Singing Higher to be Heard: The Effect of Anthropogenic Noise On Red-Winged Blackbird Song

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Abstract

Sounds are one of the most common means of communication and are essential to several species' survival and reproduction. The efficiency of acoustic signal transmission, and the ability of receivers to detect that signal, can be affected by ambient noise, such as that produced by human activities. Recent studies have suggested that animals alter the frequencies of their acoustic signals to minimize interference produced by anthropogenic noise. These changes could be a short-term adaptation to noise levels (behavioural) or a long-term adaptation in populations due to average anthropogenic noise levels (genetic change, phenotypic plasticity). A species' ability to adapt to anthropogenic noise may be a key factor in its success. It is therefore important to evaluate different species responses to noise for effective management. In this study I evaluated the effects of noise on Red-Winged Blackbird communication by assessing various parameters of their song when exposed and unexposed to noise in the vicinity of the Queen's University Biological Station, Ontario, Canada. First, I compared the songs of Red-Winged Blackbirds located in quiet marshes and along the roadside, during quiet periods. This allowed me to test if the songs in the two areas differed in the absence of anthropogenic noise, which would be suggestive of a longer-term change. The song of Red-Winged Blackbirds had increased signal tonality in areas affected by anthropogenic noise. Second, I compared the songs of Red-Winged Blackbirds from undisturbed marshes when exposed and unexposed to white noise that I broadcasted. Individuals exhibited increased signal tonality when temporarily exposed to noise, which suggests that Red-Winged Blackbirds are also capable of immediately altering their signals in response to noise. The song alterations I documented stress the importance of taking into account anthropogenic noise in conservation management. Conservation strategies such as the use of natural acoustic barriers sound adsorbent materials in new constructions, road closing during key seasons and special transportation in conservation areas are potential solutions.

Introduction

     The ways and the reasons for which animals communicate has continually sparked curiosity and fueled academic research. This research has lead to the discovery of a number of interesting tactics animals use to send signals. Examples include snakes producing vibrations (Burger, 1998), birds tapping their wings together (Hunter, 2008) and singing (Vehrencamp, 2000; Satischandra et al. 2010), and bees communicating the location of food by performing the waggle dance (Gil and Marco, 2010). In particular, research has shown that communication is often essential for reproduction and survival (Gorissen et al. 2006). For example, a closer look into the function of birds' vocalizations and songs reveals their importance in territory defense (Sogge 2007), mate attraction and mating decisions (Saether, 2002; Catchpole and Slater 1995), signaling predator presence (Fallow and Magrath 2010), and even expressing nutritional needs (Godfray, 1991; Ellis et al. 2009).

     The use of sounds is one of the most common means of communication observed in animals (Laiolo 2010). When an animal sends an acoustic signal into its environment, it must ensure that the sounds it produces are detected and recognized by the receiver for communication to occur (Park et al. 2010). The efficiency of communication can be affected by 1) signal production (e.g., signal structure, amplitude, directionality, etc.), 2) signal transmission (e.g., humidity, ambient noise, topography, etc.), and 3) signal perception (sensitivity, neuronal processing, appropriate behavioural response, etc.) (Wiley and Richards, 1982; Bradbury and Vehrencamp, 1998). A particularly well-studied example of a factor that impacts signal transmission is tree cover. Tree cover attenuates sound propagation by scattering soundwaves (Bullen and Frickle, 1982). This can favour the use of lower frequency vocalizations, which travel farther and which are less subject to attenuation through scattering in

forests (Marten and Marler, 1977; Forrest 1994), as well as narrow band signals (i.e. tonal signals), which also travel farther and suffer less distortion than frequency-rich signals in forests (Bradbury and Vehrencamp, 1998). Increased tree cover can also result in signals of longer duration, which will help increase propagation (Ey et al., 2009; Kirschel et al. 2009).

Ambient background noise is another factor that can affect signal transmission and recognition through acoustic masking. The detectability of a signal by a receiver is dependent on its signal-to-noise ratio. For a given frequency-band, signals with a signal-to-noise ratio (SNR) below a certain threshold cannot be detected by the receiver (Marten and Marler, 1977). Several species exhibit adaptations that increase their signal-to-noise ratio, thus diminishing the effects of acoustic masking on their signals. There are four main mechanisms by which animals do this. First, animals can adjust the timing of their signals. Many species (anurans, katydids, and others) use temporal adjustment and thereby avoid overlap with other species' signals (Greenfield, 1994). Second, animals can adjust the amplitude of their signals during noisier periods, thus improving their signal-to-noise ratio (Pytte et al. 2003). Third, animals can use a different type of signal, with better transmission properties, in periods with higher levels of environmental noise (Dunlop et al. 2010). Fourth, animals can adjust the pitch (frequency (Hz)) of their signals. Per example, Green Hylia (*Hylia prasina*) adjust the pitch of their songs to avoid interference by insect sounds (Kirschel et al. 2009). Certain anurans located close to streams use ultrasonic frequencies to communicate, thereby avoiding frequency interference with the broadband background noise produced by the streams (Feng et al. 2006).

Sounds produced by human activity can be another important source of ambient noise. As human population and urbanization continue to increase (United Nations, 2008) anthropogenic noise is likely to reach more animal populations. Although time has allowed animals to evolve several adaptive mechanisms to compensate for environmental noise, rapid changes in acoustic

environments due to human activity could challenge the adjustment potential of communication systems (Lengagne, 2008). Anthropogenic noise might affect breeding opportunities for species that are incapable of adapting their signals to acoustic interference, thereby contributing to a decline in density (Slabbekoorn and Peet 2003). Species' persistence in urban areas, as well as those impacted by anthropogenic noise, such as roadways, construction sites, airports, etc., requires the capability to tolerate or to adapt to environmental noise (Jung and Kalko, 2010).

A number of species exhibit compensation mechanisms that increase the probability of signal transmission and detection in environments affected by anthropogenic noise (Laiolo, 2010). Some species wait until quieter, unaffected periods to produce signals (Lengagne, 2008; Penna and Hamilton-West, 2007; Fuller et al. 2007). Others exhibit active noise-dependant change in various characteristics of their signals. For example, an increase in the amplitude of the signals produced in noisy environments (the Lombard effect) has been documented in taxa ranging from marine and terrestrial mammals, to amphibians, to birds, thus increasing the efficiency of their signaling (Parks et al. 2010; Brumm et al. 2004: Brumm and Todt, 2002; Brumm et al. 2009; Penna and Hamilton-West, 2007; Egnor and Hausser, 2006). Others prolong the duration of their signals during noisy periods, thus increasing its detection probability (Brumm et al. 2004).

Another increasingly documented anthropogenic noise-dependant compensation mechanism is a shift in the frequencies of animals' acoustic signals (Laiolo, 2010). Some species achieve this by producing syllables or song-types with higher frequencies in noisy environments (Bermudez-Cumatzin et al. 2008; Halfwerk and Slabbekorn, 2009). Others, including dolphins, birds and amphibians, demonstrate a spectral shift of a given signal when in a noisy environment (Wood and Yezerinac, 2006; Slabbekoorn and Peet, 2003). Typically, this shift is toward higher frequencies, thereby minimizing the signals' overlap with anthropogenic noise, which is

predominately concentrated in lower frequencies (Wood and Yezerinac, 2006).

The development of these vocal changes could occur via a number of mechanisms and at different time scales. Populations in noisy areas versus quiet ones might evolve different genetically-based signaling strategies that are each adapted to their local noise environments. These populations may also experience long-term adjustments due to phenotypic plasticity, through mechanisms such as passive acquisition of the portions of signals that are efficiently transmitted in spite of noise and, selective depletion of signals or portions of signals that are masked by noise. Finally, these changes could also occur as short-term behavioural adjustments to current noise levels, such as documented in Chiffchaffs (*Phylloscopus collybita*) (Verzijden et al. 2010; Patricelli and Blickley, 2006; Halfwerk and Slabbekoorn, 2009; Parris et al. 2002).

The ability to adapt to noise may be a key factor in the success of species that are affected by urbanization and human activity (Slabbekoorn and Peet, 2003; Tyack, 2008). Thus, evaluating different species' responses to ambient anthropogenic noise will become increasingly important to undertake effective conservation management and planning (Lengange, 2008). Here, I use Red-Winged Blackbirds to test the hypothesis that anthropogenic noise effects temporal and spectral characteristics of bird song.

Red-Winged Blackbirds (*Agelaius phoeniceus*) are an ideal species for studying the effects of anthropogenic noise on signaling strategies because they commonly vocalize in marshes found along noisy roads (Camp and Best, 1994). They have a repertoire of up to 8 variants of the same basic song-type, known as the "conkaree" (Kroodmsa and James, 1994), spanning between 1-5 kHz, which typically consist of a series of introductory syllables followed by a trill (Beletsky et al. 1980). The function of the introductory syllables of the Red-Winged Blackbird song remains uncertain, although it is suspected that they might serve as notes that help the singing bird acquire the attention of other birds (Smith et al. 1979). The trill is known to

facilitate species recognition and is likely the part of the song that conveys the most meaningful information (Beletsky et al. 1980). For this reason, this study will focus on the trill of the Red-Winged Blackbird song.

One particularity that distinguishes the Red-Winged Blackbird trill from the signals evaluated in other anthropogenic noise and frequency content studies is its broadband nature (Patricelli and Blickley, 2006). Studies previously conducted in acoustic laboratories have revealed that it is more difficult to detect sounds with a greater bandwidth (i.e. sounds that are less tonal; Lohr et al. 2003). Frequency-rich signals suffer greater distortion, particularly in the high frequency components, and do not travel as far as narrow band signals (Bradbury and Vehrencamp, 1998). In habitats with higher levels of natural noise (e.g., tropical ecosystems), some species have been found to converge on songs that have primarily pure tones or narrow frequency bands (Dubois and Martens, 1984; Slabbekoorn et al. 2002). However, this has yet to be documented in habitats disturbed by anthropogenic noise (Patricelli and Blickley, 2006). In the case of a broadband signal such as the Red-Winged Blackbird trill, one might then expect to observe a shift towards a more tonal trill in environments disturbed by anthropogenic noise in order to improve signal transmission.

In the first experiment of this study, I tested whether song structure was adjusted on the long-term by comparing the songs of populations living in low and high ambient anthropogenic noise. I predicted that the trill of Red-Winged Blackbirds along the roadside (high ambient anthropogenic noise) would have a significantly longer duration, more tonal energy distribution and a higher minimum frequency compared to the trill of Red-Winged Blackbirds found in marshes (low ambient anthropogenic noise). In the second experiment, I tested whether song structure was adjusted in the short-term by comparing the songs of Red-Winged Blackbirds from quiet marsh locations under normal conditions and when presented with low-frequency noise. I

predicted that the trill of Red-Winged Blackbirds would have a significantly longer duration, more tonal energy distribution and a higher minimum frequency when they were exposed to noise.

Materials and Methods
Study Area

I collected data on rainless mornings in May and June 2010 in the vicinity of Queen's

University Biological Station (44°34'0"N 76°19'26"W), 100 km south of Ottawa, Ontario,

Canada.

Long-Term Adjustment Experiment

In this experiment I compared the songs of Red-Winged Blackbirds located in quiet

marshes and in marshes along a secondary highway (Highway 15) during quiet periods. This

allowed me to test if the two populations' songs differed in the absence of anthropogenic noise,

which would be suggestive of a longer-term change due to genetic differences or phenotypic

plasticity.

Experimental Design

I recorded 3-12 songs for each of 32 males distributed across 4 marshes by the highway

(each separated by a minimum of 2 km) and an additional 32 males that were distributed across 4

quiet marshes (each separated by a minimum of 2 km). To minimize the chance of recording the

same bird on more than one occasion, recordings were made by systematically circling a marsh

or by progressing north to south along the highway. Individuals within a given marsh were

distinguished by identifying distinct visual cues such as plumage coloration, missing feathers,

and markings on feet and bills (Lank and Dale, 2001; Bretagnolle et al. 1994). Site types were

alternated daily.

Ambient Noise

The objective of this experiment was to compare Red-Winged Blackbird populations

located in areas affected and unaffected by anthropogenic noise. It was therefore important to

compare noise levels at both site types (roadside vs. marsh). A roadside census of traffic on

Highway 15 conducted by the Ministry of Transportation of Ontario (MTO) shows a high number of cars along the highway (Figure 1A). When traffic density is at its very low there is still approximately 1 car every 3 minutes. When traffic density is at its peak there are as many as 4 cars per minute.

The fairly constant presence of cars along Highway 15 suggests that roadside sites are generally noisier than the quiet marsh sites. To ensure that the levels of noise differed between sites that I qualified as exposed and unexposed to anthropogenic noise, I measured average amplitude of ambient noise at both site types and conducted counts of cars passing by to measure traffic density along the highway.

Over the course of 1 morning, I went to 8 locations at which I had previously made recordings (4 quiet marshes, 4 marshes along the roadside). At each of these locations I measured the amplitude of ambient noise at 15-second intervals for a 5-minute period using a Radio Shack Sound Pressure Level (SPL) Meter. Roadside and marsh locations were alternated after every second trial to control for temporal variation in noise.

It was also important to verify that traffic noise has the potential to cause acoustic masking of Red-Winged Blackbird trills. For this reason, I compared typical spectrograms and power spectrums of a Red-Winged Blackbird song and traffic noise to evaluate the potential for overlap (Figure 3).

Behavioural Flexibility Experiment

In this experiment I compared the songs of Red-Winged Blackbirds from undisturbed marshes when they were exposed and unexposed to white noise that I broadcasted. I evaluated the Red-Winged Blackbirds' capability to shift the spectral structure of their song in response to noise by recording a series of individuals when exposed to ambient noise.

Experimental Design

I presented a given subject with 2 sequential playback treatments over the course of approximately 6 min, while simultaneously recording his vocal response. The two treatments were run back-to-back. This procedure minimized variation in the subject-observer distance between the 2 treatments. For each trial I would wait until the individual sang a minimum of 3 songs and a maximum of 7 before beginning the next treatment. The order of the treatments was randomized for each subject. Individuals were distinguished in the same fashion as in the previous experiment.

I used artificial white noise for this experiment because unlike traffic noise, which is inextricably associated with trills, it had a clear upper limit that was lower than the trill and could hence be removed completely in the analysis. The first treatment was a control treatment, during which I played no background noise. During the second treatment I broadcasted white noise spanning between 0-1830 kHz (overlaps with some introductory syllables of the song, but not with the trill) from a Califone VoiceSaver PA-285 speaker. The amplitude was set to 89 dB, at 1 m from the speaker, which is comparable to noise levels used in similar studies (Verzijden et al., 2010). Furthermore, this compares to the typical amplitude of a car (79.43 ± 0.60dB) or truck (90.00 ± 0.00dB) that I recorded on the highway, at approximately 2 m using the SPL meter. The broad-spectrum white noise used in the 2nd treatment was produced in Adobe 2.0 and then band pass filtered using Raven Pro 1.3.

Recordings

Recordings for all experiments were made using a shotgun microphone (Audio-Technica, model 8015b) with a foam windshield connected to a digital recorder (Marantz PMD 660, format WAV, sampling rate 44.1kHz, bit-rate 16 bits). For every distinct song recorded I visually estimated the distance between the recorder and the bird (mean: 20 ± 1 m; range, 4-50 m).

Throughout the collection of data, wind speed reached a maximum of 13 m/s (Queen's University Biological Station weather station data).

Song Measurements

All recordings were analyzed using Avisoft SASLab Pro (Version 4.38). Each song was filtered using a 2 kHz high pass filter, which removed background noise without removing components of the song, and was then normalized to a peak amplitude of 0 dB. Spectrograms were made with a Fast Fourier transformation size of 1024 points, an overlap of 87.5% and using a Blackmann window, which resulted in a frequency resolution of 43 Hz and a temporal resolution of 14.5 ms.

I used Avisoft's "automatic parameter measurement" feature to select automatically the trill portion of each song. To determine the best fit parameters to detect automatically the trill I tested several setting combinations on a sub-set of songs and retained the most reliable threshold (-15 dB) and holdtime (10 ms) for the subsequent analysis of all songs. In spite of the fact that all the threshold and holdtime combinations I tested did not allow accurate automatic detection of the trill the majority of the time (likely due to frequent juxtaposition of an introductory syllable to the trill), I used the automatic detection when possible to avoid measurement bias and be able to select the best fit measurement settings without bias. In cases where the automatic detector was unable to detect accurately the trill I manually selected the beginning of the trill based on its distinct visual, audible and temporal characteristics and let Avisoft detect the remaining portion of the trill. Overall, this type of manual selection was required 89% of the time.

I took a series of spectral measurements from the trill of every song. Because the trill contains virtually no frequency modulation, I based each measure on the average of the entire trill. Measurements included duration, minimum frequency, maximum frequency, bandwidth (Figure 2), and energy distribution (25th, 50th and 75th percent quartiles as well as entropy).

Minimum frequency, maximum frequency, and bandwidth were based on a threshold of -10 dB. The quartiles characterize the energy distribution across the spectrum by dividing it into four parts that are equal in terms of spectral energy. Entropy is a quantification of the randomness of the sounds recorded: sounds that are more tonal have a smaller entropy value (a pure tone would have an entropy of 0, whereas white noise would have an entropy of 1). Although most studies of this nature also include measurements of the peak frequency in their study this measurement is less reliable for the Red-Winged Blackbird trill because it is broadband with no obvious frequency of maximum amplitude (see Figure 3A and C).

In the Long-Term Exposure Experiment for roadside recordings, I excluded any songs for which I could hear traffic noise in the background or see traffic noise in the spectrograms from the analysis. This allowed me to assess population differences in the absence of anthropogenic noise (long-term changes).

The systematic difference in background noise in the Behavioural Flexibility Experiment had the potential to induce measurement artifacts. I validated the measurement methodology of the Behavioural Flexibility Experiment by comparing the broadcasted songs of individual Red-Winged Blackbirds when exposed and unexposed to broadcasted noise. I selected 3-5 high quality songs of 20 individuals recorded during the Long-term Adjustment and Behavioural Flexibility experiments and normalized their peak amplitude to 0 dB using Sample Manager (Version 3.2.2). I broadcasted these songs from a Califone Voice Saver PA-285 setting their amplitude to 85dB spl at 1 m distance (using a Radio Shack SPL meter), to mimic the natural amplitude of songs (Patricelli et al. 2007). I then recorded each of these songs twice, exposing them to two different treatments: one with broadcasted background noise (broadband noise band pass filtered from 0-1830Hz) and one without background noise. I used the same experimental

set-up as the Behavioural Flexibility Experiment. I alternated the order of treatments after every 2 individuals.

Statistical Analyses

Statistical analyses were conducted in SPSS version 19.0. Several of the song characteristics I measured were highly correlated, thus, some needed to be eliminated. Within pairs of highly correlated variables, I retained the variable that had the highest simple correlation with the variable of interest. This left me with 50th and 75th percent quartiles, the minimum and maximum frequency, the entropy and the duration. For each experiment, I constructed separate Linear Mixed Models (LMM) for each of the measured song characteristics by entering them as the response variable. In the Long-Term Adjustment experiment the variable "site type" was included as a fixed factor, and the distance between the subject and recorder was included as a covariate with random effects. I accounted for repeated measurements of the same individual by including "individual" as a random subject factor. For the Behavioral Flexibility and Validation experiments I used the same models as in the previous experiment but replaced "site type" by "treatment type" as the fixed factor. I re-ran all models removing distance as a covariate and statistical significance remained the same for all variables of interest.

Assumptions of normality and homoscedacity were verified by inspecting histograms. I applied a cubic transformation to the entropy variable from the Long-Term Adjustment experiment to meet the model's assumptions. For all analyses results were considered significant when $p < 0.05$ and trends were considered when $0.05 < p < 0.1$. All means are reported ± standard error. I used Cohen's d as a measure of effect size in LMMs where values below 0.2 indicate a small effect size, 0.5 a medium effect size, and 0.8 a large effect size (Cortina and Nouri, 2000).

Results

Long-Term Adjustment Experiment

Ambient Noise

The mean amplitude of roadside locations (65.8 ± 1.8 dB) and marsh locations (51.7 ± 0.1 dB) showed clear differences (Figure 1B). These measurements also allowed me to measure traffic density at roadside sites which was a minimum of 1 car every 2 minutes.

A closer examination of a typical RWBB trill and typical traffic noise reveals the potential for acoustic masking (Figure 3). This implies that anthropogenic noise has the potential to mask Red-Winged Blackbird songs.

Songs

I analyzed 436 songs of 64 male Red-Winged Blackbirds (32 per site type). Once roadside songs during which a car was passing were excluded, 344 songs remained for statistical analysis (63 individuals, 32 in quiet marshes and 31 in roadside marshes). Duration of the trills did not significantly differ between habitat types ($F_{1, 53.7}$ = 1.68, p = 0.201, d = -0.44). Habitat type had a significant effect on 2 of the 5 spectral measurements evaluated. The maximum frequency of the trill was significantly lower in birds near the road ($F_{1, 54.2}$ = 10.456, p = 0.002, d = 0.81). Minimum frequency was not significantly affected by habitat type ($F_{1, 54.2}$ = 2.595, p = 0.113, d = 0.41). The energy in the 50% quartile tended to be concentrated in lower frequencies in birds along the road ($F_{1, 61.0}$ = 3.095, p = 0.084, d = 0.44) and the energy in the 75% quartile was concentrated in significantly lower frequencies in birds along the road ($F_{1, 59.3}$ = 4.413, p = 0.04, d = 0.53). Furthermore, the entropy of trills from birds near the road was significantly lower than in marshes ($F_{1, 58.6}$ = 4.599, p = 0.037, d = 0.54) (Figure 4).

Behavioural Flexibility Experiment

I analyzed 139 songs of 20 male Red-Winged Blackbirds (70 with interference, 69

without interference). Duration of the trill was not significantly influenced by the broadcast of noise ($F_{1, 119.0} = 0.004$, p = 0.960, d = 0.02). Noise had a significant effect on 3 of 5 spectral characteristics measured. Minimum and maximum frequency were not significantly affected by the interference noise (minimum frequency: $F_{1, 119.7} = 0.632$, p = 0.428, d = 0.25; maximum frequency: $F_{1, 119.7} = 0.294$, p = 0.589, d = 0.17). The energy distribution was concentrated in significantly lower frequencies in the 50% and 75% quartiles (50% quartile: $F_{1, 119.1} = 10.126$, p = 0.002, d = 1.01; 75% quartile: $F_{1, 119.2} = 4.413$, p = 0.038, d = 0.66). Furthermore, the entropy was significantly lower in the presence of noise ($F_{1, 119.7} = 7.734$, p = 0.006, d = 0.88) (Figure 5). To ensure the results of this experiment were not due to measurement artifacts, I analyzed 138 songs of 20 male Red-Winged Blackbirds (69 while broadcasting noise and the same 69 recordings without noise). Treatment type had no significant effect on any of the songs' temporal or spectral characteristics (duration: $F_{1, 117.1} = 0.004$, p = 0.951, d = 0.019; maximum frequency: $F_{1, 117.0} = 0.061$, p = 0.805, d = 0.078; minimum frequency: $F_{1, 117.4} = 0.059$, p=0.808, d = 0.077; 50% quartile: $F_{1, 116.8} = 0.718$, p = 0.398, d = -0.27; 75% quartile: $F_{1, 117.2} = 0.679$, p=0.412, d = 0.27; entropy: $F_{1, 117.2} = 0.591$, p=0.444, d = 0.24).

Discussion

I found noise dependent variation in Red-Winged Blackbird song when comparing songs that were sung in generally quiet areas versus generally noisy areas that were temporarily quiet. This suggests that noise levels induce a fairly long-term change upon this species' signals, due to genetic change or to phenotypic plasticity.

Song structure between the two site types (roadside marsh and quiet marsh) varied in terms of tonality. Overall, Red-Winged Blackbirds located along the highway had trills with a significantly smaller bandwidth (significant decrease in maximum frequency and no significant change in minimum frequency) and significantly more tonal energy distribution. Laboratory studies have shown that songs with larger bandwidths (less tonal) are more difficult to detect during noisy periods (Lohr et al. 2003). In fact, this type of association between bandwidth and noise has previously been detected in natural environments (Dubois and Martens, 1984). This might be one of the reasons for which I observed this type of difference between birdsong in habitats affected and unaffected by anthropogenic noise.

I also found noise-dependant song structure variation in Red-Winged Blackbirds from quiet marsh areas that are unexposed to regular anthropogenic noise. This suggests that Red-Winged Blackbirds are also capable of an immediate behavioural adjustment to noise. Overall, Red-Winged Blackbirds exposed to noise showed more tonal signals by concentrating their trill into lower frequencies (as shown by the decreased entropy and 50% and 75% quartiles). The background noise found in these recordings could have produced measurement artifacts. The validation experiment I conducted allowed me to confirm that the experimental methodology and measuring techniques that were used did not induce artifacts in the results obtained from this experiment.

When considering the temporal aspect of all Red-Winged Blackbird trills evaluated in this study, my results do not suggest that there are any significant differences in trill duration due to noise. We might have expected birds from generally noisy areas (roadside), or individuals that were exposed to temporary noise to prolong their songs to increase the transmission, and consequent detection, of their signals during noisy periods (Brumm et al. 2004; Warren et al. 2006; Nemeth et al. 2006). While temporal adjustment in song can procure an advantage in certain environments, these types of adjustments represent a trade-off between associated energetic costs (Fernandez-Juricic et al. 2005). The advantages related to signal transmission due to an increased trill duration in noisy environments may not be important enough for Red-Winged Blackbirds located along the highway to exhibit these changes.

The overall trend of adjustments toward lower frequencies observed in this study differs from results found in most studies concerning this topic. Nonetheless, other studies have documented a similar tendency toward lower frequencies in environments affected by anthropogenic noise (Morisaka et al. 2005). This type of adjustment might be explained by a number of factors. Lower frequencies travel farther and attenuate less than higher ones (Bradbury and Vehrencamp, 1998; Forest, 1994), thus creating an important incentive for animals to adjust their signals in this direction in noisy environments. While this type of adjustment is less intuitive considering the potential overlap between traffic noise, which is concentrated in low frequencies, and birdsong, it is possible that the decreased attenuation and longer travelling distance of lower frequencies are advantageous for species such as the Red-Winged Blackbird because their trill spans between approximately 2.75-5kHz, and traffic noise is primarily concentrated below 3kHz (Wood and Yezerinac, 2006).

Overall, my results demonstrate a difference between the songs of Red-Winged Blackbirds affected and unaffected by anthropogenic noise. These types of changes can be costly

for the species experiencing them (Parks et al, 2010; Tyack, 2008). Although vocal adjustments might allow better propagation and decreased degradation, these altered signals may decrease recognition by females or even be less attractive to them, thus leading to a decrease in mating success. If the way conspecifics interpret signals does not change alongside vocal adjustments, individuals that have altered their signals may be at a disadvantage. For example, males that have adjusted their signals may be interpreted as less threatening by conspecifics in threat displays (Patricelli and Blickley 2006). These differences may also eventually prevent mate recognition between populations that are regularly exposed to anthropogenic noise and those that are not, potentially representing the first steps of speciation (Wood and Yezerinac, 2006; Slabbekoorn and Peet, 2003; Warren et al. 2006). In addition, certain individuals may not be capable of adapting to anthropogenic noise, potentially leading to a decline in population size (Slabbekoorn and Peet, 2003). Noise may also have other adverse affects on species ecology. For example, it has been known to cause negative effects on foraging activities in bats (Schaub et al. 2008). Noise has also been documented to affect reproductive success of females, causing smaller clutches and decreasing the number of fledglings (Halfwerk et al. 2010).

We need to consider anthropogenic noise in conservation management. Levels of noise in protected areas as well as areas with species at risk must be considered for effective conservation management (Barber et al. 2010). Authorities might consider implementing various strategies to reduce anthropogenic noise in natural habitats such as creating acoustic barriers with trees along highways and around airports (Ozer et al. 2008). In urban areas we might consider using more absorbent ground covers when building, and even building sound barriers in key areas (Slabbkoorn and Rimpester 2008). Another strategy, although untested, might be to close key roads during breeding seasons (Parris and Schneider, 2009). We might also consider limiting transportation through nature reserves to sound-efficient buses (Laube and Stout, 2000), or

creating noise taxes during breeding seasons according to car type and speed, which are factors that affect noise levels (Makarewicz and Kokowski, 2007). Conservation authorities should also consider using the GIS resources available to map the effects of noise when planning management. These resources allow integration of distances, barriers, habitat types and other spatial components to calculate sound propagation and would thus allow us to create effective models to test conservation strategies before implementing them (Konstantinidis, 2005).

Although my results suggest the adaptations to noise that we observed could procure communication benefits, some recent research suggests that the signal transmission advantages procured from frequency variations are not sufficiently effective to mitigate anthropogenic noise masking (Nemeth and Brumm, 2010). Future studies evaluating the benefits of pitch (frequency) variation on signal transmission, and the response of conspecifics, would help clarify this topic. Future studies on Red-Winged Blackbirds and other species and noise could also consider looking at the amplitude and frequency modulations of songs in areas affected by anthropogenic noise and as an immediate response to noise, because these are other types of effective noise dependant adaptations previously observed in the environment that were not explored in this study (Bradbury and Vehrencamp, 1998).

Overall, my results suggest that there are modifications to birdsong when populations live in areas affected by anthropogenic noise. Acute noise also seems to be capable of inducing an immediate behavioural response that shows similar spectral effects.

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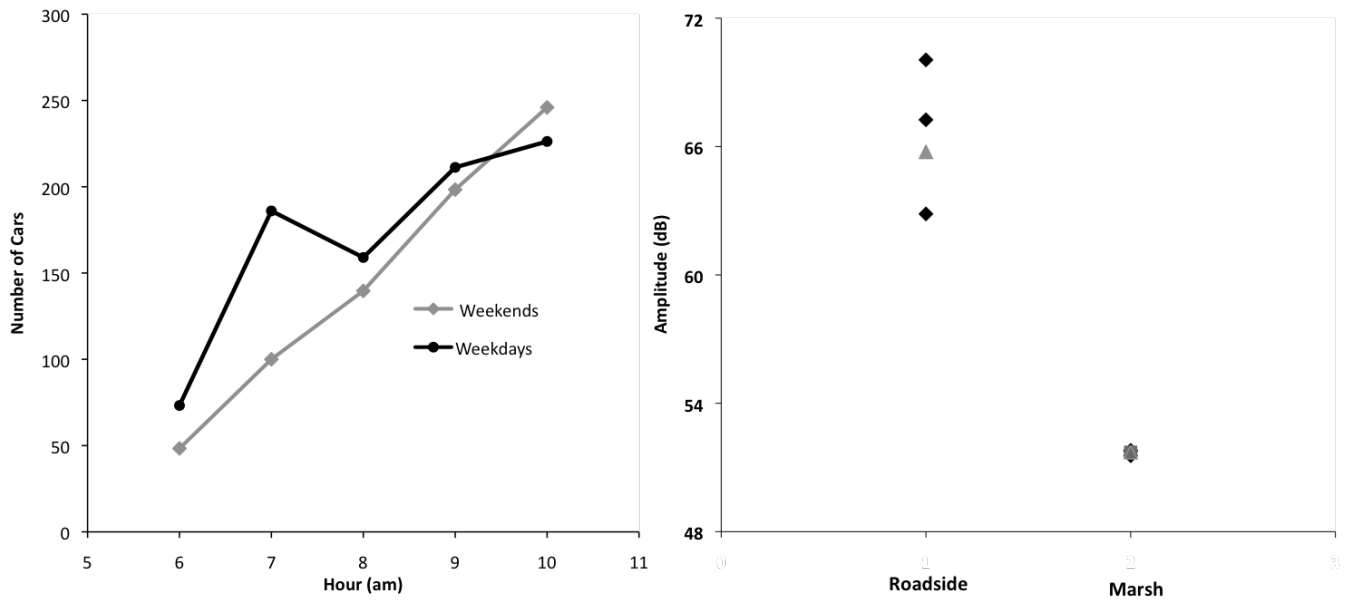
Figures

Figure 1. The degree of noise on the roadside and at marshes without anthropogenic disturbance. Panel A: The incidence of vehicles passing by per hour on Highway 15 (Ontario, Canada), at the intersection of Road 8, between 6am and 11am, as accounted for by the MTO over a week in April (n=1). Panel B: Mean amplitude of ambient noise at 4 locations on the roadside and at 4 locations marshes (black diamond) and, mean amplitude of all roadside locations and all marsh locations (grey triangle).
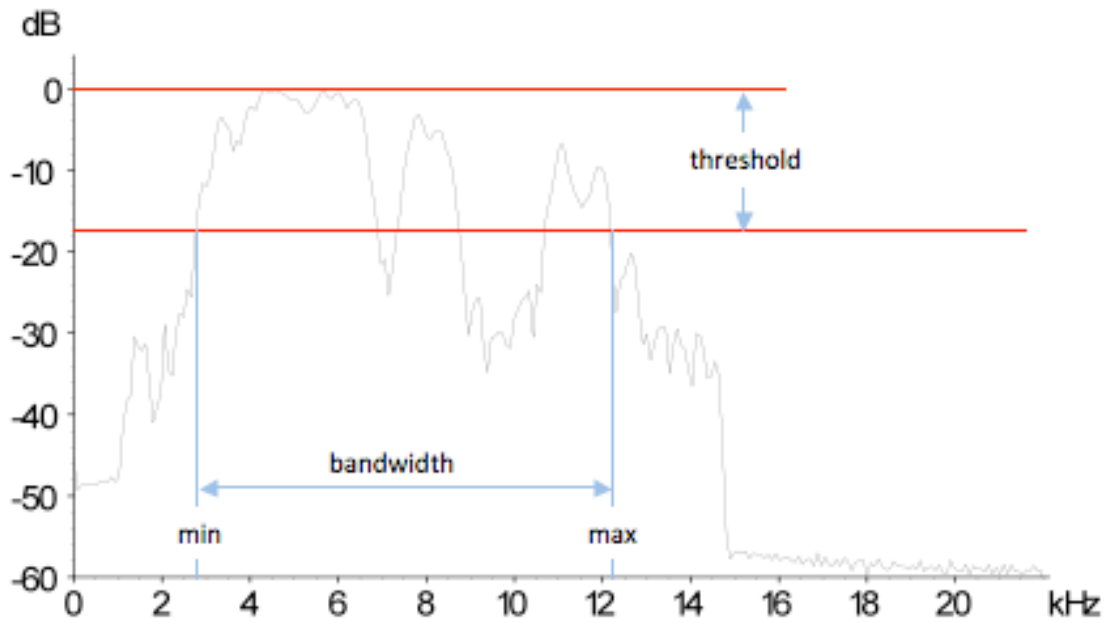
Figure 2. Defining spectral measurements. Minimum and maximum are defined in relation to the threshold set (-15dB in the case of this study) and result in a bandwidth spanning between their values. Note: This figure was taken from the Avisoft-SASLab Pro software manual, version 5.1 (Avisoft Bioacoustics 2010).
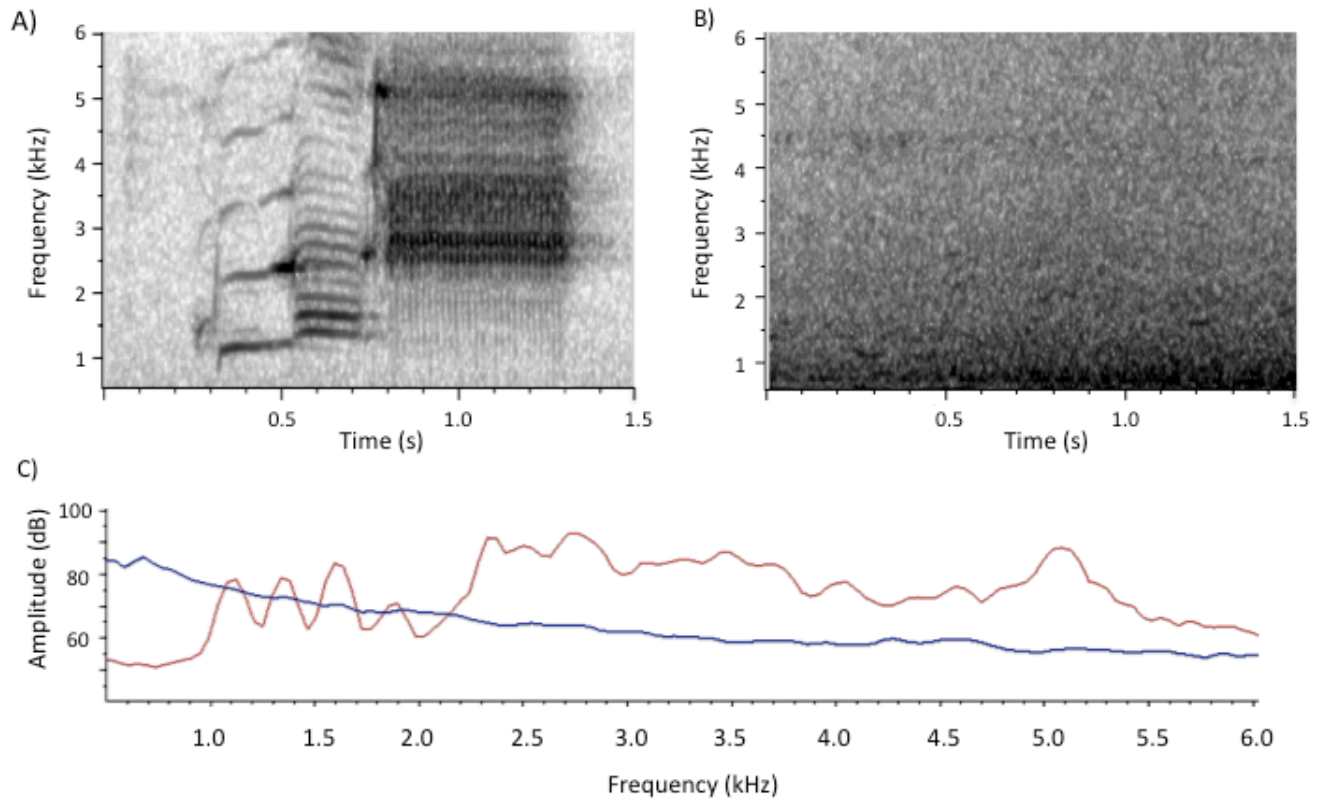
 Figure 3. The overlap between a typical Red-Winged Blackbird song and the typical sound produced by traffic noise. Spectrograms of the song (panel A) and the traffic (panel B) were produced with a Fast Fourier transformation size of 1024, an overlap of 87.5% (a brightness of 43 and contrast of 50) and, using a Blackmann window, which resulted in a frequency resolution of 43Hz and a temporal resolution of 14.5ms. Power spectrums (panel C, song in red and traffic in blue) were based on the average of the Red-Winged Blackbird song and traffic noise recordings. The various parts of this figure were aligned and combined into 1 figure using Microsoft PowerPoint 2008.
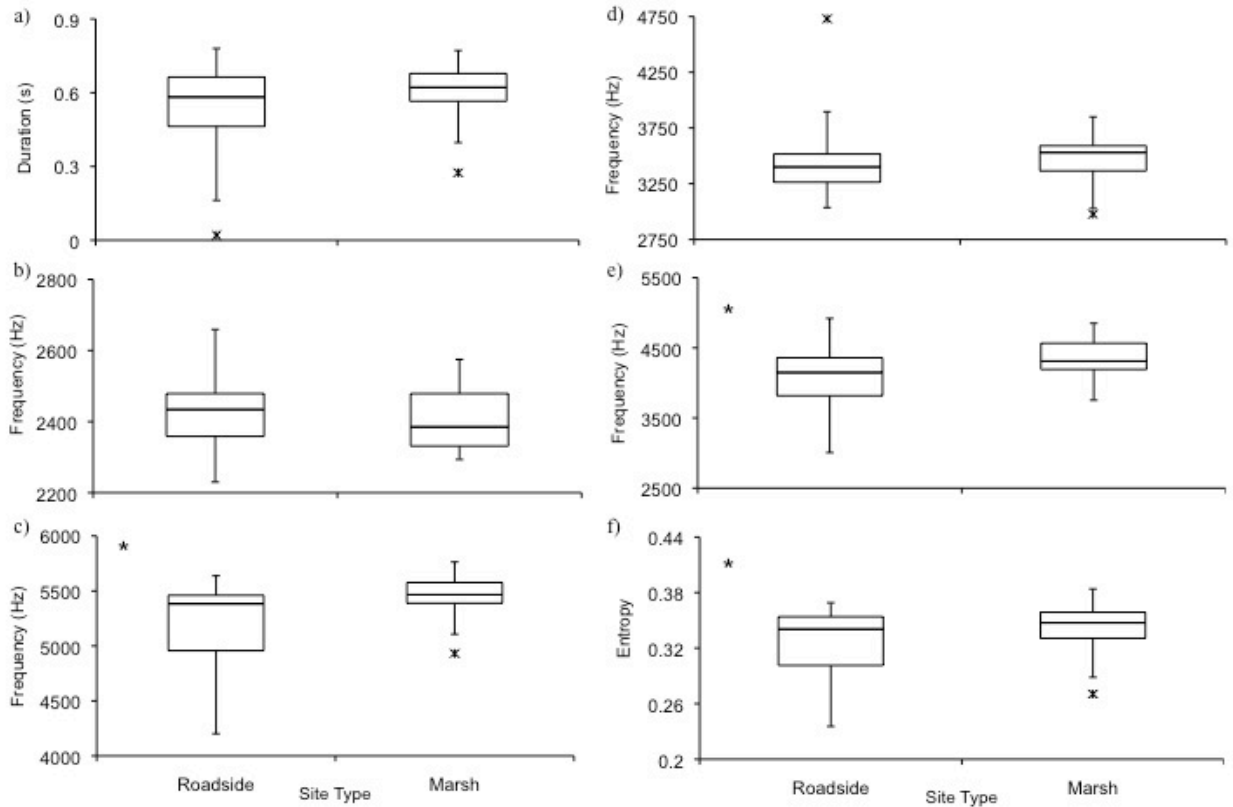
Figure 4. Temporal and spectral characteristics of the Red-Winged Blackbird trill in habitats disturbed and undisturbed by anthropogenic noise. The box plots show medians (black line), interquartile range (box) and, maximum and minimum (whiskers) of the song parameters of the birds recorded along the roadside (n=31) and in quiet marsh habitats (n=32) for: (a) duration.,(b) minimum frequency, (c) maximum frequency, (d) 50% quartile, (e) 75% quartile and, (f) entropy. Song parameters which differ significantly are indicated in the top left corner of graphs (*).
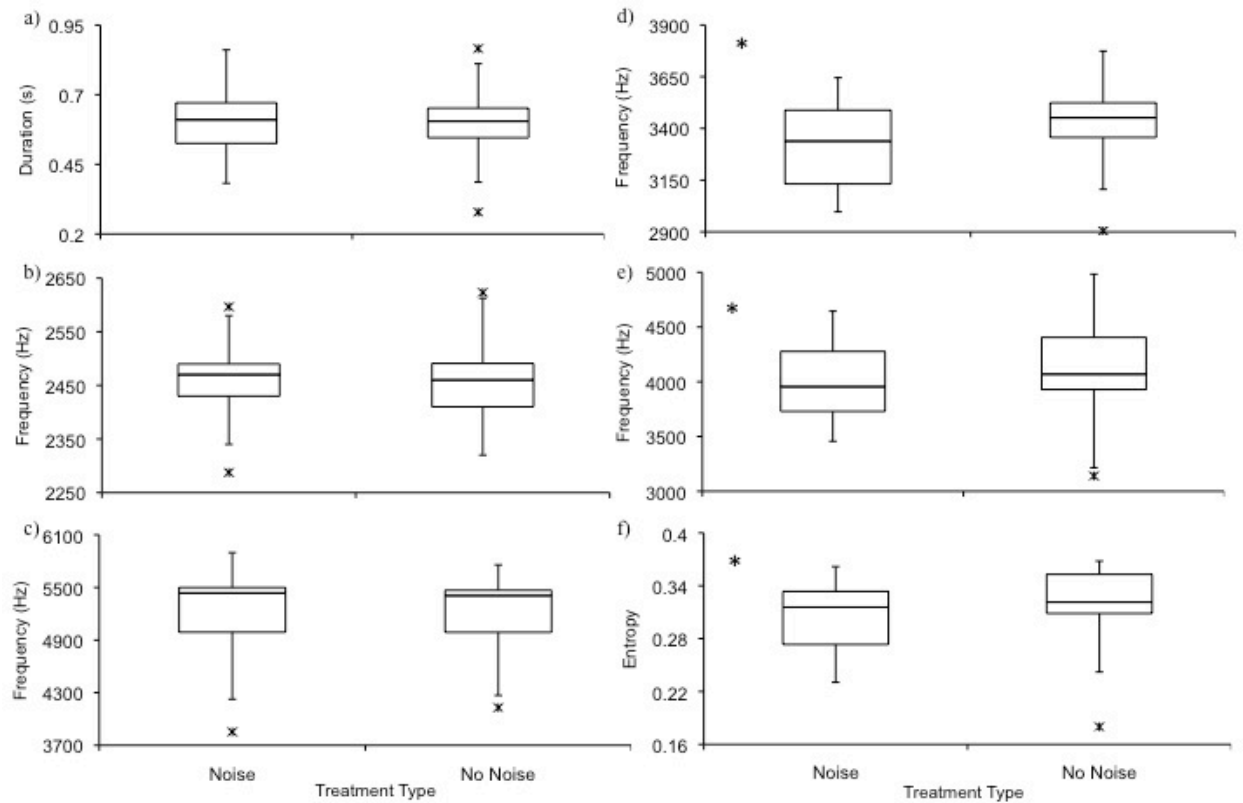
Figure 5. Temporal and spectral characteristics of the Red-Winged Blackbird trill in habitats undisturbed by anthropogenic noise in response to broadband noise. The box plots show medians (black line), inter-quartile range (box) and, maximum and minimum (whiskers) of the song parameters of the birds (n=20) trills during disturbance and without disturbance for: (a) duration, (b) minimum frequency, (c) maximum frequency, (d) 50% quartile, (e) 75% quartile and, (f) entropy. Song parameters which differ significantly are indicated in the top left corner of graphs (*).