Seasonal variability in habitat structure may have shaped acoustic signals and repertoires in the black-capped and boreal chickadees

Apol CA[1], Sturdy CB[2], Proppe DS[1]

[1]Biology Department, Calvin College, 3201 Burton St SE, Grand Rapids, Michigan, 49546

[2]Department of Psychology, Neuroscience and Mental Health Institute, University of Alberta, P217 Biological Sciences Building, Edmonton, AB T6G 2E9, Canada

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Corresponding author:

Darren S. Proppe
dsp5@calvin.edu
616-526-6662

Abstract

Many songbird species have evolved multiple vocalizations, or repertoires, that function to communicate various biological signals. More diverse repertoires may have evolved in response to the effects of seasonal variation in habitat structure on signal transmission. Such changes in habitat necessarily occur for migrating species, but they also occur for resident species that occupy deciduous forests. The black-capped chickadee (*P. atricapillus*), possesses a *chick-a-dee* call and a *fee-bee* song, but the closely related boreal chickadee (*P. borealis*) lacks a song. Consistent with the habitat variability hypothesis, the black-capped chickadee possesses a larger repertoire and primarily occupies deciduous forests, whereas the songless boreal chickadee occurs more often in coniferous forests. We explored the ecological basis of this hypothesis by recording audio playbacks of two species in two habitat types during two seasons. Specifically, we played both songs and calls of the black-capped chickadee and calls of the boreal chickadee in deciduous and coniferous habitats, prior to and after leaf-out. We measured attenuation and degradation in the re-recorded vocalizations. For black-capped chickadees, the song was less degraded than the call in post-leaf, deciduous forests. The boreal chickadee call attenuated more quickly in all treatments, but maintained its acoustic structure better than both black-capped chickadee vocalizations in coniferous forests. Our results support the hypothesis that variable habitats provided a seasonal transmission benefit for both song and call in the black-capped chickadee, but that the transmission benefit of song is lost in the less variant coniferous forests, which may underlie the absence of a song in the boreal chickadee.

Keywords: songbird, sound transmission, call, vocalization, attenuation, degradation, repertoire, season, evolution, birdsong, North American chickadees

Introduction

Acoustic signals are a key component of avian communication systems, primarily serving to attract mates and defend territories, although other functions also include alarm, announcement of food, and even declaration of individual identity (Catchpole and Slater 2008). Many songbird species have evolved multiple vocalizations, often termed repertoires, that aid in the transfer of acoustic information between individuals. Krebs (1977) posited that larger, more elaborate repertoires enhance a male's ability to attract mates and defend territories by increasing their apparent density to potential rivals, dubbed the Beau Geste hypothesis. Other benefits may include reducing habituation in the receiver (Krebs 1976), positive sexual selection (Ritchison 1995; Podos et al 2004), and optimizing the active space of the signal in variable environments (Brenowitz 1982). Multiple studies support the notion that larger vocal repertoires increase the fitness of the sender (Potvin et al 2015; Yasukawa 1981; Smith and Reid 1979: Krebs et al 1978).

But producing repertoires are also costly. While the immediate energetic cost of producing vocalizations has been debated (Oberweger and Goller 2001), their development is linked with neural signals and pathways, termed the Vocal Control System (VCS; Nottebohm 2005; Vu et al 1994), that may be expensive to develop. Vocal complexity and repertoire size is correlated with the volume of the high vocal center (HVC; Airey et al 2000; Garamszegi and Eens 2004). Development and maintenance of the HVC and other components of the VCS are costly, and investing in vocal development represents a trade-off in neural space that could otherwise be devoted to other functions (Gil and Gahr 2002). Tests of the nutritional stress hypothesis have shown that developmental conditions predict the quality and complexity of adult birdsong (Nowicki et al 2002), with lower quality nest conditions requiring offspring to dedicate a greater portion of their energy budget to growth and survival (MacDonald et al 2006). Because vocal development is costly, the benefits of vocal repertoires must outweigh the costs to be evolutionarily stable.

For the benefits of a signal to be realized, it must alter the behavior of a receiver. The social context and average distance to conspecifics are important factors (Krebs and Kroodsma 1980), but fundamentally, a signal must be audible and interpretable once it reaches the intended receiver in order to influence behavior (Maynard-Smith and Harper 2003). A primary obstacle for signal transmission is the structure of the habitat where the sender resides, which effectively attenuates and degrades the signal as it moves across distance (Wiley and Richards 1982; Patten et al 2004). But the impacts of habitat on vocal transmission vary by vegetative structure, and this variation may influence the evolution of birdsong. Morton (1975) posited that vocalizations will be structured for effective transmission and minimal degradation in the primary habitats utilized by a species, coined as the acoustic adaptation hypothesis (AAH). Further studies have confirmed that vocalizations in many songbird species are optimized for transmission in their native habitats (reviewed in Boncoraglio and Saino 2007).

Tonal (i.e., whistled) vocalizations degrade less in most habitats, but signals with high amplitude modulation (AM; i.e., trills) benefit from better maintenance of structure in open habitats (Brown and Handford 2000). In open habitats, the primary drivers of degradation are wind and temperature gradients. Pulsed signals with AM modulation reduce the impacts of these environmental gradients. In general, lower frequency signals also maintain their structure better than those produced at higher frequencies (Marten and Marler 1977), but frequency dependent effects increase with vegetation density because objects impeding transmission have a greater impact on the transmission of shorter wavelengths (i.e., higher frequency sounds; Wiley and Richards 1978; Morton 1975).

If differential sound transmission in particular habitats facilitates the evolution and complexity of vocalizations, it follows that habitats which vary in structure seasonally should favor the evolution of larger repertoires in year-round residents. For example, a trill that transmits well in an open, leafless habitat may transmit poorly once leaves emerge. A more tonal signal may be favored for transmission under the latter scenario, and maintaining two vocalizations may be the most efficient way to communicate. In turn, species living in less variable habitats (e.g., coniferous forests) may not benefit from the unique transmission properties offered by multiple vocal types, and could fail to develop - or lose - portions of their repertoire because the costs to maintain them outweighs the benefits.

Contrasting habitats and repertoire sizes exist for the black-capped (*Poecile atricapillus*) and boreal chickadee (*Poecile hudsonicus*). The black-capped chickadee resides in coniferous and deciduous forests (Foote et al 2010) and possesses two primary vocalizations for longer range communication (Smith 1997). The breeding song is used in spring and summer when deciduous forests are partially to fully foliated, although a smaller peak of singing also occurs in mid-winter (Avey et al 2007). The song is composed of two tonal notes known as the *fee* and *bee* that can be frequency shifted jointly, but are maintained at a relatively stable frequency ratio between notes (Horn et al 1992; Figure 1a). The black-capped chickadee call is used most often when leaves are absent (Avey et al 2007) and functions to mitigate flocking and foraging behavior (Smith 1997). Amplitude modulation is greater in the call, being comprised of four broader band note types referred to as A, B, C and D (Ficken et al 1978; Figure 1b). Note types can be repeated or omitted within a call, but progress in the same syntactical order. Higher frequency A, B, and C notes comprise the *chick-a* portion of the call, followed by low-frequency D notes composed of multiple harmonic bands.

In contrast, the boreal chickadee is most common in coniferous forests and possesses only a single longer range vocalization (Ficken et al 1996). Their vocalization is similar in structure and syntax to the black-capped chickadee call (McLaren 1976; Figure 1c), although A and D notes are more common than other note types (Moscicki et al 2011). The boreal chickadee call conveys flocking and foraging information, and may also be used as a breeding vocalization (McLaren 1976)

The vocalization system of these two chickadee species appears to be well suited for their native habitats. The more tonal song is used by the black-capped chickadee during periods of dense vegetation and the broadband call is used when habitats are more open. Frequency variation in song production may also be important as dominance is indicated by maintaining the frequency ratio and amplitude between the two notes at varying overall frequencies (Hoeschele et al 2009; Christie et al 2004). The more open habitats that occur during song peaks in mid-winter and in early spring may facilitate better transmission of higher frequency songs and facilitate mate selection. In contrast, the single vocalization of the boreal chickadee may be sufficient for communication in less variant forests.

The first step in determining whether habitat variability could have shaped signal design and repertoire size in these species is to demonstrate that the *fee-bee* song enhances transmission in post-leaf deciduous forests in the black-capped chickadee, and that the *chick-a-dee* call is sufficient for communication at all distances in less variant forests for the boreal chickadee. To test this habitat variability hypothesis, we compared the transmission rates of the black-capped chickadee song and call, and the boreal chickadee call in deciduous and coniferous forests before and after leaf-out occurred in deciduous vegetation. Using playback experiments, we compared attenuation (signal-to-noise ratio, tail-to-signal ratio) and degradation (cross-correlation coefficient) across distance for each vocalization. We predicted that the black-capped chickadee song would attenuate and degrade less than the black-capped call in the post-leaf deciduous forests. We also predicted that transmission of high frequency song would be less impacted in pre-leaf forests, facilitating song shifting during mate selection. We predicted that the boreal chickadee call would transmit as well or better than the black-capped vocalizations in coniferous forests. Taken together, these results would support that the boreal chickadee call is sufficient for communication in less variant boreal forests, but that the black-capped chickadee call is not sufficient in seasonally variant deciduous forests. Thus, the benefit of possessing a song is enhanced in seasonably variant habitats.

Materials and Methods

Site selection and setup

Twenty forested sites containing black-capped and/or boreal chickadee populations and negligible elevation differences were selected for playback studies from the North Saskatchewan River valley and regions surrounding Edmonton, Alberta, Canada (53.5444° N, 113.4909° W). Ambient noise was < 45 dB(A) re 20 µpa at all sites. Each site was comprised of 150 linear meters of contiguous, mature forest dominated by a single cover type and buffered by > 50 m of similar contiguous forest on either side (assessed via relevé; Benninghoff 1966). Ten sites were dominated by deciduous tree cover (deciduous; 90-100%: trembling aspen {*Populus tremuloides*}, balsam poplar {*Populus balsamifera*}, paper birch {*Betula papyrifera*}), and another ten were dominated by coniferous tree cover (coniferous; 90-100%: white spruce {*Picea* *glauca}*). Ground and shrub cover (< 1.5 m in height) included some herbaceous and deciduous plants in both forest types, although cover was generally reduced in coniferous forests. We did not avoid coniferous sites with herbaceous and deciduous ground cover, because doing so would have resulted in habitats atypical of those inhabited by boreal chickadees.

Playback experiments were conducted twice in each site during the spring and summer of 2009. All experiments occurred between 700-1100 or 1600-1800 hours in a balanced design that equalized timing across treatments. The first experiment was conducted between 21 April and 9 May 2009, a timeframe when leaves were absent on all deciduous cover and snow was absent from the forest floor (pre-leaf). The second playback experiment was conducted between 17 June and 6 July 2009 when all deciduous cover was fully vegetated (post-leaf).

Stimulus preparation and playback procedure

Each playback vocalization was recorded in the laboratory from a unique individual. All birds originated from Barrier Lake Field Research Station in the Kananaskis Valley, Alberta, Canada (51°02′ N, 115°03′ W) where both coniferous and deciduous forest are present. Birds were housed in species specific rooms at the University of Alberta in individual Jupiter parakeet cages (0.3 m wide x 0.4 m high x 0.4 m deep; Rolf C. Hagen, Inc., Montreal, Quebec, Canada) for > 1 month prior to vocal recording. All vocalizations were recorded in sound-attenuating chambers (IAC 252 Series Mini Sound Shelter; Industrial Acoustics Corporation, Bronx, New York, USA) via an AKG C 1000S condenser microphone (frequency response: 50 – 20 000 Hz; AKG Acoustics, Vienna, Austria) and a Marantz solid-state recorder (PMD 670, New York, New York, USA) during natural, non-induced, bouts of singing.

Four black-capped chickadee (BCCH) songs, four black-capped chickadee calls, and four boreal chickadees (BOCH) calls were utilized for playback experiments. Black-capped chickadee song stimuli included four unedited vocalizations (*bee* note peak frequency = 3436, 3774, 3391, 3269 Hz) chosen because they spanned the range of frequencies used by the species (Ratcliffe and Weisman 1985). Each vocalization was also frequency-shifted to simulate high (3500 Hz), medium (3200 Hz), and low (2900 Hz) *bee* note frequencies from within the range of natural frequency variation found in black-capped chickadee songs (Ratcliffe and Weisman 1985). Frequency shifting was conducted in GoldWave Version 5.12 (GoldWave, Inc., St. John’s, NF). Calls from both species were selected to incorporate typical variation in call length and note composition (Charrier et al 2004; Moscicki et al 2011).

All vocalizations were high pass filtered (1102.5 Hz), normalized, and compiled into a WAV track. Each track contained three replicates of a single vocalization separated by 5 seconds of silence. Creating individual tracks for each exemplar allowed for easy repeat playback in the field when necessary. For example, repeated playback was often required to obtain stimuli not overlapped by singing individuals. We prepared 24 total tracks for playback, including; four black-capped chickadee calls, four boreal chickadee calls, and four versions of each black-capped chickadee *fee-bee* song (natural, high, medium, low, N=16).

Within each site, we broadcasted acoustic stimuli from a location that was surrounded by > 50 m of contiguous forest consistent with the intended cover type in all directions and > 100 m along the linear transmission line (cover assessed via relevé). Vocalizations were broadcast at 80 ± 3 dB(A) SPL (measured at 1 m; fast rate and A weight; Bruel and Kjaer 2239 sound level meter; Bruel and Kjaer, Naerum, Denmark) via an Audix PH-3 speaker (25 W, frequency response 100-20,000 Hz ± 10 dB; Audix USA, Wilsonville, Oregon, USA) mounted 2 m above the ground on a microphone stand. Stimuli were produced by a Sony D-SJ301 compact disc player (44,100 Hz sampling rate, 16-bit accuracy; Sony Canada, Toronto, Ontario, Canada). Each track was presented until we aurally determined that three exemplars were free from overlap. Stimuli were recorded simultaneously at 5, 20, 40, 60, and 80 m from the sound source in a linear arrangement. Five initial playback experiments included a 100 m recording, but no vocalizations remained detectable at this distance. 5 m recordings were used as the model sound for calculating comparative transmission characteristics. Additional recording distances spanned the transmission range of chickadee vocalization. Each recording location consisted of a Marantz solid-state digital recorder (PMD 670; 44 100 Hz sampling rate, gain 2.5/10, PCM, 16 bit format) and an omnidirectional microphone (Sennheiser ME62; Wedemark, Germany) positioned vertically at 2 m above the ground atop a microphone stand.

Because temperature and humidity are also known to impact acoustic transmission (Forrest 1994; Wiley and Richards 1978) and were likely to fluctuate across time and season during the course of our experiment, we measured humidity (%) and temperature (°C) every 5 s for the duration of each playback by placing a 1-wire ibutton (DS1923; Maxim Integrated, San Jose, California, USA) at 5 m from the playback source and 2 m above the ground. Since playback experiments generally lasted < 30 minutes, we compiled the data to establish the mean temperature and humidity for each playback experiment. Because wind can impact transmission, experiments were not conducted at wind speeds > 3 on the Beaufort scale.

Analysis

To compare vocalization types across forest type and season, we analyzed the first two exemplars of each vocalization from each playback session that were clear of overlapping sounds in SIGNAL version 5.0 (Engineering Design, Berkeley, California, USA). For each vocalization we calculated 1) signal-to-noise ratio (SNR), a measure of attenuation across distance, 2) tail-to-signal ratio (TSR), a measure of both attenuation (energy lost from the signal in the time dimension) and degradation (e.g., masking of signal offset), and 3) the cross correlation coefficient (XC) between the model (5 m) and observed sounds at different distances, a measure of within-signal degradation (similar to blur ratio which assesses difference between signal rather than similarity, Dabelsteen et al 1993). SNR was calculated as: 20 log($RMS_{voc,v}/RMS_{amb,v}$), where vocalization (voc) and ambient noise level (amb) were measured in volts (v). 1 s of ambient noise was obtained near (typically < 5 s) each recorded vocalization that was free of non-ambient sounds to assess RMS_{amb}. TSR was calculated as $RMS_{tail,dB}/RMS_{voc,dB}$. To calculate $RMS_{tail,dB}$, we measured the length of the longest tail in each set of re-recorded vocalizations (i.e., at all distances) and assessed the RMS value within the time window of the same length for each vocalization in that set. Thus, each tail interval contained roughly the same level of ambient noise and varied only by the amount of energy dissipating from the signal. Lastly, we calculated XC by cross correlating the amplitude function (AF) of the model sound (5 m recording) with all other recorded distances (20, 40, 60, 80 m). The measure ranged from 0-1, with 1 representing complete similarity. Because XC is not affected by amplitude scaling, it measures signal integrity rather than amplitude attenuation (Beeman 2009).

General linear mixed models (lmer, R version 3.3.2) were built to test the effects of treatment (conif/pre-leaf, conif/post-leaf, decid/pre-leaf, decid/post-leaf) and vocal type (BOCH call, BCCH call, BCCH song {unshifted, 2900 Hz, 3200 Hz, 3500 Hz}) on SNR, TSR, and XC. All models included fixed terms for treatment, vocal type, distance, humidity, and temperature, as well at the following biologically relevant interactions: treatment*vocal type, treatment*distance, vocal type*distance, treatment*vocal type*distance, humidity*vocal type, temperature*vocal type, humidity*treatment, and temperature*treatment. Distance was log-transformed because previous work has shown that it is a better fit for transmission data (Yip et al 2017). Random effects were included for exemplar (1-4), and repeated measurements of the same exemplar (1-2). All candidate models were compared via the dredge function (package MuMIn) and ranked via AIC (Burnham and Anderson 2002). Models < 2ΔAIC from the top model are also reported. To evaluate the importance of each predictor, we summed the AIC weight of all models including each term.

Predictions from the top models are presented graphically by treatment and across distance while holding other variables constant (ggplot2). In models that retained humidity and temperature or an interaction with treatment, the mean temperature and/or humidity in each forest type was utilized as the constant rather than the overall mean. Differences in transmission properties are described where the mean difference between two vocal types or two frequencies exceeded 1) the mean of the 95% confidence intervals calculated within each vocal type and distance and 2) the effect was > 10% of the total range of values. Since SNR is calculated on a logarithmic scale, we reported difference at 5% of the value range. This second requirement, which required larger effect sizes, was included to emphasize biological relevance. Results are reported as the raw difference followed by the percentage of the range covered by the difference.

Results

SNR

The top SNR model (AIC = 55631.39, weight = 95.7%) included all the variables except the humidity by vocal type interaction. No other models fell within 2 AIC, and all retained terms had a summed weight of 1. As expected, all vocal types attenuated across distance, with pre-leaf forest conditions having generally higher SNRs than the post-leaf conditions, especially in deciduous forests (Figure 2a-h). The mean 95% confidence interval within vocal type and distance was 0.656 dB and the range was 28.64 dB. We report differences with effect sizes > 1.43 dB (> 5% of range). Black-capped chickadee songs attenuated less than conspecific calls at 5 m in post-leaf deciduous forest (+1.626 dB {5.7% of range}; Table 1). Although less pronounced, this pattern was consistent in both post-leaf forests and in the pre-leaf deciduous forest. The boreal chickadee call attenuated less than both black-capped chickadee vocalizations in short-range pre-leaf conditions, especially in coniferous forests (+1.707 dB {5.96%} compared to BCCH call; +2.086 dB {7.28%} compared to BCCH song; 5 m). This transmission advantage was not maintained at greater distance, and attenuation of the boreal chickadee call was greater than both black-capped chickadee vocalizations in post-leaf forests (i.e., -2.786 dB {9.73%} compared to BCCH call; -4.445 dB {15.52%} compared to BCCH song; 5 m post-leaf deciduous forest). Black-capped chickadee songs at 2900 and 3200 Hz attenuated less than songs at 3500 Hz in all conditions (0.312 - 2.086 ΔdB {1.09 - 7.28%}) but differed little from each other (<0.001 - 1.005 ΔdB {>1 - 3.53%}).

TSR

The top TSR model excluded the humidity by vocal type interaction and the three-way interaction between distance, treatment, and vocal type (AIC=-5152.1, AIC weight = 65.3%). The second highest model for TSR (AIC=-5150.3, weight = 25.6%, ΔAIC= 1.87) included the interaction between humidity and vocal type. No other models were within 2 AIC. The summed weights for all retained terms was > 0.98. Overall TSR patterns were similar to SNR, increasing across distance, but less so in the pre-leaf forest (Figure 3a-h). The mean 95% confidence interval within vocal type and distance was 1.99% and the range was 80.52%. Thus, we report effects where the differences between vocalizations differed by > 8.05%. TSR did differ between black-capped chickadee vocalizations (< 3.7% {4.59% of range}). TSR for the boreal chickadee call was higher (i.e., more attenuated) than both black-capped chickadee vocalizations in almost all treatments, although the difference only exceeded 8.05% at 80 m in pre-leaf deciduous forest (-8.4%, {10.43%}, compared to BCCH call, -8.6%, {10.68%}, compared to BCCH song; 80 m Table 1). Black-capped chickadee songs at 2900 Hz attenuated less than songs at 3500 Hz at greater distances in all treatments (i.e., 8.5 - 10.5% {10.56 - 13.04%} at 80 m). Songs at 3200 Hz attenuated less than song at 3500 Hz at greater distances in coniferous forests (i.e., 8.2 - 8.8% {10.18 - 10.93%} at 60-80 m), but did not otherwise differ from songs at other frequencies.

XC

The top XC model (AIC=-27885.9, weight = 72.2%) included all variables and interactions. One other model fell within 2 AIC (AIC=-27883.9, weight = 27.1%, ΔAIC= 1.95). The humidity by vocal type interaction was not retained in this second model. The summed weights for all terms retained in the top model were > 0.72. For all vocal types, XC was higher in the pre-leaf condition compared to post-leaf (Figure 4a-h). The mean 95% confidence interval within vocal type and distance was 0.4% and the range was 12.74%. Thus, we report effects where the differences between vocalizations differed by > 1.27%. The black-capped chickadee call was less degraded than its song at 5 and 20 m in all habitats (+2.0 - 7.0% {15.70 - 54.95% of range}), but the pattern reversed at greater distances in post-leaf forests (+ 1.9 - 3.1% {14.91 - 24.33%}) and in pre-leaf coniferous forests (+1.4 {10.99%} at 80 m; Table 1). The boreal chickadee call had higher XC values than black-capped calls at distances greater than 40 m in all forests. This effect was especially large in post-leaf forests (+2.3 - 3.1% {18.05 - 24.33%} in deciduous, +1.5 - 3.3 {11.7 - 25.90%} in coniferous). The boreal chickadee call was also less degraded than the black-capped chickadee song in most treatments and at most distances, although the effect was most pronounced at 5 - 20 m in coniferous forests (+1.7 - 4.3% {13.34 - 33.75%}). 3500 Hz black-capped chickadee songs were less degraded at 5 m then songs at other frequencies (+2.8 - 8.9% {21.98 - 69.86%}), but more degraded at distance beyond 40 m (-2.4 - -7.2% {18.84-56.51%})

Discussion

Here we show that seasonal variability in habitat structure impacted the transmission of boreal and black-capped chickadee vocalizations. While signal-to-noise and tail-to-signal ratios were generally similar for the song and call of the black-capped chickadee, cross correlation results demonstrated that its song is less degraded than its call at greater distances, but only in post-leaf forests. This supports the hypothesis that the song provides a distinct transmission advantage over the black-capped chickadee call in post-leaf deciduous forests, and that retaining this vocalization can enhance communication in habitats that vary seasonally. The black-capped chickadee song also degraded less then the boreal chickadee call in post-leaf deciduous forests. However, degradation of the boreal chickadee call in coniferous forests was similar to or reduced in comparison to the black-capped chickadee song. This indicates that the degradation advantage of the black-capped chickadee song is lost in the coniferous forests, potentially providing a mechanism by which less variant habitats could underlie the lack of a song in the boreal chickadee.

Although our results support the role of habitat variability, a number of alternative hypotheses must also be considered. First, we have assumed that these vocalizations are optimized by maximizing their transmission distances. However, transmission also has costs via eavesdropping by potential competitors (Mennill et al 2002) and predators (Mougeot and Bretagnolle 2000; Catchpole and Slater 2008). Some have suggested that song in the black-capped chickadee is structured for long distance communication, while calls are limited to shorter range communication (Ficken et al 1978). Our data support this, with cross correlation results revealing that black-capped chickadee calls maintain their structure better than songs at shorter distances, but that the reverse is true at longer distances.

In boreal chickadees, conspecific territories tend to be widely dispersed (Hadley and Desrochers 2008; Lait and Burg 2013), suggesting that a long range signal may not be necessary for territory defense. Further, attenuation impacted the boreal chickadee call more heavily than either black-capped vocalization in the current study. It is possible that boreal chickadees simply do not use longer range communication, which could also underlie the lack of a song. However, with an average territory size > 80 m in diameter (McLaren 1975), signaling across the distances we examined might still be necessary to communicate with a paired mate. This alternative hypothesis could be evaluated by determining whether boreal chickadees are able to detect sounds produced at lower signal-to-noise ratios. If attenuated signals can still be detected, a call that remains distinct, but not particularly loud, might facilitate longer range communication while minimizing predator and competitor eavesdropping. Notably, the boreal chickadee call maintained its structure similar to the black-capped chickadee call at short ranges and the song at longer distances. As such, the boreal chickadee call may be structured to maximize transmission quality at all distances.

A second alternative is that social interaction and sexual selection have driven the development of different vocal systems in the two chickadee species. Sexual selection underlies the development of many acoustic ornaments (Shutler and Weatherhead 1990; Buchanan and Catchpole 1997; Kunc et al 2005) and is known to favor stable frequency and amplitude ratios between the *fee* and *bee* note in the black-capped chickadee song (Hoeschele et al 2009; Christie et al 2004). It is also plausible that habitat variability and sexual selection have operated in tandem to differentiate the vocal repertoires of the black-capped chickadee, as appears to be the case for the little greenbul (*Andropadus virens*; Slabbekoorn and Smith 2002). This second alternative hypothesis is also testable. If female boreal chickadees produce copulation solicitation displays or other courtship behavior in response to black-capped chickadee song, it is unlikely that selection pressure underlies the loss of a song in the boreal chickadee because female responses would have favored song retention.

While we cannot state conclusively that the boreal chickadee lost a *fee-bee* like song from a common ancestor, phylogenetic evidence indicates that this is the most parsimonious explanation. Most of the North American chickadees (Genus *Poecile*) possess some form of the *chick-a-dee* call and *fee-bee* song (Hailman 1989). This includes the Mexican chickadee (*Poecile sclateri*, Ficken and Nocedal 1992), Carolina chickadee (*Poecile carolinensis*, Mostrum et al 2002), mountain chickadee (*Poecile gambeli*, McCallum et al 1999), and the black-capped chickadee (*Poecile atricapillus*, Foote et al 2010). A single monophyletic, brown headed clade, which includes the chestnut-backed chickadee (*Poecile rufescens*, Dahlsten et al 2002), gray-headed chickadee (*Poecile cinctus*, Hailman and Haftorn 1995) and the boreal chickadee (*Poecile hudsonicus*, Ficken et al 1996), lacks a song. Genetic evidence suggests that multiple sister clades possessing both vocalizations were derived from a common ancestor that preceded the brown-headed clade (phylogeny developed by Gill et al 2005), making it likely that the ancestral repertoire did include a song.

Similar to the boreal chickadee, other members of the brown headed clade inhabit mostly coniferous forest (Dahlsten et al 2002; Ficken et al 1996, Hailman and Haftorn 1995). Conversely, the four North American chickadee which possess a song, are found primarily within mixed and deciduous forest across much of their geographical range (Ficken and Nocedal 1992; Mostrum et al 2002; McCallum et al 1999; Foote et al 2010). Because song was most likely lost only once in the brown-headed lineage, a broader ecological and phylogenetic comparison within the Genus *Poecile* could be provide valuable information on the differential development of repertoires.

In addition to the role of habitat variability in the development of repertoires, we hypothesized that black-capped chickadee songs produced at various frequencies would transmit differently as vegetation changed. We predicted that denser vegetation would have a greater impact on the transmission of higher frequency sounds because structure more easily distorts their shorter wavelengths (Wiley and Richards 1978; Morton 1975). Notably, high frequency songs degraded less at shorter distances, possibly due to the dominance of ground effects at these distances. Degradation from reverberation and ground interference is known to be higher in lower frequency sounds (Richards and Wiley 1980). At greater distances, high frequency sounds are more attenuated and degraded by processes such as scattering, and these processes likely outweigh ground effects. In keeping with this, lower frequency songs transmitted better at greater distances in all conditions. However, effect sizes were smaller in pre-leaf forest, and songs produced at all frequencies were less attenuated and degraded in pre-leaf conditions. This pre-leaf period overlaps the timeframe when mate selection occurs (Smith 1997). Since frequency shifting is necessary to indicate dominance (Hoeschele et al 2009; Christie et al 2004), better transmission of higher frequency songs might facilitate mate selection in this species.

These results indicate that vocal signals may have been shaped by seasonable variability in habitat structure.

The effective transmission of the *fee-bee* song in all habitats suggests that it be could be maintained as the sole longer range vocal type in all chickadee species. However, information theory predicts that the length of a vocal message should correlate to the amount and complexity of information contained within it (Reznikova 2007). Unlike most songbirds, the structure of the chickadee song is much simpler than their calls (Ficken et al 1978). While important information regarding dominance and geographic distribution can be extracted from song (Hahn et al 2016; Hahn et al 2017), the chickadee call is capable of transferring more information than the song. This includes integral information about species and sex identification as well as various predator identification information (Guillette et al 2010; Templeton et al 2005). Thus, the complexity and amount of information encoded in the chickadee call likely make it more of a necessity to the vocal repertoire than the song.

Two caveats warrant discussion. First, coniferous forests were not entirely invariant. Transmission in pre-leaf coniferous forests differed from pre-leaf deciduous forests, likely due to the more open habitats found when deciduous trees are not foliated. But in some cases, signal transmission also differed between pre- and post-leaf conditions in coniferous sites, although less so than in deciduous forests. We controlled for wind in our experimental design and statistically accounted for temperature and humidity. But, ground cover and low-lying shrubs may have contributed to the observed transmission differences. Nonetheless, coniferous forests were representative of habitats used by the boreal chickadee and were less seasonally variant than deciduous forests. Second, the biological relevance of the observed transmission differences deserves further exploration. Distance was the primary driver of both attenuation and degradation in the current study. This dominant role of distance is typical of transmission studies (Mitani and Stuht 1998; Slabbekoorn et al 2002; Christie et al 2004), and previous studies have also reported small, but potentially meaningful, transmission differences that conform to the acoustic adaptation hypothesis (Wasserman 1979; Anderson and Conner 1985; Blumstein and Turner 2005). Studies that examine behavioral responses to small changes in signal transmission quality are needed to establish the biological relevance of the observed differences. But differential transmission in the two chickadee species studied here are inline with the notion that variable habitats could have played a role in shaping signals and repertoires.

The habitat variability hypothesis can be extended to migratory species as well. Migrants necessarily settle in at least two spatially distinct habitats over the course of their annual cycle (e.g., Johnson et al 2005; Rohwer et al 2009). At first glance, this would imply that migratory species should possess more distinct breeding songs and larger repertoires. However, the vegetative structure, in addition to the geographical location must vary to support this prediction. For example, the Kirtland’s warbler (*Setophaga kirtlandii*) winters in dense coppice forests and breeds in early succession Jack Pine barrens (Walkinshaw 1983; Mayfield 1960) which may not differ dramatically in their transmission properties despite their spatial separation. Comparative studies that assess structural habitat differences alongside repertoire complexity might determine whether variability is applicable more broadly in the development of repertoires. Here we show that vegetative structure may have played a role in the loss of the *fee-bee* song in the boreal chickadee. We propose that the habitat variability hypotheses, as an extension of the acoustic adaptation hypothesis, should be considered when determining what factors have driven the evolution of repertoires in animals that communicate using acoustics.

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Data Availability

The data that support the findings of this study are available online in the OSF public repository: https://osf.io/vmdbt/

References

Airey DC, Buchanan KL, Szekely T, Catchpole CK, DeVoogd TJ (2000) Song, sexual selection, and a song control nucleus (HVC) in the brains of European sedge warblers. J Neurobiol 44(1):1-6

Anderson ME, Conner RN (1985) Northern Cardinal song in three forest habitats in eastern Texas. Wilson Bull 97(4):436-449.

Avey MT, Quince AF, Sturdy CB (2007) Seasonal and diurnal patterns of black-capped chickadee (*Poecile atricapillus*) vocal production. Behav Processes 77(2):149–155. doi:10.1016/j.beproc.2007.12.004

Beeman K (2009) Signal reference guide. Version 4.04.29 / 5.04.29. Engineering Design, Berkeley

Benninghoff WS (1966) The relevé method for describing vegetation. Mich Bot 5:109-114

Blumstein DT, Turner AC (2005) Can the acoustic adaptation hypothesis predict the structure of Australian birdsong? Acta Ethol 8(1):35-44.

Boncoraglio G, Saino N (2007) Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. Funct Ecol 21:134–142. doi:10.1111/j.1365-2435.2006.01207.x

Brenowitz EA (1982) The active space of red-winged blackbird song. J Comp Physiol A 147(4):511–522. doi:10.1007/BF00612017

Brewer R (1963) Ecological and reproductive relationships of black-capped and Carolina chickadees. Auk 80:9-47

Brown TJ, Handford P (2000) Sound design for vocalizations: quality in the woods, consistency in the fields. Condor 102:81-92

Buchanan KL, Catchpole CK (1997) Female choice in the sedge warbler *Acrocephalus schoenobaenus* multiple cues from song and territory quality. Proc Roy Soc B-Biol Sci 264(1381):521-526.

Burnham KP, Anderson D (2002) Model selection and multimodel inference: a practical information-theoric approach. Springer, New York

Catchpole CK, Slater PJB (2008) Bird song: biological themes and variations. Cambridge University Press, Cambridge

Charrier I, Bloomfield LL, Sturdy CB (2004) Note types and coding in parid vocalizations. I: The chick-a-dee call of the black-capped chickadee (*Poecile atricapillus*). Can J Zool 82:769-779

Christie PJ, Mennill DJ, Ratcliffe LM (2004) Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees. Behav Ecol Sociobiol 55(4):341–348. doi:10.1007/s00265-003-0711-3

Dabelsteen T, Larsen ON, Pedersen SB (1993) Habitat-induced degradation of sound signals: quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in blackbird song. J Acoust Soc Am 93(4):2206-2220. doi:10.1121/1.406682

Dahlsten DL, Brennan LA, McCallum DA, Gaunt SL (2002) Chestnut-backed chickadee (*Poecile rufescens*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/chbchi doi:10.2173/bna.689

Ficken MS, Ficken RW, Witkin SR (1978) Vocal repertoire of the black-capped chickadee. Auk 1:34-48. doi:10.2307/4085493

Ficken MS, Nocedal J (1992) Mexican chickadee (*Poecile sclateri*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/mexchi doi:10.2173/bna.8

Ficken MS, McLaren MA, Hailman JP (1996) Boreal chickadee (*Poecile hudsonicus*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/borchi2 doi:10.2173/bna.254

Foote JR, Mennill DJ, Ratcliffe LM, Smith SM (2010) Black-capped Chickadee (*Poecile atricapillus*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/bkcchi doi:10.2173/bna.39

Forrest TG (1994) From sender to receiver: propagation and environmental effects on acoustic signals. Am Zool 34(6):644-654. doi:10.1093/icb/34.6.644

Garamszegi LZ, Eens M (2004) Brain space for a learned task: strong intraspecific evidence for neural correlates of singing behavior in songbirds. Brain Res Rev 44(2-3):187-193. doi:10.1016/j.brainresrev.2003.12.001

Gil D, Gahr M (2002) The honesty of bird song: multiple constraints for multiple traits. Trends Ecol Evol 17(3):133-141. doi:10.1016/S0169-5347(02)02410-2

Gill FB, Slikas B, Sheldon FH (2005) Phylogeny of titmice (Paridae): II. species relationships based on sequences of the mitochondrial cytochrome-B gene. Auk 122(1):121-143. doi:10.1642/0004-8038(2005)122[0121:POTPIS]2.0.CO;2

Guillette LM, Bloomfield LL, Batty ER, Dawson MRW, Sturdy CB (2010) Black-capped (Poecile atricapillus) and mountain chickadee (*Poecile gambeli*) contact call contains species, sex, and individual identity features. J Acoust Soc Am 127(2):1116–1123. doi:10.1121/1.3277247

Hadley A, Desrochers A (2008) Winter habitat use by boreal chickadee flocks in a managed forest. Wilson J Ornith 120:139-145

Hailman JP (1989) The organization of major vocalizations in the Paridae. Wilson Bull 101(2):305-343

Hahn AH, Hoeschele M, Guillette LM, Hoang J, McMillan N, Congdon JV, Campbell KA, Mennill DJ, Otter KA, Grava T, Ratcliffe LM, Sturdy CB (2016) Black-capped chickadees categorize songs based on features that vary geographically. Anim Behav 112:93-104. doi:10.1016/j.anbehav.2015.11.017

Hahn AH, Guillette LM, Hoeschele M, Otter KA, Ratcliffe LM, Sturdy CB (2017) Discrimination of male black-capped chickadee songs: relationship between acoustic preference and performance accuracy. Anim Behav 126:107-121. doi:10.1016/j.anbehav.2017.02.001

Hailman JP, Haftorn S (1995) Gray-headed chickadee (*Poecile cinctus*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/gyhchi doi:10.2173/bna.196

Hoeschele M, Moscicki MK, Otter KA, van Oort H, Fort KT, Farrell TM, Lee H, Robson SWJ, Sturdy CB (2009) Dominance signalled in an acoustic ornament. Anim Behav 79(3):657-664. doi:10.1016/j.anbehav.2009.12.015

Horn AG, Leonard ML, Ratcliffe L, Shackleton SA, Weisman RG (1992) Frequency variation in songs of black-capped chickadees (*Parus atricapillus*). Auk 109(4):847–852

Johnson MD, Sherry TW, Strong AM, Medori A (2005) Migrants in Neotropical bird communities: an assessment of the breeding currency hypothesis. J Anim Ecol 74(2):333-341.

Krebs JR (1976) Habituation and song repertoires in the great tit. Behav Ecol Sociobiol 1(2):215–227. doi:10.1007/BF00299198

Krebs JR (1977) The significance of song repertoires: the Beau Geste hypothesis. Anim Behav 25:475-478. doi:10.1016/0003-3472(77)90022-7

Krebs J, Ashcroft R, Webber M (1978) Song repertoires and territory defense in the great tit. Nature 271:539-542. doi:10.1038/271539a0

Krebs JR, Kroodsma DE (1980) Repertoires and geographical variation in bird song. Adv Stud Behav 11:143-177

Kunc HP, Amrhein V, Naguib M (2005) Acoustic features of song categories and their possible implications for communication in the common nightingale (*Luscinia megarhynchos*). Behaviour 142(8):1077-1091.

Lait LA, Burg TM (2013) When east meets west: population structure of a high-latitude resident species, the boreal chickadee (*Poecile hudsonicus*). Heredity 111(4):321-329

MacDonald IF, Kempster B, Zanette L, MacDougall-Shackleton SA (2006) Early nutritional stress impairs development of a song-control brain region in both male and female juvenile song sparrows (*Melospiza melodia*) at the onset of song learning. Proc Roy Soc B-Biol Sci 273:2559-2564. doi:10.1098/rspb.2006.3547

Marten K, Marler P (1977) Sound transmission and its significance for animal vocalization. Behav Ecol Sociobiol 2:271-290

Mayfield H (1960) The Kirtland's warbler. Cranbrook Institute of Science, Bloomfield Hills

Maynard-Smith J, Harper D (2003) Animal signals. Oxford University Press, New York

McCallum DA, Grundel R, Dahlsten DL (1999) Mountain Chickadee (*Poecile gambeli*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/mouchi doi:10.2173/bna.453

McLaren MA (1975) Breeding biology of the boreal chickadee. Wilson Bull 87(3):344-354

McLaren MA (1976) Vocalizations of the boreal chickadee. Auk 93(3):451-463

Mennill DJ, Ratcliffe LM, Boag PT (2002) Female eavesdropping on male song contests in songbirds. Science 296(5569):873. doi:10.1126/science.296.5569.873

Mitani JC, Stuht J (1998) The evolution of nonhuman primate loud calls: acoustic adaptation for long-distance transmission. Primates 39(2):171-182.

Morton ES (1975) Ecological sources of selection on avian sounds. Am Nat 109:17–34. doi:10.1086/282971

Moscicki MK, Hoeschele M, Bloomfield LL, Modanu M, Charrier I, Sturdy CB (2011) Note types and coding in Parid vocalizations: the chick-a-dee call of the boreal chickadee (*Poecile hudsonicus*). J Acoust Soc Am 129(5):3327-3340

Mostrum AM, Curry RL, Lohr B (2002) Carolina chickadee (*Poecile carolinensis*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/carchi doi:10.2173/bna.636

Mougeot F, Bretagnolle V (2000) Predation as a cost of sexual communication in nocturnal seabirds: an experimental approach using acoustic signals. Anim Behav 60:647–656. doi:10.1006/anbe.2000.1491

Nottebohm F (2005) The neural basis of birdsong. PLoS Biol 3(5):e164. doi:10.1371/journal.pbio.0030164

Nowicki S, Searcy W, Peters S (2002) Brain development, song learning and mate choice in birds: a review and experimental test of the "nutritional stress hypothesis". J Comp Physiol A Sens Neural Behav Physiol 188(11):1003–1014. doi:10.1007/s00359-002-0361-3

Oberweger K, Goller F (2001) The metabolic cost of birdsong production. J Exp Biol 204:3379-3388

Otter K, Chruszcz B, Ratcliffe L (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

Patten MA, Rotenberry JT, Zuk M (2004) Habitat selection, acoustic adaptation, and the evolution of reproductive isolation. Evolution 58:2144-2155

Podos J, Huber SK, Taft B (2004) Bird song: the interface of evolution and mechanism. Annu Rev Ecol Evol Syst 35:55-87. doi:10.1146/annurev.ecolsys.35.021103.105719

Potvin DA, Crawford PW, MacDougall-Shackleton SA, MacDougall-Shackleton EA (2015) Song repertoire size, not territory location, predicts reproductive success and territory tenure in a migratory songbird. Can J Zool 93:627-633

Ratcliffe L, Weisman R (1985) Frequency shift in the *fee bee* song of the black-capped chickadee. Condor 87:555-556

Reznikova Z (2007) Dialog with black box: using information theory to study animal language behaviour. Acta Ethol 10(1):1-12. doi:10.1007/s10211-007-0026-x

Richards DG, Wiley RH (1980) Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. Am Nat 115:381-399

Ritchison G (1995) Characteristics, use and possible functions of the perch songs and chatter calls of male common yellowthroats. Condor 97:27-38

Rohwer S, Hobson KA, Rohwer VG (2009) Migratory double breeding in Neotropical migrant birds. Proc Roy Soc B-Biol Sci 106(45):19050-19055.

Shutler D, Weatherhead PJ (1990) Targets of sexual selection: song and plumage of wood warblers. Evolution 44(8):1967-1977.

Slabbekoorn H, Smith TB (2002) Habitat-dependent song divergence in the little greenbul: an analysis of environmental selection pressures on acoustic signals. Evolution 56:1849-1858

Slabbekoorn H, Ellers J, Smith TB (2002) Birdsong and sound transmission: The benefits of reverberations. Condor 104(3):564-573.

Smith DG, Reid FA (1979) Roles of the song repertoire in red-winged blackbirds. Behav Ecol Sociobiol 5(3):279-290. doi:10.1007/BF00293676

Smith SM (1997) Black-capped chickadee. Stackpole Books, Mechanicsburg

Templeton CN, Greene E, Davis K (2005) Allometry of alarm calls: black-capped chickadees encode information about predator size. Science 308(5730):1934-1937. doi:10.1126/science.1108841

Vu ET, Mazurek ME, Kuo Y (1994) Identification of a forebrain motor programming network for the learned song of zebra finches. J Neurosci 14(11):6924-6934

Walkinshaw LH (1983) Kirtland's warbler: the natural history of an endangered species. Cranbrook Institute of Science, Bloomfield Hills

Wasserman FE (1979) The relationship between habitat and song in the White-throated Sparrow. Condor 81(4):424-426.

Wiley RH, Richards DG (1978) Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behav Ecol Sociobiol 3(1):69–94. doi:10.1007/BF00300047

Wiley RH, Richards DG (1982) Adaptations for acoustic communication in birds: sound propagation and signal detection. In: Kroodsma DE, Miller EH (ed) Acoustic Communication in Birds, vol 1. Academic Press, New York, pp131-181

Yasukawa K (1981) Song and territory defense in the red-winged blackbird. Auk 98(1):185-187

Yip DA, Bayne EM, Sólymos P, Campbell J, Proppe D (2017) Sound attenuation in forest and roadside environments: implications for avian point-count surveys. Condor 119(1):73-84. doi:10.1650/CONDOR-16-93.1

Figure legends

Figure 1. Representative spectrogram of a) black-capped song, b) black-capped chickadee call, and c) boreal chickadee call. Note types are stated above each element. Time (x-axis) varies between vocalization. The frequency spectrum (y-axis) is standardized for both call images, but is reduced for song. The songs shown are the same exemplar with the *bee* note shifted to a high (3500 Hz), medium (3200 Hz), and low (2900 Hz). A horizontal line has been added at 3500 Hz for reference.

Figure 2. Model predictions for signal-to-noise ratios (SNR) plotted by treatment. Panels a-d compare the boreal chickadee call, black-capped chickadee call, and unshifted black-capped chickadee song. Panels e-h compare frequency shifted black-capped chickadee songs. Mean humidity and temperature for each treatment was used in the calculation of predictions. Shaded ribbons represent 95% CI.

Figure 3. Model predictions for tail-to-signal ratios (TSR) plotted by treatment. Panels a-d compare the boreal chickadee call, black-capped chickadee call, and unshifted black-capped chickadee song. Panels e-h compare frequency shifted black-capped chickadee songs. Mean humidity and temperature for each treatment was used in the calculation of predictions. Shaded ribbons represent 95% CI.

Figure 4. Model predictions for cross-correlation coefficients (XC) plotted by treatment. Panels a-d compare the boreal chickadee call, black-capped chickadee call, and unshifted black-capped

chickadee song. Panels e-h compare frequency shifted black-capped chickadee songs. Mean humidity and temperature for each treatment was used in the calculation of predictions. Shaded ribbons represent 95% CI.

Table 1. Effect sizes between vocalizations for each distance and treatment. Effects are reported in ΔdB for signal to noise ratio (SNR), and Δ% for tail to signal ratio (TSR) and cross correlation (XC). Bolded results represent cases where the effect size exceeded 5% (SNR) or 10% (TSR and XC) of the ranges of values across all treatment and distances.

Effect	Treatment	Distance	BCCH call - BCCH song	BCCH call - BOCH call	BCCH song - BOCH call	BCCH song: 3500 - 3200 Hz	BCCH song: 3500 - 2900 Hz	BCCH song: 3200 - 2900 Hz
Signal to noise ratio (SNR)	Deciduous pre-leaf	5	0.088	-1.427	***-1.514***	-1.361	***-1.659***	-0.298
		20	-0.274	-0.340	-0.066	-1.033	***-1.555***	-0.522
		40	-0.455	0.204	0.658	-0.869	***-1.503***	-0.634
		60	-0.561	0.521	1.082	-0.773	***-1.473***	-0.700
		80	-0.636	0.747	1.383	-0.705	***-1.451***	-0.746
	Deciduous post-leaf	5	***-1.659***	**2.786**	**4.445**	***-2.633***	***-2.086***	0.548
		20	-0.786	**1.453**	**2.239**	***-1.472***	-1.375	0.097
		40	-0.349	0.786	1.135	-0.892	-1.020	-0.128
		60	-0.094	0.396	0.490	-0.553	-0.812	-0.260
		80	0.088	0.120	0.032	-0.312	-0.665	-0.353
	Coniferous pre-leaf	5	0.379	***-1.707***	***-2.086***	-1.333	***-2.338***	-1.005
		20	0.180	-0.485	-0.666	-1.385	***-1.981***	-0.596
		40	0.081	0.125	0.045	-1.411	***-1.802***	-0.391
		60	0.023	0.483	0.460	-1.426	***-1.697***	-0.272
		80	-0.018	0.736	0.755	***-1.436***	***-1.623***	-0.187
	Coniferous post-leaf	5	-1.010	1.208	**2.218**	***-2.397***	***-2.314***	0.082
		20	-0.466	1.115	**1.581**	***-1.835***	***-1.799***	0.036
		40	-0.194	1.068	1.263	***-1.554***	***-1.541***	0.013
		60	-0.035	1.041	1.077	-1.390	-1.390	0.000
		80	0.077	1.022	0.945	-1.274	-1.283	-0.010
Tail to signal ratio (TSR)	Deciduous pre-leaf	5	-0.035	-0.003	0.032	0.019	-0.004	-0.023
		20	-0.017	-0.044	-0.027	0.025	0.051	0.026
		40	-0.007	-0.064	-0.056	0.028	0.078	0.050
		60	-0.002	-0.075	-0.074	0.030	**0.094**	0.064
		80	0.002	***-0.084***	***-0.086***	0.031	**0.105**	0.074
	Deciduous post-leaf	5	0.011	-0.059	-0.070	0.034	0.014	-0.020
		20	0.001	-0.046	-0.047	0.049	0.050	0.000
		40	-0.005	-0.039	-0.035	0.057	0.068	0.010
		60	-0.008	-0.036	-0.028	0.062	0.078	0.016
		80	-0.010	-0.033	-0.023	0.065	**0.085**	0.020
	Coniferous pre-leaf	5	-0.025	0.002	0.027	0.004	-0.001	-0.005
		20	-0.013	-0.022	-0.008	0.045	0.067	0.022
		40	-0.007	-0.034	-0.026	0.065	**0.101**	0.035
		60	-0.004	-0.041	-0.037	0.077	**0.121**	0.043
		80	-0.001	-0.045	-0.044	**0.086**	**0.135**	0.049
	Coniferous post-leaf	5	-0.003	-0.019	-0.016	0.024	0.019	-0.005
		20	0.017	-0.026	-0.042	0.056	0.058	0.002
		40	0.027	-0.029	-0.056	0.072	0.077	0.005
		60	0.033	-0.031	-0.063	**0.082**	**0.089**	0.007
		80	0.037	-0.032	-0.069	**0.088**	**0.097**	0.009
Cross correlation (XC)	Deciduous pre-leaf	5	**0.064**	0.003	***-0.061***	**0.028**	**0.072**	**0.044**
		20	**0.028**	-0.001	***-0.029***	-0.001	**0.014**	**0.015**
		40	0.009	-0.003	-0.012	***-0.016***	***-0.015***	0.001
		60	-0.001	-0.004	-0.003	***-0.024***	***-0.032***	-0.008
		80	-0.009	-0.005	0.004	***-0.030***	***-0.044***	***-0.014***
	Deciduous post-leaf	5	**0.051**	**0.052**	0.001	**0.045**	**0.089**	**0.044**
		20	**0.016**	0.010	-0.006	0.000	0.009	0.008
		40	-0.001	-0.011	-0.009	***-0.022***	***-0.032***	-0.009
		60	-0.011	***-0.023***	-0.011	***-0.035***	***-0.055***	***-0.020***
		80	***-0.019***	***-0.031***	-0.013	***-0.045***	***-0.072***	***-0.027***
	Coniferous pre-leaf	5	**0.063**	**0.020**	***-0.043***	**0.048**	**0.060**	0.012
		20	**0.025**	0.005	***-0.020***	0.006	**0.013**	0.007
		40	0.006	-0.003	-0.009	***-0.015***	-0.010	0.005
		60	-0.006	-0.008	-0.002	***-0.027***	***-0.024***	0.003
		80	***-0.014***	-0.011	0.002	***-0.036***	***-0.033***	0.002
	Coniferous post-leaf	5	**0.070**	**0.038**	***-0.032***	**0.040**	**0.089**	**0.049**
		20	**0.020**	0.003	***-0.017***	-0.008	0.010	**0.017**
		40	-0.006	***-0.015***	-0.009	***-0.031***	***-0.030***	0.002
		60	***-0.020***	***-0.025***	-0.005	***-0.045***	***-0.053***	-0.008
		80	***-0.031***	***-0.033***	-0.002	***-0.055***	***-0.069***	***-0.014***

Figure 1.

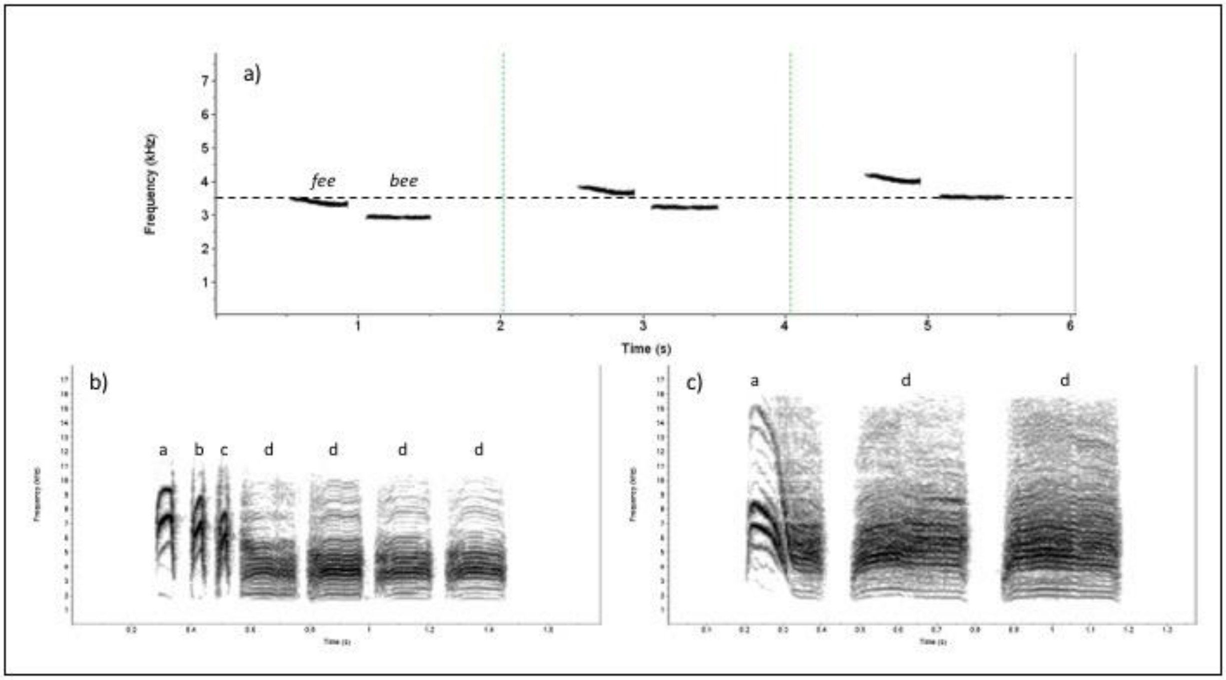


Figure 2

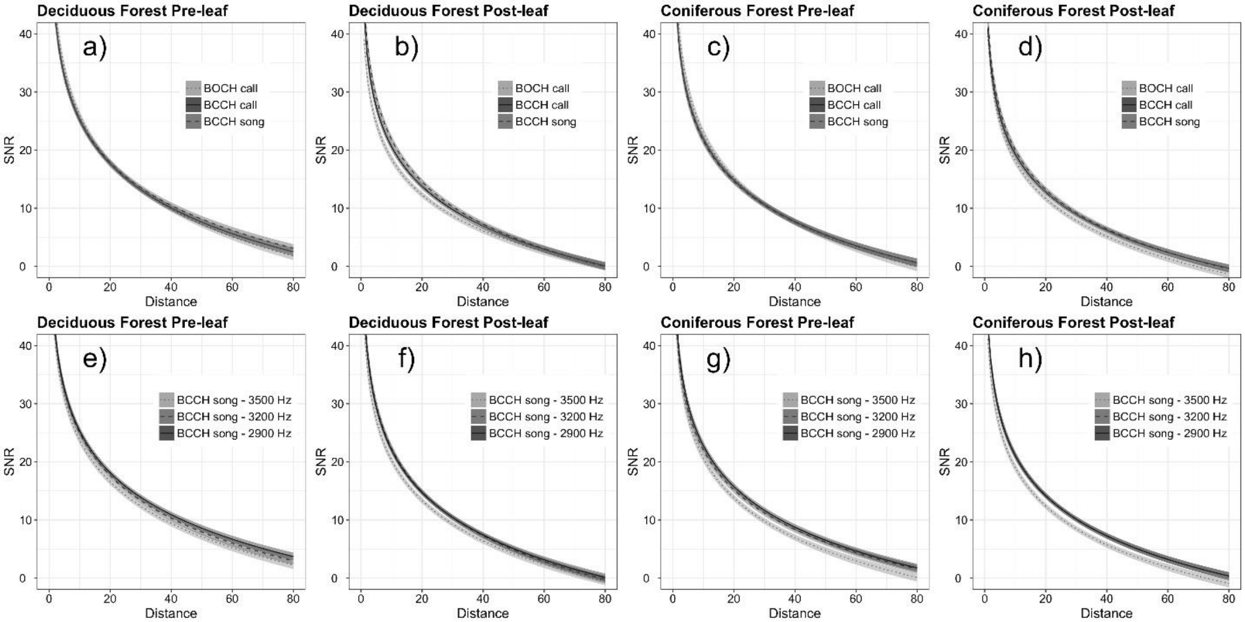

Deciduous Forest Pre-leaf
a)
Deciduous Forest Post-leaf
b)
Coniferous Forest Pre-leaf
c)
Coniferous Forest Post-leaf
d)
BOCH call
BCCH call
BCCH song
SNR
Distance
0
10
20
30
40
60
80
Deciduous Forest Pre-leaf
e)
Deciduous Forest Post-leaf
f)
Coniferous Forest Pre-leaf
g)
Coniferous Forest Post-leaf
h)
BCCH song - 3500 Hz
BCCH song - 3200 Hz
BCCH song - 2900 Hz

Figure 3

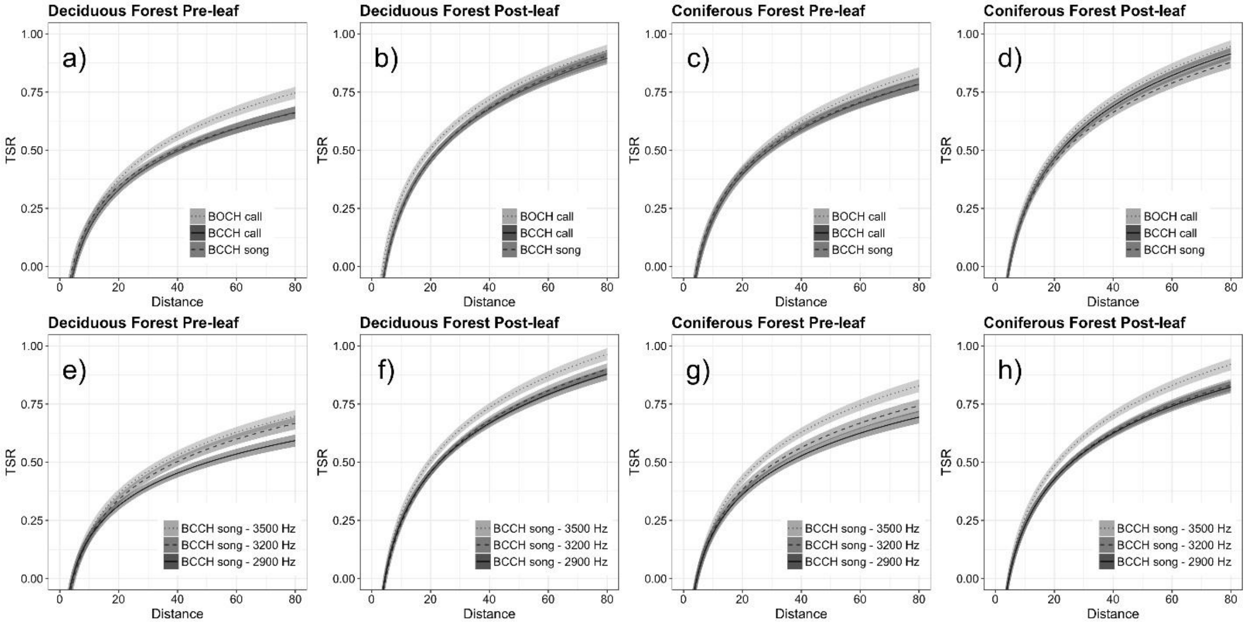
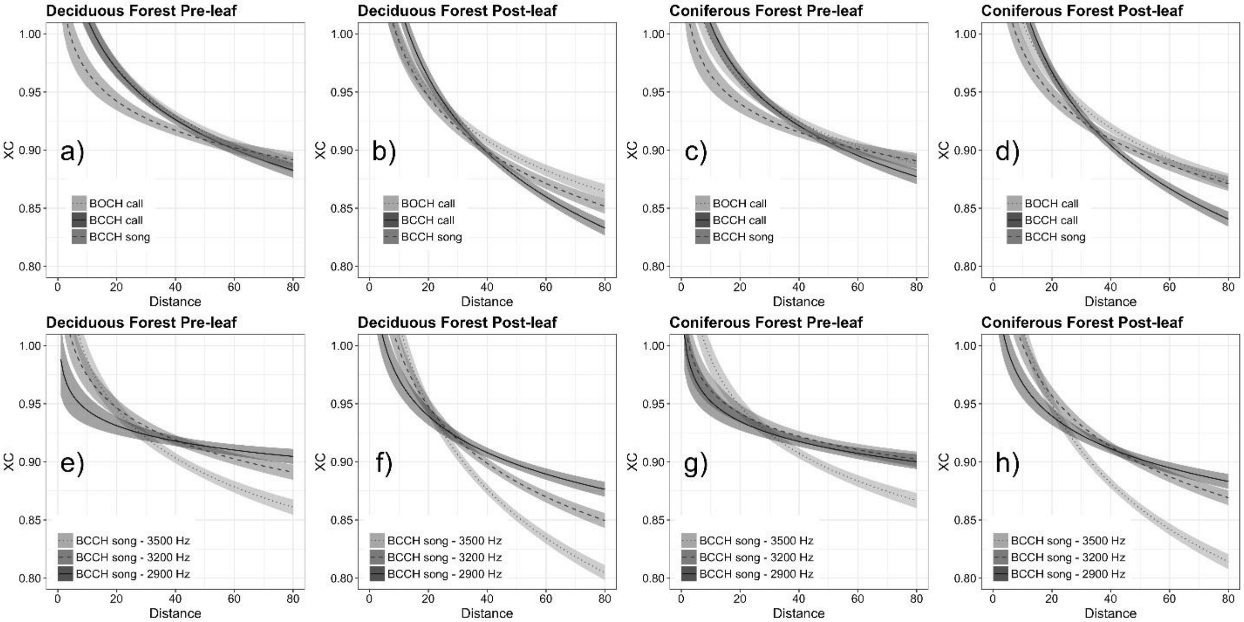

Deciduous Forest Pre-leaf
Deciduous Forest Post-leaf
Coniferous Forest Pre-leaf
Coniferous Forest Post-leaf
a)
b)
c)
d)
e)
f)
g)
h)
TSR
0.00
0.25
0.50
0.75
1.00
Distance
0
20
40
60
80
BOCH call
BCCH call
BCCH song
BCCH song - 3500 Hz
BCCH song - 3200 Hz
BCCH song - 2900 Hz

Figure 4


Deciduous Forest Pre-leaf
Deciduous Forest Post-leaf
Coniferous Forest Pre-leaf
Coniferous Forest Post-leaf
a)
b)
c)
d)
BOCH call
BCCH call
BCCH song
e)
f)
g)
h)
BCCH song - 3500 Hz
BCCH song - 3200 Hz
BCCH song - 2900 Hz
XC
1.00
0.95
0.90
0.85
0.80
Distance
0
20
40
60
80