a spectral cutoff of $-40$ dB relative to the maximum amplitude and a window size of 1024 points. Song duration was high correlated with both fee duration (Pearson's $r = 0.67$, $p < 0.001$) and bee duration (Pearson's $r = 0.78$, $p < 0.001$), thus, only song duration was retained for analysis. None of our four song variables were correlated (Pearson's $r < 0.22$), suggesting that all features were modified independently. Thus, we did not apply a correction factor for multiple tests to our $r$ value.

Overhead canopy cover was calculated by overlaying a standardized grid on each photo in Picasa 3.1 (Google 2003, Mountain View, CA, USA), counting the number of cells with $>50$% cover, and then dividing the total covered grids by the total number of grids (covered grids/108; method modified from aerial photography methods for estimation of canopy cover after Jennings et al. 1999, Stewart et al. 2007).

Ambient noise was measured directly from each audio track containing chickadee songs recorded in the field. To ensure that recordings of ambient noise were standardized, the settings (i.e. gain, recording volume, dB cutoff, etc.) on all recording equipment and the sound analysis program were standardized and maintained at the same level for the duration of the experiment. To calculate ambient noise, each track was edited into six segments of equal length and the first 1000 milliseconds (ms) in each section free from any bird vocalizations or unusual noise bursts was used for analysis. The six measurements were then concatenated to create one, 6000 ms window. Energy was measured in volts from a spectrograph for 1) all frequencies (A weighted) and 2) the 3–4 kHz bandwidth (cutoff of $-70$ dB relative to the maximum amplitude and a window size of 1024 points; similar to Slabbekoorn 2004). The 3–4 kHz bandwidth was quantified to examine the validity of using the measure of all frequencies as a representation of the masking levels experienced by chickadees in the 3–4 kHz bandwidth where they produce their song. Voltage measures were converted to decibels (dB) via the formula $\text{dB} = -20 \log_{10} (\text{Volts})$. To convert dB to sound pressure level (SPL), 1 s test sounds at 1, 3, 5, 7 and 9 kHz were played and rerecorded in the laboratory from a speaker positioned 1 m from both the microphone and recorder used in the study, and a sound level meter (Briel and Kjaer 2239, Naerum, Denmark). We developed a standard correction factor to convert the dB of recorded sounds to dB SPL by determining the correction needed to match the measured dB level of test sounds analyzed in SIGNAL with the recorded SPL readings of the same sounds measured by the sound level meter.

In some cases, multiple songs were measured from a single track or location. In the analysis this required repeated use of the same canopy cover and noise measures for multiple songs, or pooling of all variables to create one mean measurement per site. Since we were interested in overall noise or canopy cover-induced changes to song characteristics we chose to use the site mean of each variable for our analyses. To confirm the viability of this approach we determined whether variation for noise level and canopy cover or to noise levels. To ensure an appropriate range of noise levels and canopy cover, experimental sites were initially classified into four categories based on these characteristics. However, the presence of continuous frog calling in some 'quiet' sites reduced the usefulness of these
correlated with the 3–4 kHz bandwidth (Pearson’s $r^2 = 0.70$, $p < 0.001$), suggesting that higher overall noise levels represent greater levels of noise masking in the frequency range of chickadee songs (Fig. 1).

Bee note peak frequency ranged from 3069 to 3373 Hz with a mean of 3242 ± 96 Hz. A general linear model revealed that bee note peak frequency increased significantly with ambient noise ($z = 2.18, p = 0.029$; Fig. 2), but was not related to canopy cover ($z = 0.71, p = 0.448$). Bee note peak frequency increased by 5 Hz with each additional decibel of ambient noise. The 95% CI for all recorded bee songs in our sample spanned 538 Hz. Thus, for each additional decibel, chickadees increased their song frequency by approximately 1% in relation to our sampled vocal range.

Inter-note ratio ranged from 1.09 to 1.15 with a mean of 1.11. Inter-note ratio decreased significantly with decreasing canopy cover ($z = -2.87, p = 0.004$; Fig. 3), but was not related to noise levels ($z = -0.92, p = 0.358$). Neither dB ratio, nor song duration were significantly related to noise or canopy cover ($z < 1.22, p > 0.223$).

**Discussion**

We found that black-capped chickadees sang their bee notes at higher frequencies when ambient noise levels were higher. This pattern is congruent with other studies that compared song frequencies of birds in relation to noise levels (Fernandez-Juricic et al. 2005, Slabbekoorn and den Boer-Visser 2006, Wood and Yezerinac 2006, Nemeth and Brumm 2009, Parris and Schneider 2009), and is consistent with the noise-dependent frequency hypothesis (Halfwerk and Slabbekoorn 2009). In contrast, chickadee bee note frequency was not significantly related to canopy cover as would be predicted if vegetative structure was responsible for frequency changes (Morton 1975). This non-significant relationship suggests that vegetative structure may not be an important confound to the noise-dependent frequency hypothesis for the black-capped chickadee.

**Results**

Overhead canopy cover ranged from 40.2 to 92.3% with a mean of 68.7 ± 12.2%. Ambient noise for all frequencies ranged from 23.5 to 55.8 dB (SPL, A weighted) with a mean of 43.8 ± 9.9 (SPLA). This measure was highly correlated with the 3–4 kHz bandwidth (Pearson’s $r^2 = 0.70$, $p < 0.001$), suggesting that higher overall noise levels represent greater levels of noise masking in the frequency range of chickadee songs (Fig. 1).

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of these sites were separated by
were primarily located in Elk Island National Park. None
located in the City of Edmonton, and low-noise sites
(Slabbekoorn et al. 2007); variation in territory sizes and
explanations for frequency shifting that warrant further
frequencies observed in high noise sites. Other alternative
did not occur, body size is unlikely to account for the higher
song frequencies, since high frequencies are easier to produce for small-bodied individuals (Fletcher 2004). Tarsus measures from black-capped chickadees studied in our lab (n = 127; 2002–2010) captured in the Edmonton River Valley and in rural Alberta (but not Elk Island) revealed that chickadees in Edmonton are significantly larger than rural birds (17.56 ± 0.35 mm, and 16.26 ± 0.38 mm respectively; t-test: t = 2.44, p < 0.016). Based on body size, birds from our higher-noise sites in Edmonton should have sung at lower frequencies. Since this did not occur, body size is unlikely to account for the higher frequencies observed in high noise sites. Other alternative explanations for frequency shifting that warrant further research include: alteration of acoustics by human structures (Slabbekoorn et al. 2007); variation in territory sizes and resources distribution (Ripmeester et al. 2010); and vocal interference from different heterospecific species (Brumm and Naguib 2009).

The majority of our high-noise sites in this study were located in the City of Edmonton, and low-noise sites were primarily located in Elk Island National Park. None of these sites were separated by >23 km. Sites within Edmonton were separated by up to 17 km, and sites within Elk Island were separated by up to 16 km. Thus, spatial separation was nearly as extensive within each category as it was between the two sites. Further, an extensive study done by Kroodsma et al. (1999) revealed that the frequency of fee-bee songs in black-capped chickadees is not significantly related to geographic location in mainland North America. Thus, black capped chickadees appear unlikely to develop dialects based on spatial separation, and the small spatial separation between the two sites in our study is unlikely to confound our results.

While it appears unlikely that population differences between the two recording locations could accounted for our results, bee note peak frequency did differ significantly between Edmonton (ED: ED = 3295.72 ± 19.09 Hz, EI = 3180.66 ± 23.52, t$_{24}$ = 3.79, p < 0.001). Inter-note ratio, however, did not (t$_{24}$ = 1.86, p < 0.075). Because of the difference in bee note frequency, we also analyzed whether noise and canopy cover differed by location, and found that both variables differed significantly (noise: ED = 51.25 ± 1.02 dB, EI = 34.35 ± 1.68 dB, t = 8.58, p < 0.001; canopy cover: ED = 75.50 ± 2.91%, EI = 61.98 ± 2.95%, t = 3.26, p < 0.001). Thus, to determine whether either variable could account for the observed difference in bee note frequency between locations, or if our results were potentially due to another untested population level factor, we tested for differences in bee note frequency between Edmonton and Elk Island using site as the unit of replication, with one dependant variable (noise or canopy cover) added as a covariate. When added as a covariate, canopy cover failed to remove the significant difference between the two locations (F$_{1,23}$ = 8.51, p = 0.008), suggesting that this variable did not account for the observed frequency differences. However, when noise was added as a covariate, the significant difference between locations disappeared (F$_{1,23}$ = 1.70, p = 0.205). In sum, if treated as separate populations, frequency differences are still significantly related to noise levels, but not canopy cover. In addition, the observed pattern remains the same with higher song frequencies occurring at higher noise levels.

Although Elk Island sites were quieter overall, three Elk Island sites had somewhat elevated noise levels, and chickadees in these sites sang at higher frequencies than in quieter Elk Island sites. In two of these sites (label A; Fig. 2) frogs vocalized in the 2–4 kHz range during recording sessions, producing higher levels of ambient noise. Additionally, one Elk Island site (label B; Fig. 2) was located ~1 km from a major highway, and background traffic noise was audible on vocal recordings. This within-location observation of elevated bee note peak frequency with higher levels of noise adds additional support to the hypothesis that black-capped chickadees sing at higher frequencies in noisy locations. One additional site in Elk Island had relatively high ambient noise, but was not characterized by higher frequency vocalizations. This variation underscores the potential importance of other contributors to song frequency, such as social interaction with other males (Mennill et al. 2002).

The significant relationship between inter-note ratio and canopy cover may be a direct response to vegetative structure, or result from a non-random distribution of dominant males. Christie et al. (2004) found that inter-note ratio decreased in low ranking male chickadees as absolute frequency increased, but remained stable in dominant

![Figure 3. Relationship between inter-note ratio of the fee and bee note and canopy cover. The line predicting the mean inter-note ratio is derived from our general linear mixed model. Data points correspond to the observed mean inter-note ratio for each site.](image-url)
individuals. Habitat suitability models suggest that ideal canopy cover for chickadees ranges from 50 to 75% (Schroeder 1983). Our results may be due to a despotic distribution (Fretwell and Lucas 1970), where dominant male chickadees with more stable inter-note ratios procured sites with ideal canopy cover, while low ranking males with more variable and generally smaller inter-note ratios were relegated to locations with cover that fell outside this range. If this is the case, it is notable that inter-note ratios did not differ by noise levels. Perhaps by using higher song frequencies black-capped chickadees avert disturbance to vocal communication, and therefore, noise does not decrease habitat suitability for this species. Unpublished results from our lab suggest that anthropogenic noise does not affect chickadee abundance or health (Proppe et al. unpubl., Byers et al. pers. comm.), two factors which may be altered if noise was a limiting factor. Experimental evaluation of this speculative explanation may provide further insight into the intersection between habitat quality and social structure in chickadees.

For species that exhibit vocal modification, more work is needed to understand the mechanisms by which songs are adjusted. Currently, it is not known whether song frequency in most bird species a) can be changed readily in response to local conditions, b) is determined only once during song development or, c) is an evolved response. Black-capped chickadees rapidly shift song frequency in response to playbacks of conspecific song (Shackleton and Ratcliffe 1994, Mennill and Ratcliffe 2004, Foote et al. 2008), and even during spontaneous song bouts amid the dawn chorus (Ratcliffe and Weisman 1985, Horn et al. 2008). In addition, individuals from a closely related species, the great tit, exhibit modification of vocalizations to avoid overlap with simulated anthropogenic noise (Halfwerk and Slabbekoorn 2009). These features make it likely that frequency adjustments made by chickadees in response to overlapping frequencies of environmental noise results from rapid behavioural responses.

More work is needed to know whether the net effect of these adaptations is positive or negative. For example, shifted songs may be more detectable by conspecifics (Slabbekoorn and Ripmeester 2008), but their higher frequencies may be less appealing to potential mates or less repelling to potential rivals (Mockford and Marshall 2009). Future work in this area should determine whether frequency shifts represent a successful and sustainable response to increased levels of anthropogenic noise for songbirds and other taxa.

In sum, we demonstrate that black-capped chickadees sing at higher frequencies when they are exposed to anthropogenic noise. We show that this shift in frequency is more strongly associated with increased levels of anthropogenic noise than with differences in vegetative structure. We also show that inter-note ratio differs in relation to canopy cover, and suggest that non-random distribution of dominant individuals may account for this phenomenon. We suggest that further study is needed to understand the behavioural mechanisms underlying these observed frequency changes, and to identify the costs incurred by those animals that modify their vocalizations in response to anthropogenic noise. Answers to these questions could guide mitigation of anthropogenic noise for birds and many other species.

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