

**BEHAVIOURAL COMPENSATION FOR HABITAT INDUCED DIFFERENCES IN  
BLACK-CAPPED CHICKADEE (*Poecile atricapillus*) SONG TRANSMISSION**

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## **Abstract**

Sound transmission is affected by natural reverberation and frequency dependent attenuation as well as additional habitat induced degradation. Optimally-structured sound signals that minimise the effects of this habitat-induced degradation have evolved in species relying on long distance transmission of sounds. Black-capped chickadees sing a highly stereotypical song of which they are able to change the absolute frequency, and possibly adjust frequency for optimal song transmission through different habitats. I conducted a song transmission study to test the optimal frequency range through two habitat types, mature mixed forest (undisturbed) and a heterogeneous matrix of different post-disturbance seral stages resulting from logging (disturbed). By recording the entire dawn chorus of birds in either habitat, I was able to determine the differences in absolute song frequency used and compare these to information about optimal song structure derived from the transmission study. Overall, songs at three different absolute frequencies showed less evidence of frequency dependent degradation and reverberation in undisturbed habitat compared to disturbed habitat. The minimum difference between songs transmitted through disturbed and undisturbed habitats appear to be in low frequency songs. Moreover, chickadees in disturbed habitat sing at lower absolute frequency. In combination, these results suggest that chickadees are possibly able to recognise differences between the two habitat types and compensate for these differences behaviourally by shifting the absolute frequency of their song.

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## Introduction

Bird song has evolved for various functions including species recognition (Nelson, 1989), individual recognition (Lind et al, 1996; Falls, 1982) territorial defence and mate selection (Catchpole and Slater, 1995). Characteristics of the songs themselves may be critical in such recognition functions. Species recognition may be facilitated by receivers cueing in on song features with either little intraspecific variation, or elements unique from heterospecifics in the same region (Nelson, 1989). The ability to identify non-related individuals by their vocalisations is an important signal component for receivers of either sex. For example, female great tits (*Parus major*) elicit certain behaviours only in response to their mate's vocalisations, indicating they are able to identify their mate (Lind et al., 1996). Similarly, belted kingfishers (*Ceryle alcyon*) are able to identify their mates from approach calls used when entering the nest (Davis, 1986).

Song is used in territorial advertisement and defence (Catchpole and Slater, 1995), and ability of territorial males recognise and reduce response to the songs of neighbouring males, may be advantageous. This can allow a male to conserve energy by not escalating flights with neighbours with whom boundaries are already established (Catchpole and Slater, 1995). On the other hand, a resident male may view a new male as a greater threat to his territory than a resident neighbouring male and therefore invests the energy for a strong territorial defence (Catchpole and Slater, 1995).

Mate and neighbour recognition strategy may be important to females as a sexual selection mechanism. Song output by particular males may serve as an honest indicator of male quality in the process of sexual selection (Otter et al., 1997), be it for mate selection (Otter and Ratcliffe, 1996) or selection of extra pair partners (Otter et al., 1998). If males of higher quality

than their mate are advertising from neighbouring territories, the female may seek extra pair copulations (Otter et al., 1998). If such a high quality male becomes available as a possible mate, the female may even initiate divorce from her original mate (Otter and Ratcliffe, 1996).

Characteristics of the songs themselves may provide the means by which females can monitor availability of specific neighbours for mating opportunities. The key for these recognition factors is the ability of the receiver to discern the characteristics of interest of the song.

### *Communication networks*

In response to the many functions of bird song, McGregor and Dabelsteen (1995) proposed the concept of communication networks. This concept is based around the fact that long distance signals involve not only a single signaller and receiver, but numerous signallers and receivers depending on signal transmission distance and territory sizes of individuals in the network (McGregor and Dabelsteen, 1995). To enable maximisation of the signal's purpose in initiating a response from a receiver, signallers may be selected to direct the signal to the desired receiver, while simultaneously restricting information from reaching an undesired receiver (McGregor and Dabelsteen, 1995). Both of these intents can be achieved through distance cues in vocalisations, which are interpreted by the receiver through the level of degradation in the signal that has occurred over the distance travelled (Phillmore et al, 1998).

### *Sound transmission*

In order to understand the interpretation of distance cues, the physics of sound transmission and resulting signal degradation must be recognised. Signal degradation is the result of many processes including frequency dependent attenuation and reverberation (Morton, 1975; Wiley and Richards, 1982). These processes are further affected by factors such as habitat (Morton, 1975), distance (McGregor et al., 1983) and height (Dabelsteen et al., 1993).

*Attenuation*, the loss of sound intensity with distance (Bradbury and Vehrencamp, 1998), is the result of spherical spreading, atmospheric absorption, scattering and boundary interference (Wiley and Richards, 1982). Spherical spreading refers to the relationship between sound intensity and distance, which in a homogeneous environment is a sound intensity decrease equal to the inverse of the distance between signaller and receiver (Wiley and Richards, 1982; Bradbury and Vehrencamp, 1998). Attenuation is frequency dependent because of differential atmospheric absorption of sound energy depending on the wavelength of the sound (Wiley and Richards, 1982). High frequency sounds (those with small wavelengths) suffer greater absorption than lower frequency sounds.

Because bird habitat is generally not homogeneous, *scattering*, the reflection, diffraction and refraction of sound waves, further increases the amount of attenuation of sounds (Wiley and Richards, 1982). Scattering occurs both due to the interactions of sound waves with molecules in the air (Bradbury and Vehrencamp, 1998), and due to environmental complexities such as atmospheric turbulence (Wiley and Richards, 1982; Morton, 1975). Boundary interference of sound waves results from reflection of sound waves on an interfering object or the ground (Wiley and Richards, 1982).

*Reverberation* results from the scattering and reflection of sound waves that occurs in the distance between the signaller and the receiver (Wiley and Richards, 1982). The combination of echoes and scatter result in signal blurring and addition of lower amplitude sounds at the end of the signal (Bradbury and Vehrencamp, 1998). Reverberation has a large influence on the complexity of vocalisations, as sounds with high amplitude modulation or frequency modulation, such as trills with a wide variation in frequency, suffer greater reverberation effects with distance than pure tones (Catchpole and Slater, 1995). This potentially introduces an evolutionary trade-

off: how can a song evolve to transfer maximum amounts of information without reverberation decreasing transmission distance (Morton, 1975)?

#### *Behavioural modifications to deal with sound transmission limitations*

The effects of reverberation can be behaviourally controlled to some degree by birds by singers varying their perch height (Catchpole and Slater, 1995). Wrens (*Troglodytes troglodytes*) have high frequency and amplitude modulations in their songs, which creates redundancy in the vocalisation. Wrens may be able to combat the constraints of heterogeneous transmission pathways, because of the high redundancy in their song and their behavioural response by varying their singing perch height (Holland et al., 1998). Similarly, blackbirds (*Turdus merula*) can increase the transmission of their song by half to full territory length by increasing their perch heights thereby decreasing ground effects (Dabelsteen et al., 1993). The results of song degradation affect signallers, as receiver response to a degraded song is lower than to an undegraded signal (McGregor et al., 1983). However, to the receiver, the amount of signal degradation is an important indicator of signaller distance (McGregor et al., 1983; Phillmore et al., 1998). Hence, an evolutionary arms race of signallers attempting to minimise degradation with distance and receivers being able to detect distance by subtle clues has been proposed (Holland et al., 1998).

#### *Habitat specific effects on sound degradation*

Habitat has significant effects on sound degradation, due to a discrepancy in reverberation and frequency dependent attenuation in different habitat types (Fotheringham and Ratcliffe, 1995). Frequency dictates the ability of a sound wave to be able to travel around objects rather than reflect off them (Morton, 1975). Therefore, high frequency sound waves experience greater loss in energy through reflections off vegetation, where lower frequencies are

able to move around these objects (Morton, 1975). This scattering is accentuated by the presence of dense vegetation and through atmospheric turbulence (Wiley and Richards, 1982). Because of these frequency and habitat dependent differences in the amount of attenuation and reverberation of sounds, it seems logical that songs that transmit best through their environment will have an evolutionary advantage.

The Acoustic Adaptation Hypothesis states that long distance auditory signals should be structured to suffer minimum degradation (Rothstein and Fleischer, 1987), and therefore predicts selection against songs that do not propagate maximally (Morton, 1975; Hanson, 1979). Various frequency-related parameters ensure such maximum transmission distance. Morton (1975) found there to be a “frequency window” or range of frequencies at which excess attenuation is lowest. Frequencies greater than 2500 Hz or lower than 1585 Hz experience greater excess attenuation in forest habitats (Morton, 1975). Because different habitats are structurally diverse in complexity, they affect sound propagation differently and therefore the optimal frequencies of vocalising in these habitats may vary (Wiley and Richards, 1982). In addition to frequency, habitat differences also affect transmission quality of different song types. More complex songs composed of trills and rapid changes in frequency suffer increased degradation in more complex habitats such as forests as opposed to open woodland habitats (Morton, 1975).

Several studies have examined differences in sound signal transmission through different habitats (e.g. Fotheringham and Ratcliffe, 1996; Handford and Loughheed, 1991). In general, birds in open habitats sing songs with higher amplitude and frequency whereas birds in complex forested habitats tend to sing lower-frequency, tonal songs (Morton, 1975; Brown and Handford, 2000). Although the pure tone vocalisation would transmit further in open habitat in calm

conditions, trilled signals experience decreased variability in transmission quality during breezy days (Brown and Handford, 2000).

Variation in song structure is seen not only interspecifically, but also intraspecifically in generalist species that utilise variable habitats. Hunter and Krebs (1979) described this variation in Great Tits occupying forest and open woodland or parkland ecosystems. Birds in woodland ecosystems have song repertoires with a higher maximum frequency, a greater frequency range and more complex songs (Hunter and Krebs, 1979). In contrast, birds in forest habitats use the more tonal song types that suffer lower degradation and transmit greater distances in dense vegetation (Hunter and Krebs, 1979). These trends hold true across large geographic areas, with birds in different areas but with similar habitat characteristics using similar vocalisations (Hunter and Krebs, 1979). More recently, Handford and Lougheed (1991) have shown similar habitat specific trends in the trill dialects of the Rufous-collared Sparrow (*Zonotricha capensis*), with lower complexity songs being heard in more complex habitats. Interestingly, birds seem to be using the trill dialects best suited to original habitat structure even when the habitat has been altered (Handford and Lougheed, 1991).

Differential transmission does not only affect the signaller, as habitat differences in sound transmission may cause distortion in distance cues, and thereby cause the receiver to respond differently to the same signal (Fotheringham and Ratcliffe, 1995). In attempting to minimise degradation of song, it has been suggested that males are trying to withhold information about their distance from a receiver (Morton, 1975). However, continuous assessment of distance has also been shown by receivers (Fotheringham et al., 1997). Black-capped chickadees (*Poecile atricapillus*) have been shown to cue in on reverberation and frequency attenuation to judge distance of singers. However, in their native habitat, differences in both reverberation and

frequency dependent attenuation were demonstrated between open woodlands and more closed forested habitats (Fotheringham and Ratcliffe, 1995). When chickadees in these different habitat types were presented with degraded and undegraded songs, their responses to these signals did not differ, suggesting that habitat heterogeneity precluded chickadees from using song degradation as a distance cue (Fotheringham and Ratcliffe, 1995).

### *Black-capped chickadee song*

Male black-capped chickadees use a highly stereotypical two-syllable song, “fee bee” or “fee bee-ee”. In populations across most of North America, this song does not exhibit much variation, with the exception of a few island populations off the east coast of the United States (Kroodsma et al., 1999). The birds, within their repertoire, do not change song types, rather they change absolute frequency (Ratcliffe and Weisman, 1985; Hill and Lein, 1987). Individual males may switch the absolute frequency of their song during a dawn chorus (Ratcliffe and Weisman, 1985). A downward shift in song frequency has been suggested to be a more aggressive version of territorial advertisement (Hill and Lein, 1987). This suggests that higher ranking males tend to use lower frequency songs (P. Christie and L. Ratcliffe, pers. comm.).

Although considerable variation of absolute frequency of songs has been observed in black-capped chickadees, the frequency ratio within a song is highly conserved (Weisman and Ratcliffe, 1989). The fee note in an undegraded chickadee song has a slight downward sweep in frequency, the glissando. Through degradation, this glissando is lost (Weisman et al., 1990). This loss is quantified by measuring the frequency ratio of the start and end of the fee note; a decreasing ratio indicates a lost glissando (Weisman et al., 1990). The frequency ratio of  $fee_{end}$  to  $bee_{start}$  is also highly conserved with a lower frequency in the bee note than in the fee note (Weisman et al., 1990). Weisman et al. (1990) found only 1.7% and 1.6% variation between

males in frequency ratios of  $f_{e_{start}}$  to  $f_{e_{end}}$  and  $f_{e_{end}}$  to  $f_{b_{start}}$ , respectively. These ratios are conserved if a bird changes the absolute frequency of its song (Weisman et al., 1990).

The importance of the conserved nature of song frequencies has been tested in various studies (Weisman and Ratcliffe, 1989; Weisman et al., 1990; Shackleton et al., 1992). When chickadees were presented with songs with above or below normal absolute frequencies, decreased social response was observed (Weisman and Ratcliffe, 1989). When the glissando is lost in the fee note, territorial males respond less strongly and act less territorial than to an unaltered song, a response much like if the singing male is far away from the receiver (Shackleton et al., 1992). Further, when females were presented with songs with an altered glissando or altered between note ratios, the number and duration of copulation displays given in response decreased significantly (Ratcliffe and Otter, 1996). This indicates that a loss of certain song structures may lead to an inability by the singing male to induce the desired response in the receiving female. Further, evidence also exists that a male's ability to sing a stereotyped song is related to its quality, which is indicated by relative flock rank (Chruszcz, 1996). Hence, the ability of males to produce the highly stereotypical songs of the population may be an indicator used by females in sexual selection (Chruszcz, 1996). Further, too great an alteration of frequencies may alter an individual's ability to recognise a conspecific, as certain song parameters in chickadee song are thought to act as species recognition cues (Weisman et al., 1990). Both males and females have lower response to heterospecific song than to altered chickadee song indicating that both sexes are able to identify conspecifics by song (Ratcliffe and Otter, 1996).

*The effects of habitat on song transmission and singing behaviour of black-capped chickadees*

Habitat differences in sound transmission have been demonstrated numerous times (e.g. Morton, 1975; Fotheringham and Ratcliffe, 1995). Further, it has also been shown that birds structure their long distance songs so as to attain optimal transmission of their signal (Morton, 1975; Brown and Handford, 2000). However, these trends have generally been established interspecifically (Morton, 1975), or when these trends were tested intraspecifically, it was across a large geographic area (Hunter and Krebs, 1979). Differences in signaller benefits and receiver reactions to degraded and undegraded songs have been well established in black-capped chickadees (Weisman and Ratcliffe, 1989; Ratcliffe and Otter, 1996).

In sub-boreal areas, post-stand replacement disturbance ecosystems are characteristically very dense in composition due to the emergence of early seral deciduous vegetation when compared to undisturbed areas. To generalist species that occupy both pre- and post-disturbance habitats these changes in vegetative structure can have great impacts on many aspects of their life history, including their ability to vocalise optimally, to advertise and defend territory. If a highly stereotyped song, such as that of the black-capped chickadee, continues to be used in this post-disturbance habitat, the denser vegetation will likely lead to increased reverberation and attenuation of song, decreasing the song's ability to reach maximum amounts of receivers. Past study of bird song suggests that lower frequency songs are transmit better through a denser medium than do high frequency songs (Morton, 1975). As black-capped chickadees are able to alter the absolute frequency of their song (Ratcliffe and Weisman, 1985), males able to distinguish between these different habitat types potentially have the ability to alter their absolute song frequency and compensate for habitat induced differences in sound transmission. Hence,

black-capped chickadees are ideal for testing behavioural modification for habitat induced transmission differences.

This study is focussing on the effects of physical habitat disturbance on optimal black-capped chickadee song transmission in two habitat types (disturbed and undisturbed) and relating these differences to whether chickadees compensate for any differences.

## **Methods**

### *Study site*

The study site is located near the Prince George campus of the University of Northern British Columbia (53°54'N, 122°49'W), and is divided into two habitat types (figure 1), disturbed (treatment) and undisturbed (control). In the disturbed site, the disturbance history involves logging of most of the area in 1962 and subsequent agricultural activities. In 1989, areas within this site were planted with a monoculture of lodgepole pine (*Pinus contorta*). The remainder of the site was left to regenerate naturally. The unlogged area of this site composes approximately 10% of the area and is structurally similar to the undisturbed site. The disturbed site is currently a recreational area complete with a trail-network. This site is characteristically heterogeneous consisting of a mosaic of willow (*Salix* sp.), Alder (*Alnus crispa*) approximately 5-7 m in height, lodgepole pine monoculture plantations of approximately 5 m in height and intermixed with young deciduous shrubs, and the uncut mature site that is characteristically similar to the undisturbed area. In contrast, the adjacent undisturbed site is a homogenous mature mixed forest that has not sustained large scale disturbance for 80 years. The dominant canopy trees are trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), hybrid spruce (*Picea glauca x engelmannii*), lodgepole pine (*Pinus contorta*), intermixed with subdominant species including subalpine fir (*Abies lasiocarpa*), douglas fir (*Pseudotsuga menziesii*), and

black cottonwood (*Populus balsamifera* var. *trichocarpa*). The average canopy height is 20-25 meters. The understory component of the control site is less well developed than in the disturbed site, and is characteristically less than one meter in height. Characteristic species include willow, alder, prickly rose (*Rosa acicularis*), high-bush cranberry (*Viburnum edule*), raspberry (*Rubus* sp.) and areas of devil's club (*Oplopanax horridus*).

### *Transmission Study*

Songs of territorial male Black-capped Chickadees were recorded in spring 2000. These songs were later digitised using Avisoft – SASLab Pro. (Specht, 2000). Six songs, two at each of three different frequencies, were chosen as stimuli (low frequency  $bee_{start}=2.9$  kHz, middle frequency  $bee_{start} = 3.2$  kHz and high frequency  $bee_{start} = 3.5$  kHz).

Songs were broadcast along two transmission lines through each two different habitat types (figure 2), undisturbed and disturbed using a Marantz PMD 430 recorder and Sony SRS-A45 speaker. The broadcast volume was held constant at 73 +/- 3dB, which was standardised using a Radio Shack 33-2055 digital sound meter at a 5 m distance. Songs were recorded at 5, 25, 50 and 100 m distances using a Marantz PMD 430 recorder and a Sennheiser ME 67 microphone at 1, 3 and 5 meter heights. In total, 288 songs were recorded and analysed using sonagrams created in Avisoft – SASLab Pro. (Specht, 2000).

Sonagrams were used to measure the durations (in seconds) of song notes (fee and bee) and the internote interval (time between fee and bee). The frequency (Hz) of peak amplitude (dB) at the beginning and end of fee and bee notes were measured by taking spectral slices at 10% and 90% of the duration of each song element (figure 3).

The effects of reverberation and frequency dependent attenuation were measured using 4 factor ANOVAs (factor 1 = habitat, factor 2 = distance, factor 3 = height, factor 4 = frequency class).

The effects of reverberation were tested using the duration of song elements (fee, bee and internote interval). The effects of frequency dependent attenuation were determined from within song frequency ratios ( $fee_{start}/fee_{end}$  and  $fee_{end}/bee_{start}$ ).

#### *Frequency shifting in different habitats*

Relative dominance ranks of colour banded males within flocks of Black-capped Chickadees were determined in March 2000 from observing males at feeders and scoring aggressive interactions. Males were classified as either high or low ranking within their flocks, based on the outcome of interactions between themselves and flockmates. High-ranking males were alpha males within their own flock. Low ranking males were beta males in two-male flocks or gamma or lower in flocks with more than two males. In total, 52 males were colour banded and assigned relative dominance ranks.

Songs of 26 territorial Black-capped Chickadee males were recorded in disturbed and undisturbed habitats in spring 2000 by entering the males' territories at the beginning of the dawn chorus (0430-0530 PST). In order to evaluate a male's average song frequency, the entire chorus of each male was recorded using Marantz PMD 430 recorders and Sennheiser ME 67 and Audio Technica ATB-815a microphones. To control for possible environmental effects, a roughly paired design of males in disturbed and undisturbed habitats was used. Whenever possible, one male in disturbed and one male in undisturbed habitat were recorded each day. In total, 15 males in disturbed and 11 males in undisturbed habitat were recorded. This discrepancy is a result of mechanical failure in the field or failure of males to sing choruses where we suspected.

Songs of each male were digitised using Avisoft SASLab – Pro (Specht, 2000). The absolute frequency (kHz) of every song was determined by measuring the frequency at the start

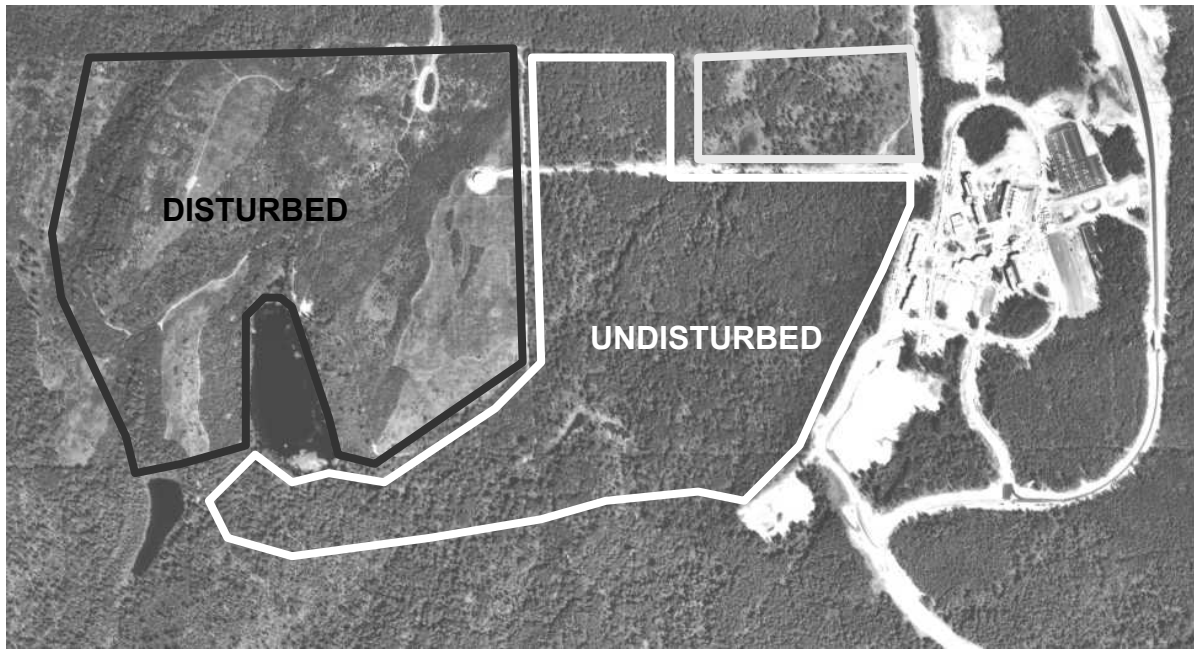


Figure 1: Aerial photo of study site showing spatial distribution of disturbed and undisturbed habitats.

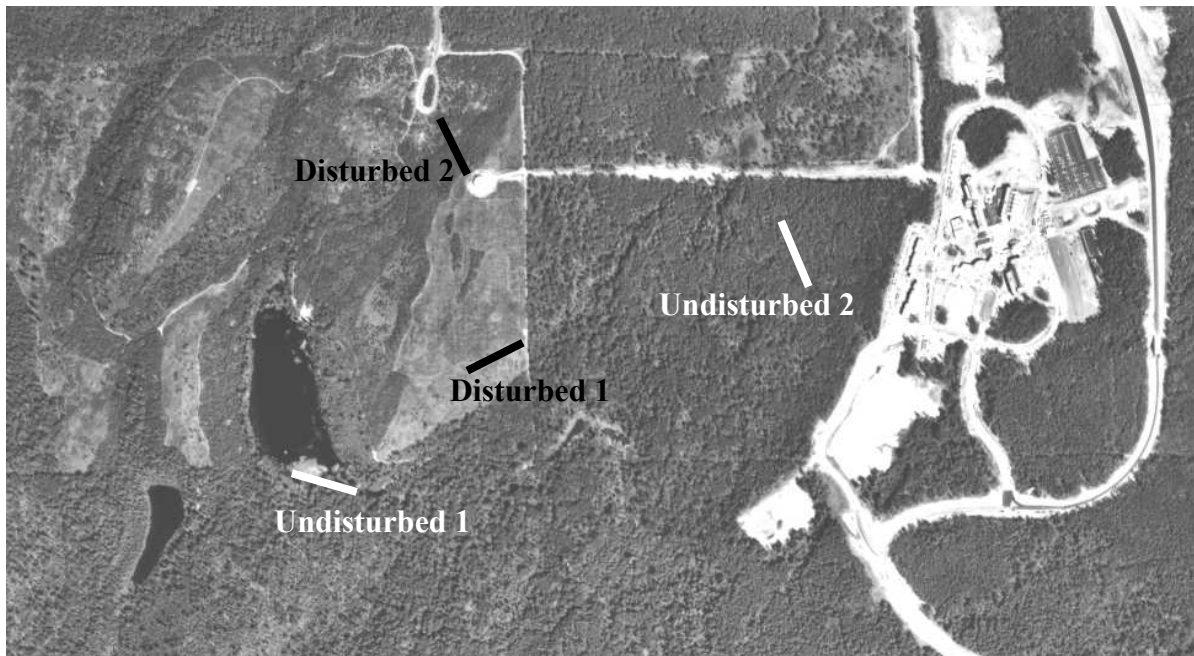


Figure 2: Aerial photo of study site showing the locations of the transmission lines in each of the two habitat types.

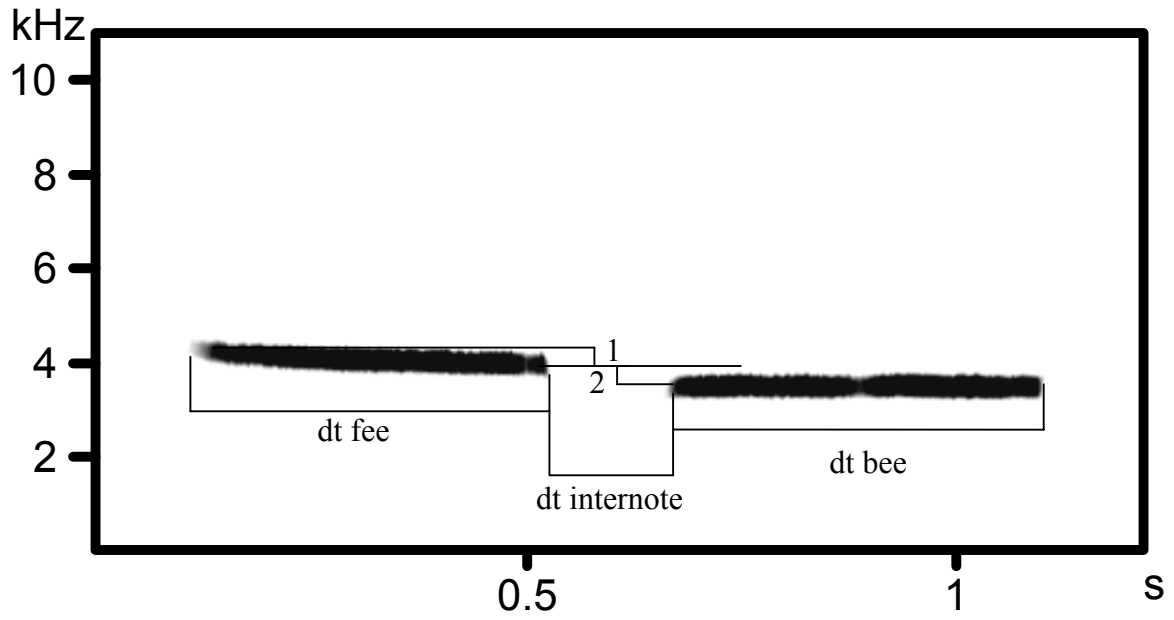


Figure 3: Sonograph of an undegraded chickadee song, showing the duration of the fee note ( $dt_{\text{fee}}$ ), duration of the bee note ( $dt_{\text{bee}}$ ) and interval between the two notes ( $dt_{\text{internote}}$ ). Numbers 1 and 2 refer to the intranote ( $fee_{\text{start}}/fee_{\text{end}}$ ) and internote ( $fee_{\text{end}}/bee_{\text{start}}$ ), respectively.

of the bee note on a sonogram (figure 3). The average song frequency of each male was determined by calculating a weighted average of all the songs of a chorus. To test for a difference in average song frequencies of males in disturbed and undisturbed habitats, a Mann-Whitney U test was used.

## **Results**

### *Transmission Study*

There were significant effects of distance and frequency on the duration of the fee and bee notes and the internote interval (table 1). Both fee and bee note intervals were found to decrease with distance and at high frequencies. In the fee note, low frequency songs suffered similar reverberation effects in disturbed and undisturbed habitats. Although overall, habitat and height were not significant factors in the duration of the fee note (table 1), significant differences in the note's duration exist at medium and high frequencies between the two habitat types (figure 4). At high frequencies, song duration drops significantly in both disturbed and undisturbed habitats, indicating a loss in glissando due the increased scattering of the high frequencies. Overall, when compared to the stimulus note, the fee note suffers lower reverberation effects in undisturbed than in disturbed habitat (figure 4). Further, when compared to the stimulus, a significant decrease in the duration of the internote interval (figure 5) is seen at all frequencies in both habitat types indicating that a significant amount of scattering is occurring. In disturbed habitats, the shortest internote interval, and therefore the greatest amount of scatter at the end of the fee note, is seen at medium frequencies, whereas scatter is less in low and high frequencies.

Overall, in the duration of the bee note, a weak trend of decreasing note duration with increasing height was observed (table 1). Trends of habitat, height or frequency on the duration of the bee note were insignificant as a whole. However, when compared to the stimulus song, at

low and medium frequencies the bee note is longer in undisturbed than in disturbed habitat (figure 6). On the contrary, at high frequency, this trend, although not significant, switches to a shorter duration song in undisturbed habitat.

Overall, there is a significant habitat effect on the intranote ratio ( $fee_{start}$  to  $fee_{end}$ ), suggesting a differential loss of the frequency sweep of the fee note in disturbed habitat. Further, there is an overall trend of frequency affecting this ratio, but distance and height are not significant factors affecting the ratio (table 1). The change in intranote ratio in songs travelling through undisturbed habitat is negligible in comparison to the stimulus songs, especially at low and high frequencies (figure 7). However, in disturbed habitat, when comparing low and high frequency songs to the stimulus ratios, there is evidence of a decreased intranote ratio, and therefore an overall glissando loss.

A trend of decreasing ratio of  $fee_{end}$  to  $bee_{start}$  was observed with habitat, height and frequency being significant factors (table 1). When comparing transmission differences between the two habitat types, the internote frequency ratio is significantly lower in undisturbed habitat than in disturbed habitat, indicating significant differential frequency dependent attenuation between the two habitats (figure 8). When further comparing these differences to the stimulus song, it is evident that low frequency songs transmitting through disturbed habitat are not significantly different from stimulus song with respect to internote ratio. However, at high song frequencies, the internote ratio of songs transmitting through undisturbed habitat, closely simulate the internote ratio of the stimulus songs.

Table 1: Results of four-factor ANOVA (factor 1=habitat, factor 2=distance, factor 3=height, factor 4=frequency of stimulus). Table shows effects of these factors on variables describing the transmission of black-capped chickadee song.

| <b>Dep.Variable</b> | <b>Factor</b> | <b>F-ratio</b> | <b>df</b> | <b>p value</b> |
|---------------------|---------------|----------------|-----------|----------------|
| dt Fee              | Habitat       | 2.316          | 1         | 0.13           |
|                     | Distance      | 12.471         | 3         | <0.001         |
|                     | Height        | 1.573          | 2         | 0.21           |
|                     | Frequency     | 101.912        | 2         | <0.001         |
| dt Bee              | Habitat       | 1.151          | 1         | 0.284          |
|                     | Distance      | 21.783         | 3         | <0.001         |
|                     | Height        | 2.654          | 2         | 0.073          |
|                     | Frequency     | 20.82          | 2         | <0.001         |
| dt internote        | Habitat       | 0.392          | 1         | 0.532          |
|                     | Distance      | 13.243         | 3         | <0.001         |
|                     | Height        | 1.782          | 2         | 0.171          |
|                     | Frequency     | 2.099          | 2         | 0.125          |
| fee(s)/fee(e)       | Habitat       | 7.7            | 1         | 0.006          |
|                     | Distance      | 1.864          | 3         | 0.137          |
|                     | Height        | 0.082          | 2         | 0.921          |
|                     | Frequency     | 2.726          | 2         | 0.068          |
| fee(e)/bee(s)       | Habitat       | 16.203         | 1         | 0.031          |
|                     | Distance      | 5.144          | 3         | 0.098          |
|                     | Height        | 0.942          | 2         | 0.006          |
|                     | Frequency     | 1.908          | 2         | 0.011          |

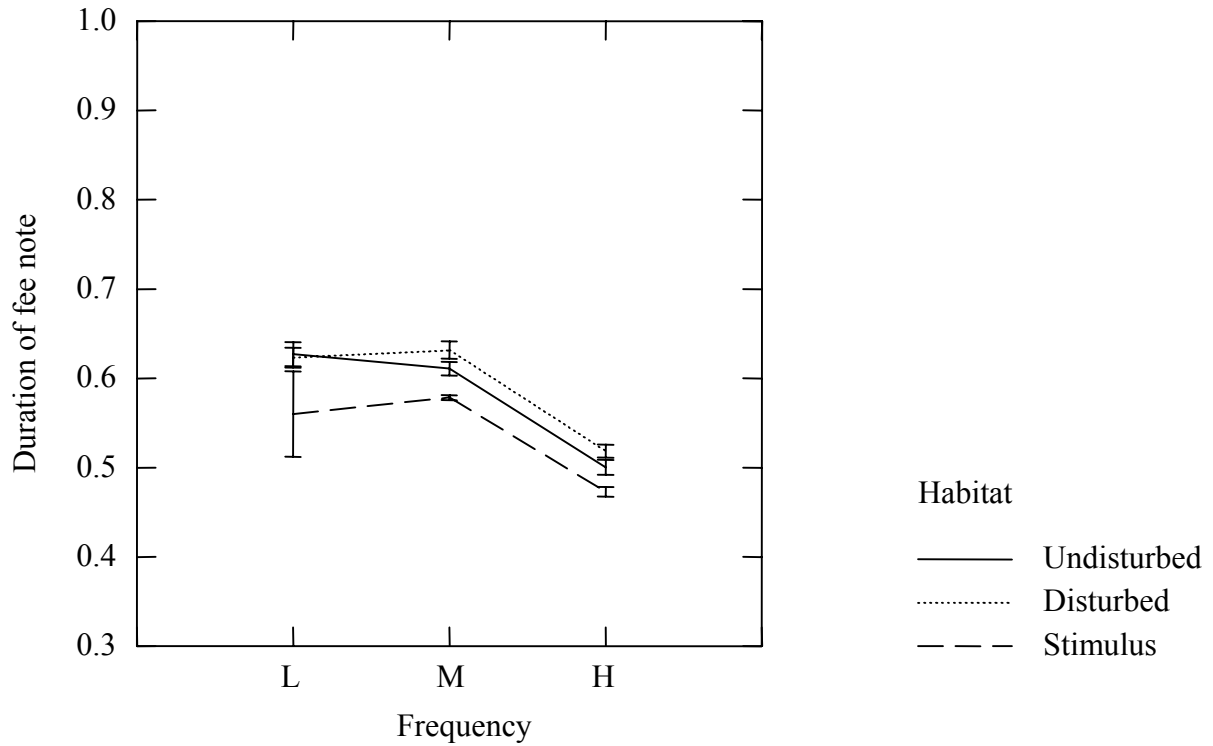


Figure 4: Comparison of the duration of the fee note of black capped chickadee songs transmitted through different habitats (disturbed and undisturbed) at three different frequencies (low, medium, high). Values are averaged over all distances (5, 25, 50, and 100m) and heights (1, 3 and 5 m). Error bars shown indicate standard error.

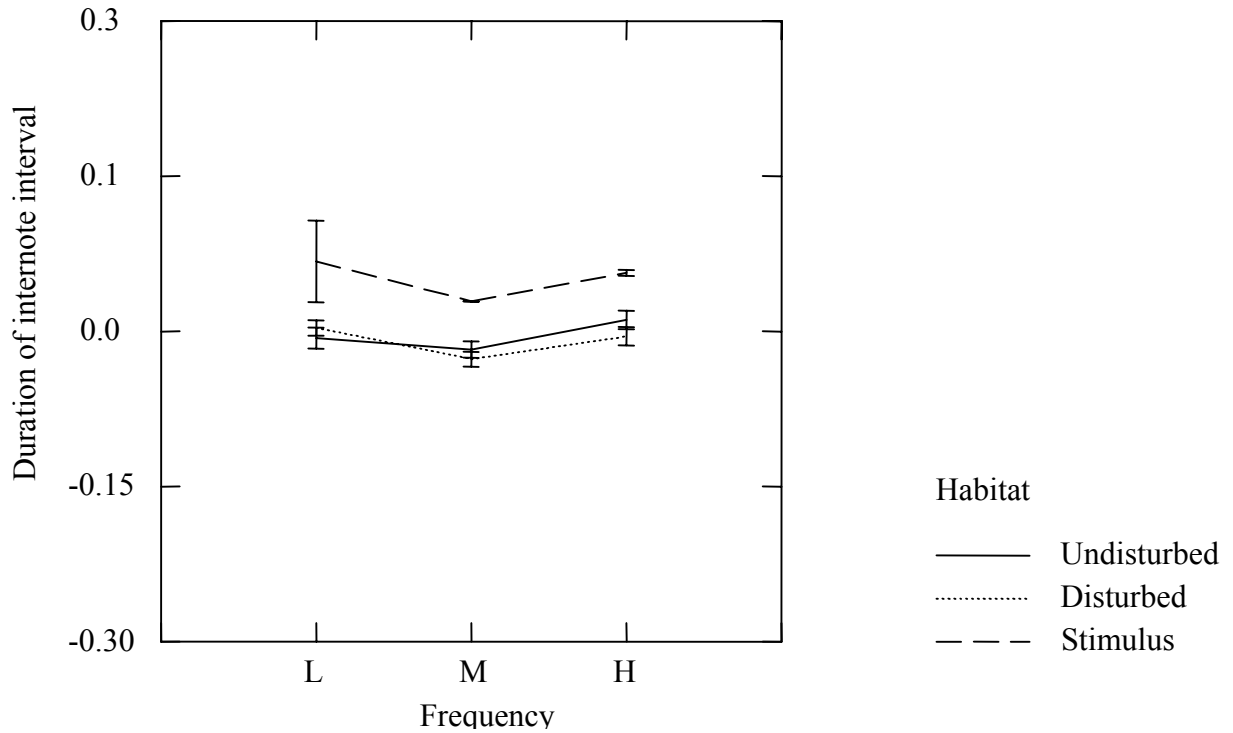


Figure 5: Comparison of the duration of the internote interval of black capped chickadee songs transmitted through different habitats (disturbed and undisturbed) at three different frequencies (low, medium, high). Values are averaged over all distances (5, 25, 50, and 100m) and heights (1, 3 and 5 m). Error bars shown indicate standard error.

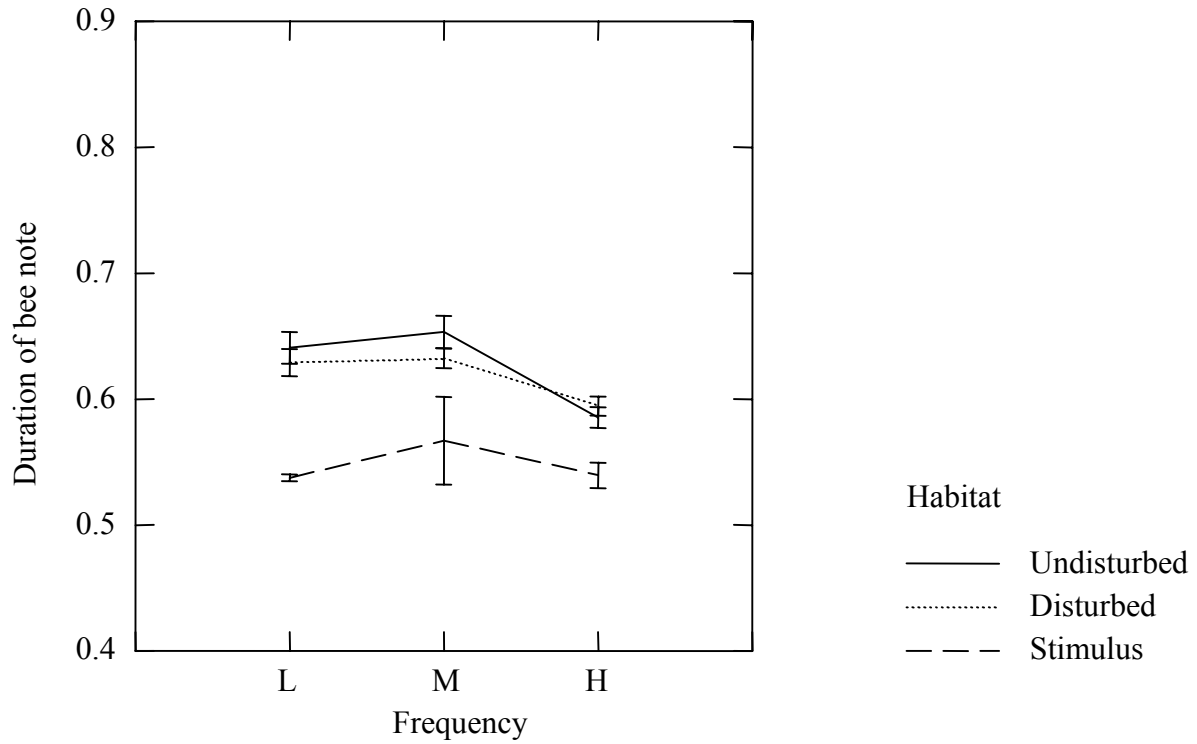


Figure 6: Comparison of the duration of the bee note of black capped chickadee songs transmitted through different habitats (disturbed and undisturbed) at three different frequencies (low, medium, high). Values are averaged over all distances (5, 25, 50, and 100m) and heights (1, 3 and 5 m). Error bars shown indicate standard error.

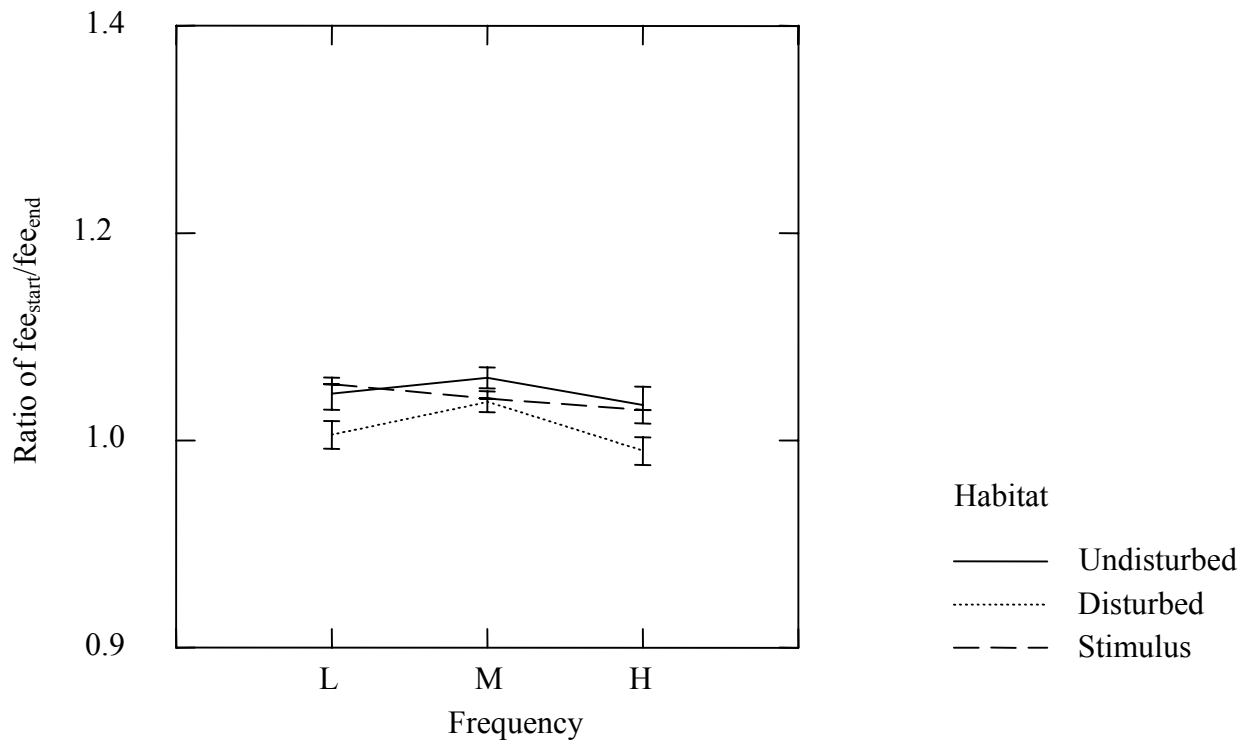


Figure 7: Comparison of the intranote frequency ratio  $fee_{start}/fee_{end}$  of black capped chickadee songs transmitted through different habitats (disturbed and undisturbed) at three different frequencies (low, medium, high). Values are averaged over all distances (5, 25, 50, and 100m) and heights (1, 3 and 5 m). Error bars shown indicate standard error.

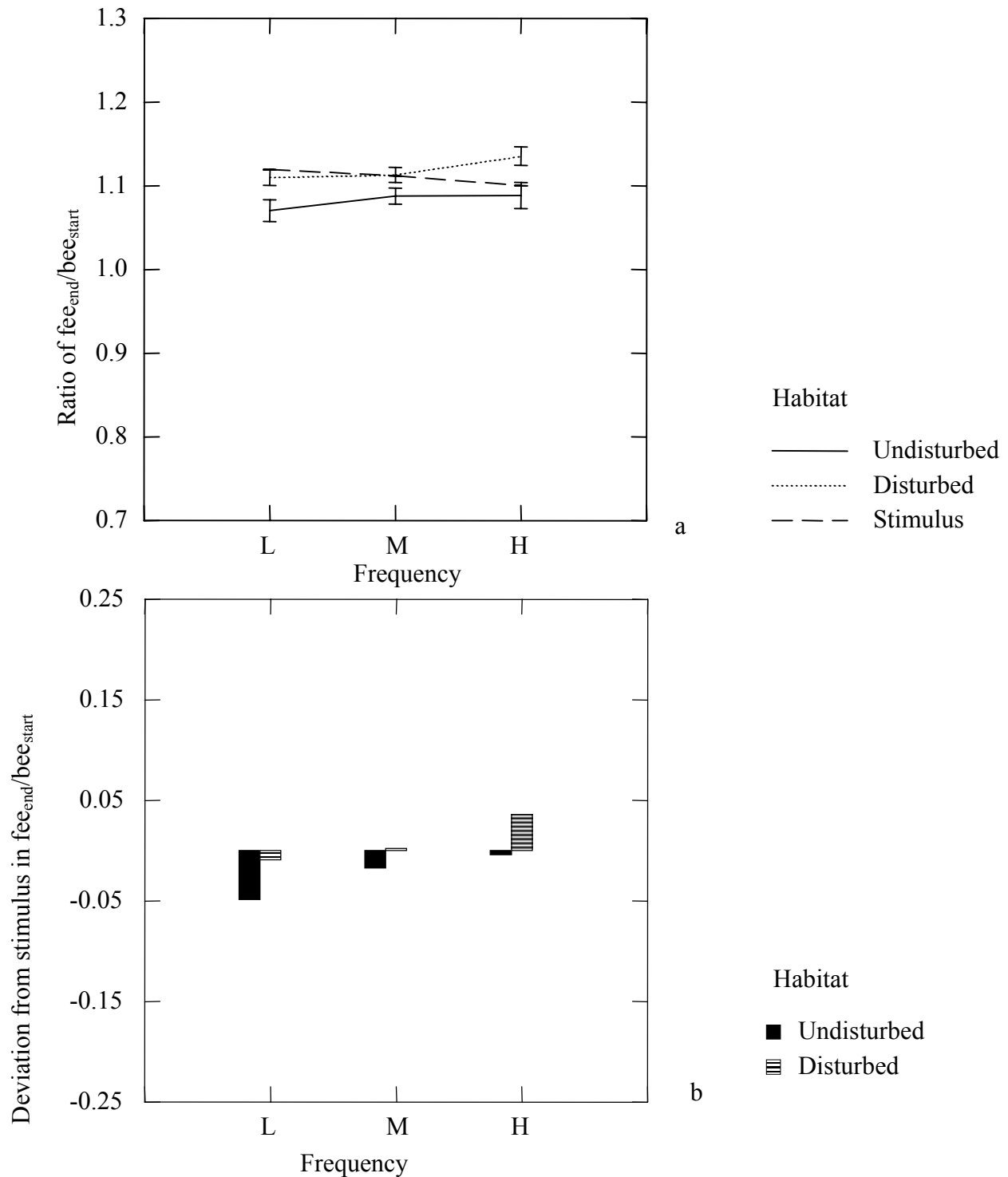


Figure 8: a) Comparison of the internote frequency ratio  $fee_{start}/fee_{end}$  of black capped chickadee songs transmitted through different habitats (disturbed and undisturbed) at three different frequencies (low, medium, high). Values are averaged over all distances (5, 25, 50, and 100m) and heights (1, 3 and 5 m). Error bars shown indicate standard error. b) Deviation of values from the stimulus ratios in disturbed and undisturbed habitats.

### *Frequency shifting in different habitats*

Because more high ranked birds in disturbed and low ranked birds in undisturbed habitats were recorded, the effect of rank on song frequency was tested. There was no influence of rank on frequency sung by low and high-ranking males in this population ( $U=44.000$ ,  $df=1$ ,  $N=21$ ,  $p=0.439$ ). There is however a significant trend in the average song frequencies of males in disturbed and undisturbed habitats ( $U=126.000$ ,  $df=1$ ,  $N=21$ ,  $p=0.024$ ). The average song frequency of males in disturbed habitats is lower than that of males in undisturbed habitats. To control for daily differences in environmental conditions, a Wilcoxon test for day was conducted for days were birds were recorded in both disturbed and undisturbed habitats. The difference in average song frequency in the different habitats continues to be significant ( $Z=1.995$ ;  $df=8$ ;  $p=0.05$ ) (figure 9).

## **Discussion**

### *Transmission Study*

The results from the transmission study indicate differential degradation due to frequency dependent attenuation and reverberation in disturbed and undisturbed habitats.

Lower frequency songs suffer less habitat-induced reverberation than higher frequency songs. Songs in disturbed habitat are longer than songs in undisturbed habitat, due to extra scattering at the end of the song. The denser vegetation in disturbed habitats as well as the heterogeneity in habitat types likely cause this extra scattering. By comparison, undisturbed habitats are characteristically homogenous and have less dense vegetation and therefore cause less scatter. Further, the loss of note duration at high frequencies can be attributed to a loss in glissando due increased scattering of the high frequency wavelengths.

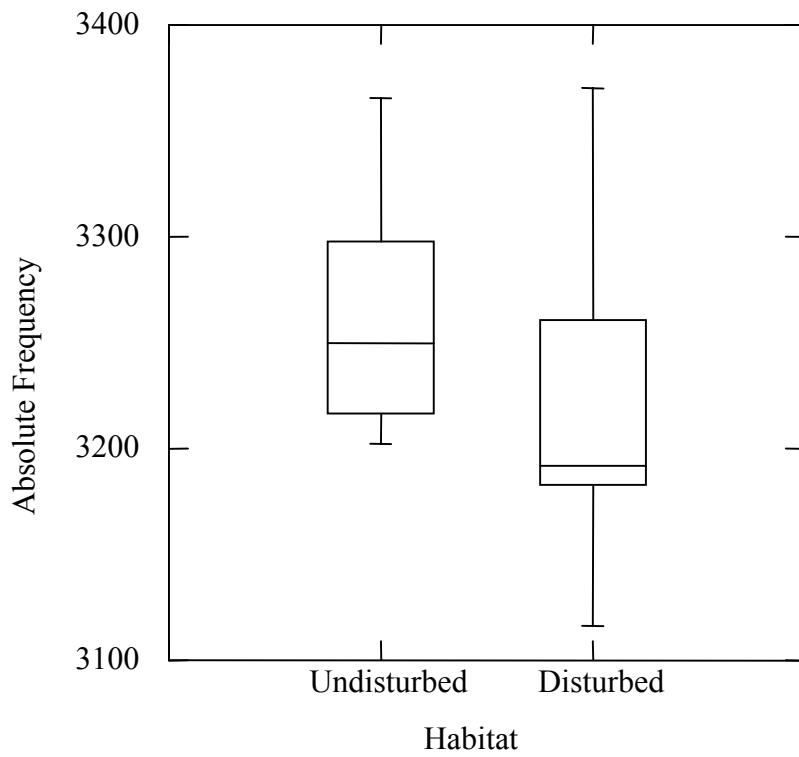


Figure 9: Difference in absolute frequency sung by black-capped chickadees in undisturbed and disturbed habitats. Difference tested using Mann Whitney U test ( $U=126.000$ ,  $df=1$ ,  $N=21$ ,  $p=0.024$ ).

The internote interval is a good indication of whether the change in duration is due to increased scattering at the end of the song, or due to a loss in the glissando at the beginning of the fee note. The longer internote interval at medium and high frequencies in undisturbed habitat indicates less scattering at the end of the fee note in this habitat. Hence, in disturbed habitats, the fee note is suffering greater glissando loss as well as greater scattering at the end of the song. Furthermore, the decreased duration of the fee note at high frequencies in both habitats is a function of not only decreased scatter but a disproportionately high a loss in glissando. Overall, the fee note suffers greater effects of reverberation in disturbed than undisturbed habitats, especially at high frequencies. The trend in frequency dependent reverberation is less strong in undisturbed habitats, indicating that scattering at the end of the fee note is less variable with changing frequencies.

Like in the fee note, there are differential effects of reverberation on the bee note, ultimately affecting the note's length. The increased duration of the bee note in undisturbed habitat is likely an indication of increased scattering at the end of the bee note (Morton, 1975) as the tonal nature of the bee note does not suggest loss of any song components. As was seen in the fee note, a significant decrease in the duration of the bee note occurs at high frequencies, in both disturbed and undisturbed songs. It seems that the greatest amount of reverberation in the bee note is occurring at medium frequency songs and in undisturbed habitat. However, at high frequencies, although not statistically significant, a trend of greater reverberation in songs in disturbed habitats is seen. Hence, at high frequencies, in both the fee and the bee note, reverberation effects are greater in disturbed habitats. Disturbed habitats are characterised by high amounts of vegetation and high heterogeneity, which are likely to cause this increased scattering. However, it remains that at low and medium frequencies, greater amounts of

scattering are occurring in undisturbed than disturbed habitat in the bee note. A possible hypothesis to explain this phenomena is there may not be as much selection on the production of a song that minimises the amount of scattering at the end of the bee note. Playback experiments that have been conducted on the response to changing song variables have shown response to earlier song parameters such as frequency ratios (Ratcliffe and Otter, 1996). The scattering of the bee note is the last variable of the song a receiving bird hears. Likely, by this point, the information portrayed by the song has been received, and therefore this parameter may be of lower importance in the transmission of the signal.

Intranote and internote frequency ratios,  $fee_{start}$  to  $fee_{end}$  and  $fee_{end}$  to  $bee_{start}$ , are indicators of frequency dependent attenuation of song (Fotheringham and Ratcliffe, 1995). The intranote ratio of  $fee_{start}$  to  $fee_{end}$  indicates the amount of glissando in the song, which is highly stereotyped in undegraded songs. Significant differences in this ratio exist between the two habitat types, with a significantly lower ratio in disturbed habitat. This indicates a greater glissando loss when song transmits through disturbed, rather than undisturbed habitat

Glissando loss has important fitness consequences because females show a lower response to songs with an altered glissando (Ratcliffe and Otter, 1996). If the glissando is lost, females may not perceive the altered song as an intraspecific signal (Ratcliffe and Otter, 1996). Accordingly, if males have a decreased ability to successfully advertise to females, their ability to form a pair bond may decrease. Hence, evolution and utilisation of a song that suffers the least loss in glissando with transmission through its habitat would be optimal.

The internote ratio of  $fee_{end}$  to  $bee_{start}$  is highly conserved in birds singing their song (Shackleton et al., 1992). Similar species and individual recognition cues as in the  $fee_{start}$  to  $fee_{end}$  ratio have been shown to exist in this internote frequency ratio. As with the intranote ratio

described above, a decreased receiver response is observed from songs when the internote ratio changes (Ratcliffe and Otter, 1996). In this study, the stimulus songs show a decreasing trend in the internote ratio with increasing frequency. However, when the songs were broadcast through the different habitats, an increase of internote ratio with frequency is evident. Low frequency songs in disturbed habitat and high frequency songs in undisturbed habitat compare best to the ratio of stimulus songs. The internote ratio is an indication of frequency dependent attenuation. Therefore, when compared to the stimulus song, songs transmitting through disturbed habitat suffer greater attenuation at high frequencies and lower attenuation effects at low frequencies. Conversely, songs transmitting through undisturbed habitat suffer less attenuation at high frequencies when compared to the stimulus song.

In conclusion, this study showed differences in the transmission of chickadee songs through disturbed and native undisturbed habitats. Overall, transmission quality decreases due to increased reverberation and attenuation in disturbed habitats. However, this decrease in quality is minimized in the transmission of low frequency songs. Conversely, the costs associated with transmitting high frequency songs in undisturbed habitat are less because of a) decreased amounts of habitat induced song degradation, and b) decreased required transmission distances.

#### *Frequency shifting in different habitats*

To optimise the production of advertisement song, optimal singing behaviour should reach as many females in as many territories as possible. As the dawn chorus is known to be a period of intersexual signalling in chickadees (Otter and Ratcliffe, 1993), there should be selection on males to modify their singing behaviour to maximise transmission. The strategy of maximum transmission distance becomes even more complex when the birds inhabit a mosaic of disturbed habitat, which can cause irregular spacing between territories of breeding black-capped

chickadees (Fort and Otter, personal communication). This irregularity in disturbed habitat causes the amount of suitable habitat to be spread unevenly through the landscape leading to variation in territory shape and size, further leading to the differences in singer and receiver distances. Song transmission in disturbed habitat results in increased frequency dependent attenuation and reverberation than song transmission through undisturbed habitat, especially at high frequencies. It is not surprising then that I found males in disturbed habitats opting to sing lower frequency songs than males in undisturbed habitats. Although high frequencies sung in undisturbed habitat attenuate more than low frequencies, the costs to the birds singing those high frequencies are lower than the costs to birds in disturbed habitat. This is because a bird's song in undisturbed habitat a) has lower overall degradation rates and b) may not need to transmit as far to reach receivers in neighbouring territories. Because of the associated costs of sound transmission through the different habitat types, it is an optimal strategy for birds to compensate for additional habitat induced degradation in disturbed habitats by producing songs that transmit maximally. By using the lower frequency songs in their repertoire in disturbed habitats, male black-capped chickadees may maximise the possible transmission distance of their song.

Differences in the song type and structure have been shown in birds occupying different habitats. However, these studies have traditionally examined interspecific differences in singing behaviour to describe optimal song structure with respect to habitat at the species level (e.g. Morton, 1975; Fotheringham et al., 1997). When differences in singing behaviour in different habitats were examined intraspecifically, it involved comparison between populations at a large geographic scale (Hunter and Krebs, 1979; Handford and Loughheed, 1991). This study is providing evidence that a population of black-capped chickadees within a centralised area are singing songs that transmit optimally through the habitat in which individuals hold territories. By

making these behavioural adjustments, it suggests that the birds are able to recognise the difference between the native undisturbed and disturbed habitats, unlike Handford and Loughheed's (1991) findings in rufous-collared sparrows (*Zonotrichia capensis*). Even after a habitat had been altered by disturbance, the sparrows continued to sing songs that were optimally adapted to the original native habitat. A possible explanation for this difference is a greater phenotypic plasticity in black-capped chickadees. Even if the rufous-collared sparrows were able to recognise the differences in habitats, they may not possess the plasticity to adjust their behaviour and sing songs that are optimally suited to the altered habitat, as chickadees do.

Finally, black-capped chickadees in disturbed habitats sing dawn choruses at significantly lower absolute frequencies than in undisturbed habitats. This suggests that chickadees are recognising and compensating for differences in habitat by singing to maximise the transmission of their song.

#### *Further study*

Differences in passerine singing behaviour with habitat modification remain largely unstudied at small population wide scales. Hence, subsequent studies should firstly attempt to replicate the results found here. Further, the mechanism of recognition between habitat types remains largely unstudied. Potentially, the recognition could be due to negative and positive feedback from singing at certain frequencies, implying a learning stage to optimal song production in different habitats. Also, chickadees and birds that do not compensate behaviourally for habitat differences in their singing, such as rufous-collared sparrows, should be compared for potential differences in phenotypic or genotypic plasticity.

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