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Title: Anthropogenic noise affects song structure in Red-winged Blackbirds (*Agelaius phoeniceus*)

Short title: Anthropogenic noise affects birdsong

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SUMMARY

Anthropogenic noise can mask animal signals that are critical for communicating information about food, predators, and mating opportunities. In response to noise masking, signallers can potentially improve acoustic signal transmission by adjusting the timing, frequency, or amplitude of their signals. These changes can be a short-term modification in response to transient noise, or a long-term modification in response to chronic noise. An animal's ability to adapt to anthropogenic noise can be critical to its success. In this study, we evaluated the effects of anthropogenic noise on the structure of Red-winged Blackbird song. First, we manipulated the presence of anthropogenic noise by experimentally broadcasting either silence or low-frequency white noise to subjects inhabiting quiet marshes located away from roadsides. Subjects exhibited increased signal tonality when temporarily exposed to low-frequency white noise, suggesting that Red-winged Blackbirds can alter their signals rapidly in response to sudden noise. Second, we compared songs produced in quiet marshes located away from roadsides to songs produced during quiet periods at roadside marshes that are normally noisy. This allowed us to test if birds that are exposed to chronic anthropogenic noise exhibit altered song structure during temporarily quiet periods. Subjects residing in roadside marshes that are normally polluted with anthropogenic noise sang songs with increased tonality during quiet periods. Overall, our results show that anthropogenic noise influences the structure of birdsong. These effects should be considered in conservation and wildlife management.

Key words: anthropogenic noise, behavioural plasticity, birdsong, communication, conservation, Red-winged Blackbird, song structure

INTRODUCTION

Acoustic communication is common among animals and is often essential for survival and reproduction (Bradbury and Vehrencamp, 1998; Catchpole and Slater, 1995). For example, acoustic signals can be used to defend territories (Sogge et al., 2007), attract mates (Catchpole and Slater, 1995; Saether, 2002), alert others to the presence of predators (Fallow and Magrath, 2010), and solicit food (Godfray, 1991; Ellis et al., 2009). For acoustic communication to occur, sounds must be detected and recognized by the receiver (Bradbury and Vehrencamp, 1998; Parks et al., 2011). The efficacy of communication can be influenced by many factors occurring at three distinct stages, including signal production (*e.g.*, signal structure, amplitude, directionality), signal transmission (*e.g.*, humidity, ambient noise, topography), and signal perception (*e.g.*, sensitivity, neuronal processing, appropriate behavioural response) (Bradbury and Vehrencamp, 1998; Wiley and Richards, 1982). Disruption of any one of these stages can impede communication.

Anthropogenic noise is a growing problem for many animals because it can mask their acoustic signals and lower their signal-to-noise ratio below a critical detection threshold (Halfwerk et al., 2010; Lohr et al., 2003; Pohl et al., 2009). Furthermore, as the human population grows and global urbanization continues, anthropogenic noise is likely to influence more animal populations. Although time has allowed animals to evolve several adaptive mechanisms to compensate for environmental noise, rapid anthropogenic changes could challenge the compensatory mechanisms of many communication systems (Lengagne, 2008). Anthropogenic noise produced by roads, construction sites, and airports, for instance, might affect breeding in species that are incapable of tolerating noise or unable to modify their signals to compensate for acoustic interference (Halfwerk et al., 2010; Slabbekoorn and Peet, 2003; Tyack, 2008). Therefore, evaluating responses to anthropogenic noise will become increasingly important for effective conservation and management of many animal species (Lengange, 2008).

Several animals exhibit adaptations that increase their signal-to-noise ratio and thus diminish the effects of acoustic masking. There are at least five mechanisms by which animals can increase signal-to-noise ratio. First, animals can produce longer signals that are easier to detect (Brumm et al., 2004; Ey et al., 2009; Kirschel et al., 2009), or, as is seen in certain anurans and katydids, they can adjust signal timing so that their signals do not overlap with conspecific, heterospecific, or anthropogenic sounds (Fuller et al., 2007, Greenfield, 1994; Lengagne, 2008). Second, animals can increase signal-to-noise ratio by increasing signal amplitude during noisy periods (Pytte et al., 2003). This type of adjustment is known as the Lombard effect and has been observed in marine and terrestrial mammals, as well as birds (Brumm and Todt, 2002; Brumm et al., 2004; Brumm et al., 2009; Egnor and Hauser, 2006; Parks et al., 2011). Third, animals, such as Humpback Whales (*Megaptera novaeangliae*) and House Finches (*Carpodacus mexicanus*), can use a different type of signal that has better transmission properties during periods of high environmental noise (Bermúdez-Cuamatzin et al., 2009; Dunlop et al., 2010). Fourth, animals can increase the tonality of their signals, since tonal signals transmit more efficiently than broadband signals through noisy environments (Lohr et al., 2003). For example, in habitats with high levels of natural noise (*e.g.*, tropical forests), some species have been found to converge on songs that have primarily pure tones or narrow frequency bands (Dubois and Martens, 1984; Slabbekoorn and Smith, 2002). Fifth, animals can adjust the pitch of their signals to improve signal transmission (Laiolo, 2010). Green Hylia (*Hylia prasina*), for example, avoid interference from insect sounds by decreasing the pitch of their songs (Kirschel et al., 2009), whereas certain anurans avoid interference from low-frequency stream noise by communicating with ultrasonic frequencies (Feng et al., 2006). In environments influenced by human activities, frequency shifts are usually towards higher frequencies, which minimize overlap with low-frequency anthropogenic noise (Slabbekoorn and Peet, 2003; Wood and Yezerinac, 2006).

Red-winged Blackbirds (*Agelaius phoeniceus* Linnaeus 1766) are an ideal species for studying the effects of anthropogenic noise on acoustic signalling because they commonly inhabit marshes located along noisy roads (Camp and Best, 1994). During the breeding season, Red-winged Blackbirds produce songs that vary in frequency from 1 to 5 kHz, and which typically consist of a series of introductory syllables followed by a broadband trill (Beletsky et al., 1980; Kroodsma and James, 1994). 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).

In this study, we examine the effects of anthropogenic noise on trill structure. In the first part of our study, we experimentally manipulated the presence of anthropogenic noise by broadcasting silence or low-frequency white noise to Red-winged Blackbirds in locations that normally do not experience traffic noise. This experimental approach allowed us to test for possible short-term plasticity in song structure. We predicted that trills would have a significantly longer duration, more tonal energy distribution, and a higher minimum frequency when they were produced during playback of low-frequency white noise. In the second part of our study, we compared songs that were produced during quiet periods by birds living near normally noisy roadsides to songs that were produced by birds living in locations that do not experience traffic noise. This allowed us to test for possible long-term changes in song structure. We predicted that the trill of Red-winged Blackbirds in marshes along noisy roadsides would have a significantly longer duration, more tonal energy distribution, and a higher minimum frequency, as compared to the trill of individuals found in quiet marshes.

MATERIALS AND METHODS

Study area

We collected data on rainless mornings in May and June 2010 in the vicinity of the Queen's University Biological Station (44°34'N 76°19'W), approximately 100 km southwest of Ottawa, Ontario, Canada.

Song structure during transient anthropogenic noise

We tested whether Red-winged Blackbirds from undisturbed marshes adjusted the structure of their trills in response to experimentally broadcasted low-frequency white noise. We presented a given subject with two sequential playback treatments over the course of approximately 6 minutes, while simultaneously recording its vocal response (recording details provided below). For each trial, we continued the first treatment until the subject sang between 3 and 7 songs. We commenced the second treatment immediately after the first and continued it until the subject sang another 3 to 7 songs. Treatment order was randomized for each subject.

The two treatments were a silent control treatment in which we broadcast continuous silence, and an experimental noise treatment in which we broadcast continuous low-frequency white noise. To create the experimental noise treatment, we generated broad-spectrum white noise in Audition software (version 2.0; Adobe, San Jose, CA, USA) and then filtered the noise (bandpass filter, 0-1830 Hz) in Raven (version 1.4 Pro; Cornell Lab of Ornithology Bioacoustics Research Program, Ithaca, NY, USA). We chose an upper bandpass filter frequency of 1830 Hz because this frequency was lower than the minimum frequency of Red-winged Blackbird trills (minimum frequency of trills observed in our chronic noise experiment = mean ± s.e.m., 2420 ± 6 Hz; range, 2150 - 2790 Hz; see below). Thus, the experimental low-frequency white noise could be removed completely in the analysis without removing the lower frequencies of the trill, thereby enabling us to measure trill structure without those measurements being affected by the white noise. Furthermore, the average spectrum of our experimental noise approximated that of typical traffic noise, which has its dominant spectral energy below 1830 Hz (Cornillon and Keane, 1977; Halfwerk et al., 2010; Wood and Yezerinac, 2006).

Trials commenced when we identified a previously untested subject. To minimize the chance of testing the same bird on more than one occasion, we selected subjects by systematically circling a marsh. Individuals within a given marsh were distinguished by identifying distinct visual cues, such as plumage coloration, missing feathers, and markings on the feet and bill (Bretagnolle et al., 1994; Lank and Dale, 2001). If subjects could not be distinguished reliably using visual cues, then we separated trial locations by at least 200 m, which is further than the average territory diameter of Red-winged Blackbirds (Picman, 1987). Once a subject was identified, the observer approached the subject to within 5-30 m (23 ± 1 m, mean ± s.e.m.), placed a loudspeaker (Califone, model PA-285, frequency response 200-5000 Hz; San Fernando, CA, USA) 1-3 m beside the observer, and connected the loudspeaker to a digital playback device (Apple iPod; Cupertino, CA, USA). The volume on the loudspeaker was set so that the amplitude of the experimental stimulus measured 89 dBC (C-weighted decibels) SPL (sound pressure level) at a distance of 1 m (measured with a RadioShack sound level meter, model 33-4050, slow response; Fort Worth, TX, USA). This amplitude is comparable to that used in another study (86 dBA SPL at a distance of 1 m; Verzijden et al., 2010) and is typical of general highway traffic (mean ± SD: 72 ± 18 dBA SPL at roadside, with 25% of all measurements > 88 dBA SPL; Lengagne, 2008) and heavy commercial truck traffic (10 – 90% range: 76 – 86 dBA SPL at a distance of 7.5 m; Stephenson and Vulkan, 1968).

Subjects were audio-recorded throughout the trial using a digital recorder (Marantz PMD 660, WAVE format, 44.1 kHz sampling rate, 16 bits; Mahwah, NJ, USA) and a shotgun microphone (Audio-Technica, model 8015b; Stow, OH, USA) that was fitted with a foam windscreen.

Song structure following chronic anthropogenic noise

We compared Red-winged Blackbird songs produced in quiet marshes to those produced in marshes along a noisy roadside (Provincial Highway #15, Ontario, Canada) during temporarily quiet periods. We recorded 3-12 songs for each of 32 males distributed across four highway marshes (each separated by a minimum distance of 2 km), and an additional 3-12 songs for each of 32 males that were distributed across four non-highway 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. If individuals could not be distinguished reliably using visual cues, we separated recording locations by at least 200 m (Picman, 1987). We alternated our recordings daily between highway and non-highway marshes. Recordings were made using the recording apparatus described in the transient noise experiment above. The distance between the recorder and bird was estimated for each recording (mean ± s.e.m., 20 ± 1 m; range 4-50 m).

Data from the Ministry of Transportation of Ontario indicate high levels of traffic along Highway 15 (Fig. 1A): 0.3 – 4 cars per minute, with a speed limit of 80 km/h. To confirm that the level of ambient noise differed between highway and non-highway marshes, we measured the average amplitude of ambient noise in each. Over the course of one morning, we went to eight typical recording locations distributed across four of our study sites (2 highway, and 2 non-highway). At each site, we measured the amplitude of ambient noise at 15-second intervals for a 5-minute period (measured with the same sound level meter identified above). Roadside and non-roadside locations were alternated after every second trial to control for possible temporal variation in noise.

Measuring song structure

We analyzed all recordings using AviSoft SASLab Pro (version 4.38; R. Specht, Berlin, Germany). First, we saved each song into a separate sound file that contained 1 s of silence both before and after the song (WAVE format, 16-bits, 44100 Hz sampling rate). We then filtered all songs, regardless of the experiment or experimental treatment from which they were derived, with a 2-kHz high-pass filter, which removed natural and experimental background noise without removing components of the trill. Finally, we normalized songs to a peak amplitude of 0 dB and created a separate spectrogram for each song (1024 point FFT; 87.5% overlap; Blackman window; 43-Hz frequency resolution; 2.9-ms temporal resolution).

We used Avisoft's "automatic parameter measurement" feature (threshold setting: -15 dB; holdtime: 10 ms) to select automatically the trill of each song. Automatic detection always identified the end of the trill, but could not always distinguish between the introductory syllables and the onset of the trill. In these cases, we selected the onset of the trill manually by looking for the start of this syllable on the spectrogram. With the trill selected, we collected multiple measurements: trill duration and the minimum frequency, maximum frequency, and energy distribution (25th, 50th, and 75th percent quartiles, as well as entropy) of the averaged frequency spectrum. Minimum frequency was considered the lowest frequency that exceeded -15 dB, whereas maximum frequency was considered the highest frequency that exceeded -15 dB. Quartiles were defined as the frequencies that divided the spectrum into four parts that were equal in terms of spectral energy. Entropy was defined as the randomness of sound: a pure tone has an entropy value near 0, whereas white noise has an entropy value near 1. For roadside recordings, we did not analyze any songs for which we could hear traffic noise in the background or see traffic noise in the sound spectrogram.

A concern in the transient noise experiment was that the broadcasted low-frequency white noise could have directly affected the measurements of song structure (Verzijden et al., 2010). This seems unlikely, however, since our 2-kHz high-pass filter should have completely removed the low-frequency white noise without affecting trill structure. Nevertheless, we conducted a validation procedure similar to that used by Verzijden et al. (2010) to ensure that our measurements were not affected directly by the experimental treatment. To achieve this, we replicated our transient anthropogenic noise experiment, but, instead of recording live subjects, we recorded simulated subjects that could not have changed the structure of their songs between the two experimental treatments. Thus, any treatment effects detected by our measurements in this validation procedure would be artifacts caused by the experimental broadcast of low-frequency white noise. In our validation procedure, we simulated 20 subjects by broadcasting pre-recorded songs from 20 different Red-winged Blackbirds at 20 different locations in a marsh habitat. We broadcast songs at natural amplitude (85 dBC SPL at a distance of 1 m) (Patricelli et al., 2007) through a loudspeaker (Califone, model PA-285; San Fernando, CA, USA) placed 1-3 m beside the observer. Simultaneously, we broadcast silence (*i.e.*, the control treatment described above) or noise (*i.e.*, the experimental treatment described above) through a second loudspeaker (Califone, model PA-285) placed 17-30 m in front of the observer, and then repeated the procedure using the opposite treatment. Consequently, the only difference between treatments was the presence or absence of experimental low-frequency white noise (*i.e.*, song structure was held constant between the treatments). This allowed us to determine whether the broadcast of noise influenced our measurements of birdsongs.

Statistical Analyses

The 25% quartile was highly correlated with the 50% and 75% quartiles, so we removed it from the analysis to avoid conducting independent analyses on non-independent response variables. We constructed separate linear mixed models for each of the measured song characteristics by entering them as response variables. In each model, we included treatment (silence versus low-frequency white noise in the transient noise experiment) or habitat type (roadside versus non-roadside in the chronic noise comparison) as a factor with fixed effects and the distance between the subject and recorder as a covariate with fixed effects. We accounted for repeated measurements of the same individual by including "individual" as a subject factor with random effects.

Assumptions of normality and homoscedasticity were verified by inspecting histograms.

The entropy variable in the chronic noise experiment was not normally distributed, but was corrected with a cubic transformation prior to analysis. Results were considered statistically significant when $p \leq 0.05$, and non-significant trends were considered when $0.05 < p \leq 0.10$. Means are reported ± 1 standard error and distance effects are described using unstandardized regression coefficients (B±SE). All statistical analyses were conducted in PASW for Mac (version 19.0; Armonk, NY, USA).

RESULTS

Song structure during transient anthropogenic noise

We analyzed 140 songs from 20 male Red-winged Blackbirds (69 songs during silent control treatment; 71 songs during experimental noise treatment). Experimental noise treatment did not affect trill duration (linear mixed model: treatment effect, $F_{1,118}$=0.009, P=0.927; distance effect, $F_{1,100}$=0.791, P=0.376, B±SE=0.002±0.002), minimum frequency (treatment effect, $F_{1,116}$=0.633, P=0.428; distance effect, $F_{1,47}$=0.189, P=0.666, B±SE=-0.700±1.610), or maximum frequency (treatment effect, $F_{1,119}$=0.231, P=0.632; distance effect, $F_{1,52}$=2.413, P=0.126, B±SE=-15.308±9.854). Experimental noise treatment did affect entropy, however, with trills produced during playback of low-frequency white noise being significantly more tonal than trills produced during the silent control (linear mixed model: treatment effect, $F_{1,118}$=7.293, P=0.008; distance effect, $F_{1,73}$=4.746, P=0.033, B±SE=-0.001±0.001). The increased tonality during the experimental noise treatment was due to the spectral energy of the trill being concentrated in lower frequencies. Specifically, the 50% and 75% quartiles were significantly lower during the experimental noise treatment than during the silent control treatment (linear mixed models: treatment effect for 50% quartile, $F_{1,118}$=9.789, P=0.002; distance effect for 50% quartile, $F_{1,67}$=0.785, P=0.379, B±SE=-3.259±3.677; treatment effect for 75% quartile: $F_{1,117}$=3.949, P=0.049; distance effect for 75% quartile, $F_{1,60}$=5.201, P=0.026, B±SE=-14.494±6.355; Fig. 2).

We conducted a validation procedure to ensure that our measurements of song structure were not influenced by the presence of low-frequency white noise. We analyzed 138 songs from 20 simulated male Red-winged Blackbirds (69 songs during playback of the silent control stimulus and the same 69 songs during playback of experimental noise). In marked contrast to our analysis of live subjects, experimental noise did not affect any of the temporal or spectral characteristics of the simulated songs (linear mixed models: treatment effect for duration, $F_{1,116}=0.004$, $P=0.951$; distance effect for duration, $F_{1,18}=6.639$, $P=0.019$, $B\pm\mathrm{SE}=0.009\pm0.004$; treatment effect for minimum frequency, $F_{1,117}=0.059$, $P=0.808$; distance effect for minimum frequency, $F_{1,18}=2.128$, $P=0.162$, $B\pm\mathrm{SE}=3.755\pm2.574$; treatment effect for maximum frequency, $F_{1,117}=0.061$, $P=0.805$; distance effect for maximum frequency, $F_{1,18}=0.013$, $P=0.910$, $B\pm\mathrm{SE}=-4.178\pm36.347$; treatment effect for entropy, $F_{1,121}=0.591$, $P=0.444$; distance effect for entropy, $F_{1,17}=0.611$, $P=0.445$, $B\pm\mathrm{SE}=-0.001\pm0.002$; treatment effect for 50% quartile, $F_{1,117}=0.718$, $P=0.399$; distance effect for 50% quartile, $F_{1,18}=0.026$, $P=0.874$, $B\pm\mathrm{SE}=-1.667\pm10.396$; treatment effect for 75% quartile, $F_{1,117}=0.678$, $P=0.412$; distance effect for 75% quartile, $F_{1,18}=0.600$, $P=0.449$, $B\pm\mathrm{SE}=-10.084\pm13.023$). This demonstrates that the changes observed in the songs of the subjects of our playback experiment were not an artifact of the experimental noise treatment.

Song structure following chronic anthropogenic noise

The mean amplitude of ambient noise at roadside locations (65.8 ± 1.8 dBC SPL) was higher than the ambient noise observed at non-roadside locations (51.7 ± 0.1 dBC SPL), owing to a minimum of 1 car every 2 minutes passing on the highway (Fig. 1B). In addition, the power spectrum of a typical Red-winged Blackbird trill overlaps that of typical traffic noise, thereby revealing the potential for acoustic masking (Fig. 3).

We recorded 436 songs from 64 male Red-winged Blackbirds (32 in roadside marshes; 32 in non-roadside marshes). We excluded 92 songs because they contained obvious traffic noise, resulting in 344 songs from 63 individuals for our comparison of roadside versus non-roadside songs (32 individuals from non-roadside marshes, 31 individuals from roadside marshes). In general, results were similar to the transient anthropogenic noise experiment. Habitat type (*i.e.*, roadside versus non-roadside) did not affect trill duration (linear mixed model: treatment effect, $F_{1,60}=0.337$, $P=0.564$; distance effect, $F_{1,318}=2.058$, $P=0.152$, $B\pm\mathrm{SE}=0.001\pm0.001$) or minimum frequency (treatment effect, $F_{1,59}=2.751$, $P=0.103$; distance effect, $F_{1,148}=1.174$, $P=0.280$, $B\pm\mathrm{SE}=0.938\pm0.866$). Habitat type did affect trill entropy, however, with trills recorded in roadside marshes being significantly more tonal than trills recorded in non-roadside marshes (linear mixed model: treatment effect, $F_{1,61}$=6.027, P=0.017; distance effect, $F_{1,324}$=12.470, P<0.001, B±SE=-0.0003±0.0001; Fig. 4). The increased tonality of trills recorded along noisy roadsides was again due to the spectral energy of those trills being concentrated at lower frequencies. The maximum frequency and the 75% quartile were both significantly lower for trills recorded along noisy roadsides than for trills recorded in non-roadside marshes (linear mixed models: treatment effect for maximum frequency, $F_{1,52}$=10.273, P=0.002; distance effect for maximum frequency, $F_{1,117}$=0.354, P=0.553, B±SE=-2.235±3.757; treatment effect for 75% quartile, $F_{1,60}$=4.712, P=0.034; distance effect for 75% quartile, $F_{1,148}$=0.941, P=0.334, B±SE=-3.057±3.152; Fig. 4). The 50% quartile also tended to be lower for trills recorded in noisy roadside marshes than for trills recorded in quiet non-roadside marshes, though the effect was not statistically significant (linear mixed model: treatment effect, $F_{1,61}$=3.477, P=0.067; distance effect, $F_{1,211}$=1.785, P=0.183, B±SE=-2.158±1.615; Fig. 4).

DISCUSSION

We tested whether anthropogenic noise affects the structure of Red-winged Blackbird song using two complementary approaches. First, we used playback to manipulate the presence of anthropogenic noise in pristine marshes, far from busy roadsides. Subjects exposed to transient experimental low-frequency white noise immediately adjusted the structure of their songs by increasing signal tonality, which demonstrates a high degree of behavioural plasticity in the singing behaviour of this species. The change in tonality was not a measurement artifact created by the presence of experimental noise, since we did not observe the same result when we replaced live subjects with simulated subjects that could not alter the structure of their songs. In the second part of our study, we compared song structure between populations that differ naturally in terms of chronic anthropogenic noise. Subjects that live near a busy highway, where they encounter chronic anthropogenic noise, produced songs with increased tonality during temporarily quiet periods, demonstrating that long-term exposure to chronic anthropogenic noise has lasting effects on Red-winged Blackbird song.

Our results demonstrate an overall increase in signal tonality caused by an emphasis of lower frequencies when Red-winged Blackbirds are exposed to anthropogenic noise. This effect has not been observed previously in response to anthropogenic noise, though a similar effect has been observed in response to natural noise. Large-billed Leaf-warblers (*Phylloscopus magnirostris*) and several species of frogs (Genus: *Rana*, Subgenus: *Paa*) live near the noisy torrents of the Nepal Himalayas. Compared to congeners living in habitats devoid of torrents, these species produce signals with increased tonality (Dubois and Martens, 1984). The reasons for increasing signal tonality in noisy environments, however, remain unclear. One possible reason is that higher frequencies attenuate more rapidly than lower frequencies (Bradbury and Vehrencamp, 1998; Forest, 1994). Re-distributing spectral energy from higher frequencies to lower frequencies could therefore enhance signal transmission in noisy environments. This strategy could be particularly effective for Red-winged Blackbirds living along roadsides because the lower frequencies contained in their trills (2.75 – 5.0 kHz) generally exceed the higher frequencies produced by traffic (traffic noise is concentrated below 3 kHz) (Cornillon and Keane, 1977; Halfwerk et al., 2010; Wood and Yezerinac, 2006). Another possible reason for increasing tonality in noisy environments is that narrow-band signals are easier than broadband signals for receivers to discriminate from background noise (Lohr et al., 2003). The reason for this is that the energy in a tonal signal is concentrated in the frequency domain, which increases its signal-to-noise ratio in the part of the spectrum containing the signal (Lohr et al., 2003). It is unclear whether tonal signals are also easier to detect when the signal and background noise occupy completely different parts of the frequency spectrum, as was the case in our transient noise experiment. Research on humans, however, suggests that the noise stimulus could still have disrupted the detection of trills and given subjects incentive to modify trill structure, even though the frequencies of the noise stimulus did not overlap the frequencies of the trill (Martin and Pickett, 1970; Berglund et al., 1996; Vinnik et al., 2011). Finally, it is also possible that increased tonality is not an adaptation to noisy environments, but a non-adaptive side-effect of another mechanism such as the Lombard Effect (Lu and Cooke, 2009).

There are several strategies that animals can use to improve signal detectability in noisy environments, other than increasing signal tonality, yet we did not detect any of these alternative strategies in our study. For example, prolonging signals is a common strategy for increasing signal detectability (Brumm et al., 2004; Nemeth et al., 2006; Warren et al., 2006), yet the trill duration in our study did not differ between all treatments. It is possible that Red-winged Blackbirds are unable to prolong their trills, or that there are energetic costs associated with prolonging trills that outweigh the potential benefits (Fernández-Juricic et al., 2005). Another strategy for increasing signal detectability in noisy environments is to increase signal amplitude. Future studies, using an amplitude-calibrated recording system, would facilitate quantitative measurement of whether Red-winged Blackbirds modify the amplitude of their songs. Many species improve signal detectability by increasing the minimum frequency of their songs, which, due to the low-frequency nature of anthropogenic noise, can reduce masking effects (*e.g.,* Bermúdez-Cuamatzin et al., 2009; Kirschel et al., 2009; Ripmeester et al., 2010; Verzijden et al., 2010). In our study, the minimum frequency of trills did not differ between treatments, perhaps because the frequency range of Red-winged Blackbird trills (2.75 – 5.0 kHz) exceeded the frequencies contained in our experimental low-frequency white noise (0 – 1.83 kHz) and exceeded the majority of frequencies produced by traffic (again, traffic noise is concentrated below 3 kHz) (Cornillon and Keane, 1977; Halfwerk et al., 2010; Wood and Yezerinac, 2006). Finally, some species increase signal detectability in noisy environments by producing an alternative type of signal with better transmission properties (*e.g.,* Bermúdez-Cuamatzin et al., 2009; Dunlop et al., 2010). Red-winged Blackbirds have only a single song-type, however, so this strategy is not an option for this species.

Our results demonstrate that Red-winged Blackbirds modify the structure of their songs in the presence of anthropogenic noise. Although such modifications presumably facilitate signal transmission and detection, the modifications can also impose significant costs on the signaller (Parks et al., 2011; Tyack, 2008). For example, females could have difficulty recognizing modified songs, or could be less attracted to males that produce modified songs (Patricelli and Blickley, 2006). Structural modifications to song could also have consequences that are manifested during intrasexual interactions. For example, males that have adjusted their signals could be interpreted by other males as less threatening, thereby compromising their ability to defend a territory (Patricelli and Blickley, 2006). If males with altered songs are unable to attract a mate or defend a territory, then populations affected by anthropogenic noise may gradually disappear. Alternatively, if females prefer the songs of their local males, then roadside and non-roadside populations may become reproductively isolated, which would constitute the first steps of speciation (Slabbekoorn and Peet, 2003; Warren et al., 2006; Wood and Yezerinac, 2006). Conservation authorities should therefore consider a number of strategies for reducing anthropogenic noise in protected areas and areas with species at risk (Kam-wah, 2005; Barber et al., 2010).

Future studies should focus on how the structural changes observed in the current study affect signal transmission and signal perception. For example, does increased signal tonality improve signal transmission in a noisy environment? Do receivers discriminate between more tonal and less tonal songs, and, if so, do these differences in song structure affect the signaller's survival and reproductive success (Nemeth and Brumm, 2010; Verzijden et al., 2010)? The results we present here show that Red-winged Blackbirds modify their acoustic mating signals in response to anthropogenic noise, and that animals living in areas with chronic exposure to high noise levels show long-term changes to their song structure.

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Fig. 1.

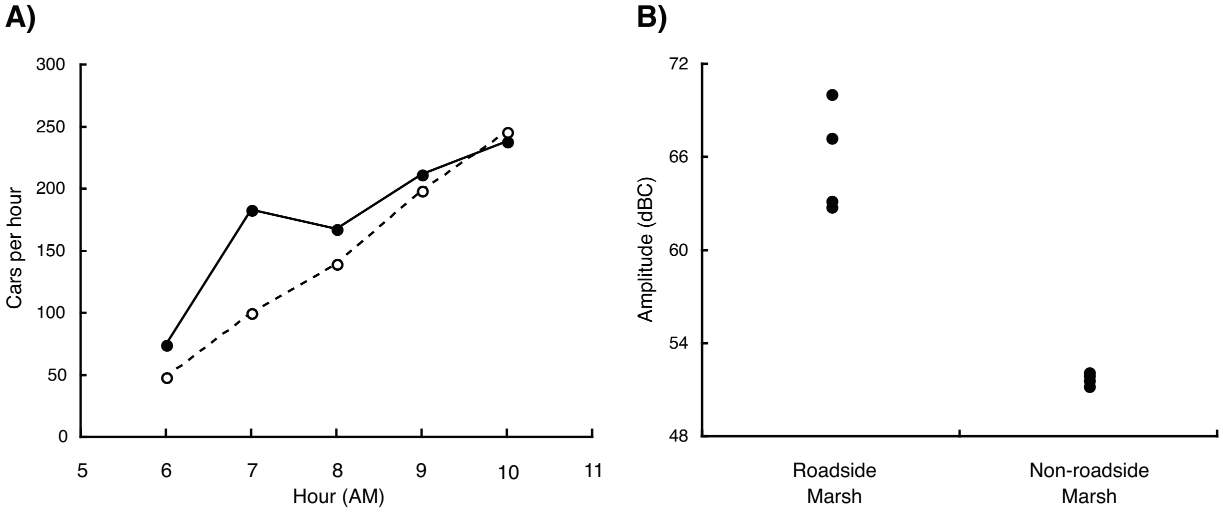

Fig. 1. Ambient noise at roadside and non-roadside marshes where Red-winged Blackbirds were recorded. (A) The average daily incidence of vehicles on Highway 15 (Ontario, Canada) at the intersection of Road 8, between 06:00 h and 11:00 h, as measured by the Ministry of Transportation of Ontario (MTO) during 1 week in April, 2007. Filled circles with solid lines indicate weekday traffic (N = 5 days) and open circles with hatched lines indicate weekend traffic (N = 2 days). (B) Amplitude of ambient noise at 4 roadside recording locations is significantly higher than at 4 non-roadside recording locations on Highway 15. Each data point is an average of sound pressure measurements that were obtained at 15-s intervals over a 5-min period.

Fig. 2.

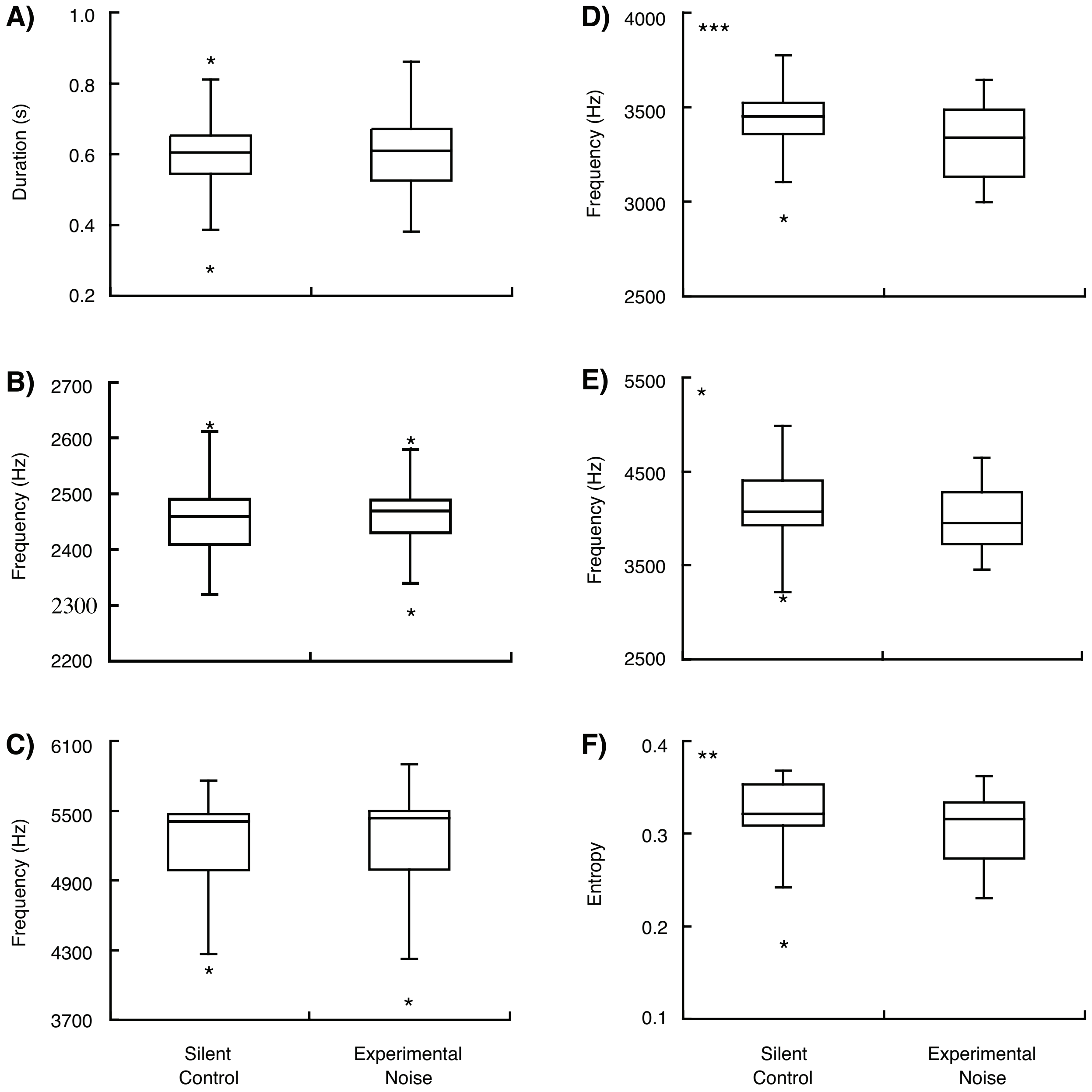

Fig. 2. Variation in the structure of Red-winged Blackbird songs during the transient anthropogenic noise experiment. Each subject (N=20) was presented with a silent control treatment, in which we broadcast silence, and an experimental noise treatment, in which we broadcast low-frequency white noise. Box plots show the median (black line), inter-quartile

range (box), minimum value within 1.5 inter-quartile ranges of the lower quartile (lower whisker), maximum value within 1.5 inter-quartile ranges of the upper quartile (upper whisker), and minimum and maximum outliers (asterisks) for 6 song parameters measured from the trill component of the birds' songs: (A) duration, (B) minimum frequency, (C) maximum frequency, (D) 50% quartile, (E) 75% quartile and, (F) entropy. For each parameter, each datapoint is the average of all songs produced by a given individual. Statistically significant differences are indicated by asterisks in the top left of each panel (* for $P \le 0.050$, ** for $P \le 0.010$, and *** for $P \le 0.005$).

Fig. 3.

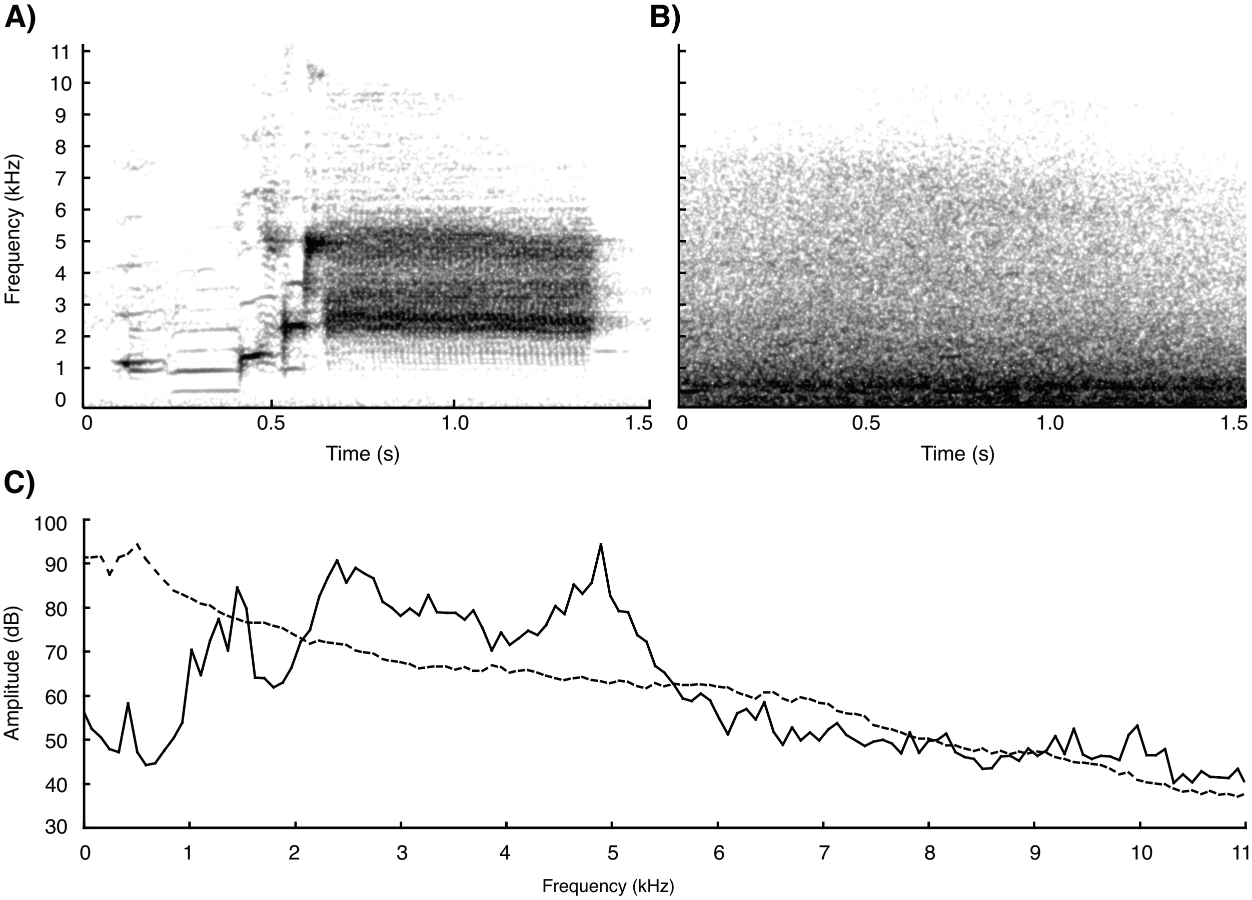

Fig. 3. The masking effect of traffic noise on a typical Red-winged Blackbird song. Spectrograms of the song (A) and the traffic noise (B) were produced using a 1024-point FFT, 87.5% overlap, and a Blackman window, which resulted in a frequency resolution of 43 Hz and a temporal resolution of 2.9 ms. Panel C shows averaged power spectrums of the Red-winged Blackbird song (solid line) and the traffic noise (hatched line).

Fig. 4.

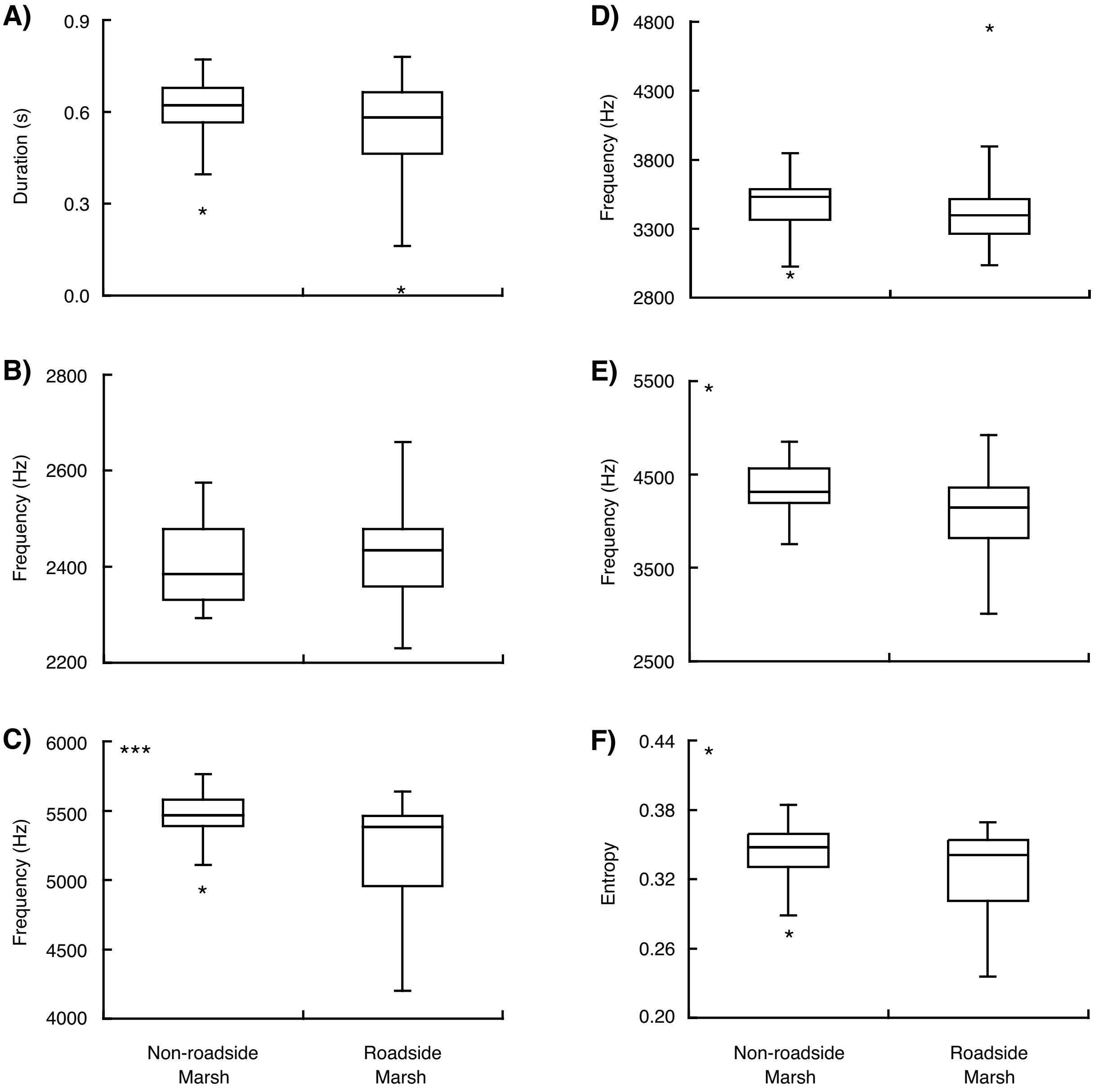

Fig. 4. Variation in the structure of Red-winged Blackbird songs for subjects that were recorded in quiet non-roadside marshes (N=32) and in noisy roadside marshes when traffic was temporarily absent (N=31). Box plots show the median (black line), inter-quartile range (box), minimum value within 1.5 inter-quartile ranges of the lower quartile (lower whisker), maximum value within 1.5 inter-quartile ranges of the upper quartile (upper whisker), and minimum and

maximum outliers (asterisks) for 6 parameters measured from the trill component of birds' songs: (A) duration (B) minimum frequency, (C) maximum frequency, (D) 50% quartile, (E) 75% quartile and, (F) entropy. For each parameter, each datapoint is the average of all songs produced by a given individual. Statistically significant differences are indicated by asterisks in the top left of each panel (* for $P \leq 0.050$, ** for $P \leq 0.010$, and *** for $P \leq 0.005$).