**RESEARCH ARTICLE**

Curry, C.M., Antze, B., Warrington, M.H., Des Brisay., P., Rosa, P. and **Koper, N.** 2018. Ability to alter song in two grassland songbirds exposed to simulated anthropogenic noise is not related to pre-existing variability. Bioacoustics. 27:105-130.

DOI: 10.1080/09524622.2017.1289123

© 2017. This manuscript version is made available under the CC-BY-NC-ND 4.0 license http://creativecommons.org/licenses/by-nc-nd/4.0/

**Ability to alter song in two grassland songbirds exposed to simulated anthropogenic noise is not related to pre-existing variability**

Authors: Claire M. Currya,b\*, Bridget Antzea (bridget\_antze@hotmail.com), Miyako H. Warringtona,c (MWarring@sgu.edu), Paulson Des Brisaya (pauldesbrisay@gmail.com), Patricia Rosaa (patriciarosa.udem@gmail.com), and Nicola Kopera (Nicola.Koper@umanitoba.ca)

aNatural Resources Institute, University of Manitoba, 303-70 Dysart Road, Winnipeg, MB, Canada R3T2N2, telephone: +1 204-474-8373

bPresent address: Oklahoma Biological Survey, University of Oklahoma, 111 E. Chesapeake St, Norman, OK, USA 73019, telephone: +1 405-325-1985

cPresent address: Department of Biology, Ecology & Conservation, St. George's University, University Centre, True Blue, Grenada, telephone +1 473-444-4175

\*Corresponding author. Email: curryclairem@gmail.com, telephone: +1 405-325-1985

# Funding acknowledgement

This work was supported by grants to NK via Natural Sciences and Engineering Research Council of Canada (grant number CRDPJ 432934-12); Cenovus Energy; the Manitoba Research and Innovation Fund and Canadian Foundation for Innovation (grant number 18787), and the University of Manitoba’s Clayton Riddell Faculty of Environment, Earth, and Resources. CMC was additionally supported by U.S. Department of Agriculture grant USDA-NIFA 2013-67009-20369 to E.S. Bridge.

# Conflict of Interest Statement

Some funding for the research was provided by Cenovus Energy to NK (supporting all other coauthors excepting MHW). The funding from industry had no effect on the research or our conclusions. Cenovus Energy contributed safety training and helped identify potential research sites, but all research was designed, analyzed, written and submitted for review by the co-authors without industry input, to maintain integrity.

# Abstract

Organisms encounter noise naturally in the environment. However, increasing prevalence of human-caused noise seems to be resulting in behavioural changes in many animals that can affect survival and reproduction. Not all species react the same way to noise; some adjust their vocal signals while others do not. We hypothesized that species with more variability in their vocal signals would be better able to adjust their signals to be audible over anthropogenic noise. We tested this within a large-scale manipulative experiment by recording songs of two grassland songbirds, Baird’s sparrow (*Ammodramus bairdii*) and Savannah sparrow (*Passerculus sandwichensis*), both of which are found in areas increasingly affected by energy extraction noise. We compared these species because Savannah sparrows have more variability in their songs geographically and temporally compared to Baird’s sparrows. We recorded both species’ songs before, during, and after high-fidelity playbacks of oil well drilling noise. Surprisingly, both species changed parts of their songs in the presence of noise (Baird’s sparrow usually decreasing frequency and Savannah sparrow increasing frequency) and these changes were not related to seasonal, song, or syllable variability. We suggest instead that acoustically heterogeneous environments may favor the evolution of species that are capable of adjusting their songs in response to variable ambient noise.

Keywords: mixed-grass prairie, energy development, Savannah sparrow, Baird’s sparrow, signalling, plasticity

# Introduction

Organisms encounter noise and acoustic interference in their natural habitat, whether from other organisms, atmospheric conditions (Snell-Rood 2012), or landscape features (Gough et al. 2014) and structure (Morton 1975; Wiley & Richards 1978; Ey & Fischer 2009). Indeed, varying levels of background noise can cause divergence in song structure among populations (Slabbekoorn & Smith 2002; Kirschel et al. 2009; Ripmeester et al. 2010). However, anthropogenic noises are increasingly prevalent in terrestrial and aquatic habitats due to traffic (Parris & Schneider 2009), urban noises (Luther & Derryberry 2012), ships (Slabbekoorn et al. 2010), energy extraction (Bayne et al. 2008), and many other sources. Anthropogenic noise can affect natural systems at multiple levels, from altering signal learning (Peters et al. 2012) and behaviour (Nowicki et al. 2002; Halfwerk & Slabbekoorn 2009; Lynch et al. 2015) of individuals to community-level changes in species interactions (Francis et al. 2012) and community composition (Francis, Ortega, et al. 2011a).

Not all species react the same way to noise: sensitivity to noise in birds varies with diet and vocal frequency (Parris & McCarthy 2013; Francis 2015). Closely related species may have completely different responses to noise (Francis, Ortega, et al. 2011b). Species with more variable or plastic songs may be able to adjust their songs more readily (Tumer & Brainard 2007; Slabbekoorn & Ripmeester 2008), either due to individual plasticity (Garcia et al. 2009; Verzijden et al. 2010; Bermudez-Cuamatzin et al. 2011) or by cultural evolution, whereby songs or song elements used in the population change as each generation learns (Catchpole & Slater 2008). For example, birds with many song types in their repertoires may use particular songs that are more easily heard over background noise (Halfwerk & Slabbekoorn 2009) or in their acoustic environment (Derryberry 2007). Either change (individual plasticity or differential use of songs in repertoires) could lead to longer term cultural shifts if certain songs or frequency ranges are more perceptible in noisy environments (Pohl et al. 2009).

Habitat fragmentation and degradation from energy extraction, including negative effects of anthropogenic noise (Bayne et al. 2008), are now significant threats to grassland birds (Askins et al. 2007; Van Wilgenburg et al. 2013). Noise associated with energy extraction can cause avoidance of noisy areas and behavioural changes in birds ranging from grouse to passerines (Habib et al. 2006; Francis, Paritsis, et al. 2011; Blickley et al. 2012), and can change community structure (Francis et al. 2012). Nonetheless, few studies have documented effects of noise from energy infrastructure on grassland songbirds, particularly declining grassland specialists, such as Baird's sparrow, a species of Special Concern in Canada (Green et al. 2002; COSEWIC 2012). In contrast, Savannah sparrow is widely distributed and abundant, although its population trends vary by region and management practice (Wheelwright & Rising 2008). For example, where both species occur in the central Breeding Bird Survey region (between the Mississippi River and the Rocky Mountains), between 1966 and 2013 Savannah sparrows have increased by 0.42% per year whereas Baird’s sparrows (which occur only in this region) have declined by 2.93% per year (Sauer et al. 2014). Baird’s sparrow nesting success appears to be more sensitive to the presence of energy infrastructure than Savannah sparrow nesting success (Ludlow et al. 2015), but how noise contributes to their differing sensitivity is unknown. We hypothesized that Baird’s sparrow populations might be more sensitive to anthropogenic development than Savannah sparrows because they are unable to adapt acoustically to an anthropogenically noisy environment.

Baird’s and Savannah sparrows both sing high-frequency songs, with only one song type learned by each male (Green 1992; Bradley 1994; Burnell 1998; Wheelwright et al. 2008). Baird’s sparrow songs are almost invariant; in recordings of 309 individuals from 1959-1991, only 13 main song types were found across the range, along with half a dozen unique variants recorded from only one individual each (Green 1992). In contrast, among Savannah sparrow selects song elements from multiple tutors during learning that are then combined to create their own song (Wheelwright et al. 2008). This has resulted in some Savannah sparrow populations changing in common song elements over time despite a shared overall structure (Bradley 1994; Williams et al. 2013). To our knowledge, no previous studies have examined the relationship between the number of song types observed and a species’ overall song plasticity. However, a species with multiple song types or less stereotyped song types is defined to have more variability within its vocal repertoire than a species with fewer or more stereotyped song types (Byers 1995). Birds can use variability within songs to modify acoustic signals in the presence of acoustic disruptions (Tumer & Brainard 2007). Thus, our focal species’ differing learning patterns suggest both significantly more potential for song plasticity in Savannah (potentially hundreds or thousands of unique song types) compared with Baird’s sparrows (13 song types) and that such plasticity might lead to a better ability to adjust song in the presence of acoustic disruptions. As understanding behavior is critical to help mitigate effects of energy extraction (Northrup & Wittemyer 2013), comparing the effects of energy extraction on acoustic behaviour of species that differ in potential song plasticity within this region may help us understand the mechanisms underlying these effects.

Untangling the effects of noise from the presence of infrastructure itself can be difficult (Lackey et al. 2012), and is important because changes in population structure and behaviour associated with industrial activity also could be due to the structure itself, habitat alteration, or human activity. One approach is to simulate infrastructure noise pollution by broadcasting noise in an otherwise undisturbed landscape (McClure et al. 2013; Shannon et al. 2014; Rosa et al. 2015; Ware et al. 2015). Such experimental tests can identify responses to noise independently from correlated effects such as avoidance of inappropriate habitat (Habib et al. 2006; Ludlow et al. 2015) that co-occur with anthropogenic infrastructure. In the case of migratory birds, we can set up noise playback systems before or after a migratory study species returns to breed in an area (Rosa et al. 2015). This is important when evaluating effects of noise *per se*, because birds that have settled into territories near infrastructure may be different from birds that have settled in undisturbed landscapes (Halfwerk & Slabbekoorn 2009). Adding anthropogenic noise after the birds arrive thus allows us to examine behaviour from a sample of the whole population, and not just the reactions of individuals that chose to settle in a noisy area.

Our objective was to determine if song and syllable-level variability corresponded to which parts of the song change when birds are exposed to anthropogenic noise and whether this differs by species. Our high-fidelity playbacks of oil well drilling noise began after birds had settled on the sites, allowing us to sample the full range of responses to noise without the confounding effects of birds selecting sites based on the disturbance itself (e.g., Habib et al. 2006). We used recordings of oil well drilling noise because it is particularly loud and is known to produce strong avoidance in wildlife (Blickley et al. 2012; Jakes 2015), perhaps because it influences communication. We first compared song and syllable variability between the two species, and predicted that Baird’s sparrows, which have substantially fewer song types across their range than Savannah sparrows, would have less variability in song parameters. Second, we tested whether functional units of songs for each species changed in response to high-fidelity playbacks of oil well drilling noise. At the population level, we predicted that the species with more existing song variability would be more likely to change whole song and syllable characteristics due to the greater underlying plasticity of their vocal repertoire. Understanding how behavioural plasticity relates to song adjustments in noise will help us determine *a priori* which species and habitats may be more sensitive to noise pollution to implement cost-effective mitigation of anthropogenic noise pollution.

# Methods

## Ethics compliance statement

This study was approved under the University of Manitoba Council on Animal Care (F12-010/1), Alberta Environment and Sustainable Resource Development (Research Permit #55492 Collection Licence #55491), and Canadian Fish and Wildlife Service (permit 11-MB/SK/AB-SC007).

## Study site

The study was conducted southeast of Brooks, Alberta (49° 0' 0.004" to 50° 53' 56.475" N; 110° 0' 2.757" W to 112° 28' 44.473" W). Oil and gas extraction is prevalent in the region (Alberta Government 2012) with well pad densities averaging 1.3 oil wells/km2 and 8.0 gas wells/km2 (J.N. Daniel, unpublished data). We surveyed birds at three grazed, mixed-grass prairie sites, typical vegetation including native forbs and grasses (*Hesperostipa comata*, *Koeleria macrantha*, *Pascopyrum smithii*) and scattered shrubs (*Artemisia cana*). From May-July, the study region receives an average of 41.0-64.5 mm of rain with average daily temperatures of 11.3-18.3 °C; daily winds range from still to exceeding 30 km/hr (Environment Canada 2015). The sites were free of external noise pollution, centred at least 800 m from adjacent oil extraction activities.

## Experimental design: playback

Each of the three sites contained a high-fidelity broadcast system; elsewhere we demonstrate that the quality, amplitude, and attenuation of sound from these playback systems closely matches sound emitted from real energy infrastructure (Rosa et al. 2015). Each broadcast system played noise from one of three different active drilling rigs, which had been recorded in the surrounding regions in September-October 2013 using 3 Zoom H4N handheld recorders (Zoom, Tokyo, Japan; 48-kHz sample rate, 24-bit Waveform Audio File Format [WAV] ﬁles) each recording for 65 mins from 3 different key locations on the drilling rig. We recorded the 3 stages of operation of the 3 different drilling rigs (i.e. drilling, laying casing and waiting on cement). We edited out non-relevant background noise using Cubase LE AI Elements 6 software (Steinberg Media, Technologies, Hamburg, Germany), and loaded the amplified WAV files onto 8GB iPod Nanos (Apple Inc., Cupertino, CA). These rigs emitted typical sound from drilling operations in the area in terms of sound amplitude, frequency, and duration of operations. Drilling noise is a broadband sound, consisting of a wide frequency range from 0 Hz to 21 kHz, with more energy in the lower frequencies (Figure 1). The noise playback was broadcast at an average of 88 dB(C) at 10 m (C-weighted time-average sound pressure level for broadband sound; LCeq). Playback units were powered by 5 150-W (8.7-A) solar panels (SunForce Products, Montreal, Quebec, Canada) charging 4 deep-cycle golf cart batteries providing power to 2 Mackie SRM350v2 loudspeakers (LOUD Technologies, Woodinville, Washington, USA) and an iPod. The electrical components were protected in a raised wooden box with two screened openings beside the solar panels. The entirety of the set-up was surrounded by a metal technical fence (Boomers Services, Brooks, Alberta, Canada) measuring 7.3 m (l) x 4.9 m (w) x 1 m (h) to prevent access by cattle. See Rosa et al. (2015) for a detailed description of the broadcast system.

We confirmed fidelity for the broadcasts in the current study using a Brüel & Kjær, 2250 SPL meter-frequency analyzer (Brüel & Kjær, Denmark) along transects radiating away from the playback structure to ensure the noise amplitude reflected the transect SPLs previously measured at actual drilling rigs (Rosa et al. 2015). Sound pressure levels at sites broadcasting drilling noise were significantly higher compared to sites without noise-producing infrastructure (Satterthewaite estimate with unequal variances, df=877.7, t=49.68, *p*<0.001). Each site had playback infrastructure present from May-August 2014, with a playback period lasting 10 days (a typical drilling period in this region) (Site 1: 11:06am June 3 to 11:06am June 13; Site 2: 5:24pm May 31 to 5:24pm June 10; Site 3: 10:47am June 7 to 10:47am June 17). During broadcasting periods, sound was broadcast nonstop and we monitored system functions and performance approximately every 2 – 5 days (mean interval length = 3.1 days, SD = 1.7) to ensure continuous broadcasting. We recorded songs before, during, and after these noise playbacks.

## Study species

Baird's sparrows sing only one song type per individual and approximately 13 song types are known across the range, with no known regional or historical variation (Green 1992; Green et al. 2002). Green et al. (2002) described slight variations in the number of repeated syllables, in the type of trill, and in the presence or absence of a final syllable within a song type. Baird’s sparrow songs typically include one or two parts (depending on the song type): introductory notes; and a “trill”, which can be divided into an initial longer syllable (Borror 1961) followed by the main trill. Sometimes a third part, a few final notes, is added onto a song type. Trills can be alternating or single frequency and do not occur in all song types (Green et al. 2002).

Savannah Sparrows also sing one song type per individual (Bradley 1994; Burnell 1998), but there is extensive regional (Bradley 1977; Pitocchelli 1981; Sung & Handford 2006) and historical (Bradley 1994; Williams et al. 2013) variation in song types. The song typically includes four parts: introductory notes; middle complex syllables; a buzz; and final syllables (sometimes a trill) (Burnell 1998; Williams et al. 2013). An individual may vary the number of repeats within a song type (this study) and there is also minor seasonal variation in frequency (Chew 1981). Syllables incorporated into these parts are learned by a given male from multiple tutors, so a Savannah Sparrow creates its song from many syllable combinations (Wheelwright et al. 2008) within the species’ “grammar” (Chew 1981). This is unlike Baird’s sparrows, where an individual generally learns one of the 13 song types, and potentially selects from an even smaller subset depending on to which of the song types they have been exposed.

## Song recording and measurements

Before, during, and after playbacks of drilling noise, we recorded vocalizations of free-living, unbanded Baird’s sparrows and Savannah sparrows from 17 May-04 July 2014 (a 48 day span) at the three study sites. We sampled singing males within a ca. 400-m radius of the site centre points where the playback equipment was located. We analysed 1-4 songs (median 3, mean 2.83) for each Savannah sparrow and 1-5 songs (median 3, mean 2.97) for each Baird’s sparrow per individual within each treatment period. Vocalizations were recorded as uncompressed audio (WAV files at 48 kHz sampling rate, 16-bit resolution) using Zoom H4N Digital Recorders with built-in stereo microphones angled at 90° at maximal recording volume.

We systematically searched for males in a non-overlapping pattern through the site so as to avoid sampling the same territory twice within treatment periods, assuming that individual males would not alter their territory within one visit. On subsequent visits at each treatment (before, during, and after noise) we sampled each site again, and thus assumed that we sampled some of the same individuals repeatedly among treatment periods. To control for repeated sampling of the same sites, and for analysis of multiple songs from each individual, we used individual nested within site as random variables in all syllable-level analyses (see models in the following section). With one exception, we did not visit the same area of the site on subsequent days, to avoid sampling the same individual within a treatment and site. One site was visited twice within the same treatment, but in that case we were conservative and excluded individuals that could not be distinguished by differing song types.

To record songs, we pointed the microphone directly at singing males at the closest approach distance possible for the individual (this ranged from 16-45 m for Savannah sparrows and 19-56 m for Baird’s sparrows). After recording, we calculated distance from bird to observer and distance from bird to infrastructure using GPS units. We recorded approximately 30 seconds of ambient noise immediately after the song recordings by pointing the directional microphones straight up at the male’s perch location. This allowed us to capture the noise conditions under which the song was generated. Temperature gradients and wind can change sound transmission (Morton 1975; Wiley & Richards 1978) and create feedback noise, so we only recorded during standardized conditions (wind speed ≤15 km/hr before 13:00).

To measure sound parameters for song and syllables, we used Raven Pro 1.5 Beta (Bioacoustics Research Program 2014), with settings standardized across recordings (Hann window size=512 samples, frequency grid DFT size=512 samples, grid spacing=93.8 Hz, time grid 50% overlap with 256 sample hop size). We used Raven Pro Beta 1.5’s “Paste Selection (Border) Mode” with “shrink by decibel level threshold” feature to select regions with boundaries 24 dB below peak frequency, allowing selections to be consistent between files, species, and levels of background noise (Podos 1997). A few individuals had high background noise but distinct signals, and in those cases we selected the -24 dB threshold manually. We used the first 1-5 (median= 3) songs where no other notable sounds overlapped with the focal sound. Therefore some songs are sequential, while others may be several minutes apart. As the recordings were recorded in stereo, we chose songs from the channel with the highest peak amplitude. For each selection, we extracted four frequency parameters, one temporal parameter, entropy, and one amplitude parameter (Charif et al. 2010): 5% low frequency (Hz), 95% high frequency (Hz), 90% frequency bandwidth (Hz, the range between the 5 and 95% frequencies), peak frequency (Hz, the frequency at which maximum power occurs), duration (seconds), aggregate entropy (measures the sound’s disorder using the energy distribution in the selection from the spectrogram), and average power (decibels) from the selection spectrum.

We corrected average power for both for background sound levels (following Bradbury & Vehrencamp 1998) and for distance from bird to observer (following Brumm 2004). The original amplitude measurement in Raven Pro is unitless and was corrected by 8.8, empirically determined to bring the value to the actual amplitude for our recording devices, measured using a Brüel & Kjær frequency analyzer. Background-corrected amplitude and then actual amplitude were calculated as follows.

Background-corrected Amplitude=10\*log10 (10((Original Raven Song Measurement-8.8)/10)-10((Raven Background Measurement-8.8)/10))

Actual Amplitude=20\*log10 (Distance of Observer to Bird)+mean(Background-corrected Amplitude)

To measure background sound levels for the average power correction, we selected a region of the spectrogram that was the same duration and frequency range as the adjacent song just after or before the song with typical background noises (no sounds that did not occur during the song measurements, such as another bird singing).

To measure environmental ambient noise, we selected 30 seconds at 0-24 kHz (the frequencies recorded by our devices) out of the ambient noise recording taken at the bird’s perch location, resulting in one ambient noise measurement per individual from the spectrogram. A few recordings had <30 seconds of ambient noise available, and in those cases we used 20 seconds.

Both species’ songs were measured as whole songs and as syllables. For Savannah sparrows, nine syllables were found at our study sites (Figure 2). Syllables were based on previous work in this species (Burnell 1998; Williams et al. 2013) with three new syllables (M.H. Warrington et al., in review). Because Baird’s sparrows were previously only classified by song types and sections, we created syllable classifications based on syllable shape (ascending, descending, flat, and repetition of notes within the syllables) within trill or introduction and final sections (Green 1992). We then combined syllables that were often mistaken for one another during classification by two independent observers, resulting in a total of nine syllable types that distinguish the song types (Figure 3). Both species had variable numbers of syllable repeats within individuals. To distinguish song types, we lumped repeated syllables or repeats of syllable clusters (memes) (Burnell 1998) to create a unique ordering of syllables. This resulted in song types that are distinguishable by syllable sequence for both species; the syllable-sequence-based song types for Baird’s sparrow mapped to the previous classifications (Green 1992; Green et al. 2002).

## Analysis and Statistics

*Ambient noise*

We evaluated whether our recorded ambient noise at the male’s singing perch was related to predicted noise values during noise playback. This tested whether our handheld recorders accurately measured ambient noise from the treatment. We used linear mixed models in the packages ‘lme4’ (Bates et al. 2011) and ‘lmerTest’ (Kuznetsova et al. 2015) in R 3.2.1 (R Core Team 2015).

Ambient noise = predictednoise + wind + (1|Site)

The predicted values were calculated using the amplitude of the playback, distance to playback, and weather (relative humidity, station barometric pressure, and temperature) (International Standards Organization 1993; International Standards Organization 1996) for 21 birds during playback only. We used birds during playback because before and after playback there was no point source of noise from which to predict sound degradation and thus noise. Weather variables were included because they are required by the ISO standard calculations for degradation of sound. Relative humidity, station barometric pressure, and temperature values were recorded in the field at the singing male’s location, at approximately 1.5 m above the ground, immediately after song recording, using handheld Kestrel Pocket Weather Meters (models 2000, 3500, and 4500; Kestrelmeters.com, Birmingham, MI).

*Population song and syllable variability*

We compared whether song features were more variable for Savannah sparrows than in Baird’s sparrows. First, we counted the number of song types per species. Although we expect the number of Savannah sparrow song types to be more than the number of Baird’s sparrow song types based on previous literature, we wanted to confirm whether this difference existed at the local scale of our three sites. Next, we checked for equality of variance for each species during quiet treatments (before and after playback) using a robust (median) Levene’s test for equality of variances (Fox et al. 2012; Sokal & Rohlf 2012). We tested during quiet treatments only in both this and the following test because we were interested in whether natural variability (both between species and intra-individual) resulted in differential responses to noise. We also calculated coefficient of variation (with small sample size correction; Sokal & Rohlf 2012) for each song and syllable parameter during quiet treatments (before and after playback). We compared coefficient of variation between species with a Wilcoxon rank sum test.

*Responses to noise*

We used linear mixed models in the packages ‘lme4’ (Bates et al. 2011) and ‘lmerTest’ (Kuznetsova et al. 2015) in R 3.2.1 (R Core Team 2015) to evaluate effects of ambient noise and date on song parameters.

Song parameter = ambientnoise + relativedate + (1|site/individual)

Before, during, and after noise playback treatments were correlated with date, so treatments were not completely distinguishable from seasonal effects. Seasonal change in song is known in Savannah sparrows (Chew 1981) and from other species (Lampe & Espmark 1987; Smith, Brenowitz, Wingfield, et al. 1997), and appears to be a result of changes in photoperiod and hormones (Smith, Brenowitz, & Wingfield 1997). Hence, we used ambient noise as a proxy for treatment, and we accounted for seasonality using the count of days since the first recording date of the season (“relative date”) as a covariate to account for seasonal changes in song features over the 48-day span of recordings.

A second model was run during noise playback only, using data from a shorter 14-day time span (between 02 June and 16 June 2014) to eliminate effects of seasonality.

Song parameter = ambientnoise + (1|site/individual)

Because we ran a large number of models, we also report effect sizes for each model to ensure that results have biological significance and are not simply due to chance. We used the R package ‘MuMIn’ (Bartoń 2009) for estimating marginal and conditional R2 for each model. Marginal R2 indicates how much variance is due to fixed effects, while conditional R2 includes both fixed and random effects.

Finally, to allow us to see if one species changed more elements of its songs compared to the other, we tallied the number of significant adjustments to noise from the two models by species. We then used a χ2 test to determine whether adjustments in response to noise (from either model) were more common than expected by chance in song and syllable parameters in either species. Each mixed model was run on a single species, as the two species contain no common syllables, so this test allowed us to see if one species changed more elements of its songs compared to the other.

*Response to noise*

We evaluated whether more variable song parameters were more likely to be changed in response to noise, at two scales. For population-level song variation, we tested whether the probability of a parameter being altered in response to noise was related to having higher variance in that parameter, for both species, using a χ2 test. For syllable variation, we used a Wilcoxon rank-sum test to compare whether the coefficient of variation was higher in parameters that changed with noise.

Finally, to determine if adjustments in response to noise were more common than expected by chance in song and syllable parameters that had seasonal changes, we used a χ2 test.

# Results

## Ambient noise

The ambient noise recorded at perch sites (n=21) during noise playback showed a significant positive relationship with ISO-predicted noise (Figure 4; β=0.77±0.19, *p*<0.001) and wind (β=1.93±0.54, *p*=0.002).

## Population song and syllable variability

Baird’s sparrows at our three study sites sang 11 song types (n=29; nbefore=8, nduring=13, nafter=8). All but one matched the Green (1992) song types; the remaining song type was found in only one individual and was unique to our study. Savannah sparrows at our three study sites sang 16 song types (n=29; nbefore=13, nduring=8, nafter=8), not significantly more than song types of Baird’s sparrows (χ2=0.93, df=1, *p*=0.34). When we compared syllable sequences (including repeats), Baird’s sparrows had marginally higher numbers of sequences compared to Savannah sparrows (54 vs. 38; χ2=2.78, df=1, *p*=0.095), suggesting Baird’s sparrows varied the number of syllable repeats within a song type more often than Savannah sparrows.

All whole-song parameters except aggregate entropy (F1,109=1.18, *p*=0.28) showed inequality of variance between the two species (Figure 5). Baird’s sparrow had higher variance for 95% high frequency (F1,109=44.44, *p*<0.001), 90% frequency bandwidth (F1,109=4.15, *p*=0.044), and average power (F1,102=8.86, *p*=0.004), whereas Savannah sparrow had higher variance for duration of song (F1,109=19.95, *p*<0.001), 5% low frequency (F1,109=6.26, *p*=0.014), and peak frequency (F1,109=6.79, *p*=0.01).

Mean coefficient of variation for Savannah sparrow (16.7%) and Baird’s sparrow (15.0%) syllables and songs were not significantly different (W=1657, p=0.76, n=119). Number of individuals and observations (each syllable or song) for each coefficient of variation calculation are given in Table 1.

## Response to Noise

In analyses with ambient noise and season as a covariate or during noise playback only (Table 1), both species changed nearly all parameters in response to ambient noise; Savannah sparrow did not change two parameters: delta time (duration) and 90% frequency bandwidth. Table 1 shows sample sizes for number of songs (observations) and number of individuals in each syllable and song analysis. Savannah sparrow changed 6/10 syllables and song in the presence of noise, and Baird’s sparrow changed 5/8 syllables and song (not all syllables had sufficient sample size to analyse) in the presence of noise. For Savannah sparrow, 9/66 analyses (13.6%) of song and syllables showed differences in the presence of noise, whereas in Baird’s sparrow 10/56 analyses (17.9%) of song and syllables showed differences. We compared a total of 122 models and as such, we additionally note that many of the changes in response to each unit of noise were at effect sizes that suggest biological significance. For example, many changes in frequency were ca. 10-50 Hz per unit increase in noise for Baird’s sparrows (with ca. 20-30% fixed variance explained) and up to 50 Hz in Savannah sparrows (with >40% fixed variance explained). Models for syllable duration and syllable power in Savannah sparrows also explained ca. 10-40% of variance. These effect sizes suggest that most changes we saw were actual responses to noise and not spurious results. There was no significant difference in the number of models that changed with noise for Baird’s sparrow or Savannah sparrow (χ2=0.15, df=1, *p*=0.70). Baird’s sparrow changed frequency and entropy parameters in three introductory syllable types and both increased and decreased power in two trill syllables. One trill syllable became shorter. Savannah sparrow increased power in syllables A, B, and C (introductory to mid-song syllables), altered frequency parameters in D, F, and I (trills and buzzes in middle and ends of songs), and altered entropy in E and D. Only syllable B shortened in duration.

## Relationship of noise to variability

Song parameters that had a higher variance were not more likely to change in response to noise (χ2=0, df=1, *p*=1). There was no relationship between which syllables or song parameters had seasonal changes and adjustment in response to noise (χ2<0.001, df=1, *p*=0.98). Syllable parameters that had a higher coefficient of variation were not more likely to be adjusted in response to noise (Table 1; Wilcoxon’s signed rank test, W=722, p=0.38, n=115).

# Discussion

Baird’s sparrow showed more variability than we expected considering the geographically and temporally fixed nature of its song in comparison to Savannah sparrow song (Bradley 1977; Pitocchelli 1981; Green 1992; Bradley 1994; Green et al. 2002; Sung & Handford 2006; Wheelwright et al. 2008; Williams et al. 2013). Despite range-wide differences between the species in song type variability, both Savannah sparrow and Baird’s sparrow adjusted their songs in the presence of noise. Finally, contrary to our predictions, variability at the song, syllable, and seasonal levels did not influence the ability of individuals to adjust their songs or syllables. Therefore, differences in population trends for the two species are unlikely to be caused by differences in overall signal production plasticity. Further research with multiple species would be needed to determine if our results hold as a general trend in song plasticity and ability to adjust to anthropogenic noise. Nonetheless, our results clearly disprove our hypothesis that Baird’s sparrows are more sensitive to anthropogenic development than Savannah sparrows because Baird’s sparrows lack the ability to alter their songs in noisy environments.

Although both species changed their songs in the presence of noise and over the season, the strategies for alterations differed between species. Baird’s sparrow shifted energy to produce the loudest sounds at lower frequencies, while Savannah sparrow shifted frequencies away from the low-frequency drilling noise. This strategy of decreasing peak frequency to increase transmission range has been found in other species (Marten et al. 1977) including as a response to increasing ambient noise (Potvin et al. 2014). Avoiding masking by shifting frequency away from noise is also a common strategy in many species (Patricelli & Blickley 2006; Laiolo 2011; Lampe et al. 2012). A study assessing impacts of road noise on birds showed that species with relatively lower frequency songs (i.e. between 2000 and 4000 Hz) were more prone to avoid roadways than species with higher frequency songs (Rheindt 2003), and Baird’s Sparrow songs are at a slightly lowered frequency than Savannah Sparrow songs. This may contribute to Baird’s sparrows’ avoidance of areas very near oil well infrastructure and of associated roads (Nenninger 2016), in addition to avoidance of structural habitat changes (Ludlow et al. 2015).

Our study was designed to allow for continuous comparison based on the effects of noise amplitude while accounting for seasonal changes in song characteristics. We suggest that future noise studies should also account for season as such changes are likely to be common based on hormonal dependencies (Smith, Brenowitz, & Wingfield 1997). An alternative design would be to record birds at control sites throughout the same timeframe and then compare differences between the control and treatment sites before, during, and after noise playback; however, we were unable to follow this protocol due to logistical constraints and relatively small sample sizes.

These species’ respective signal enhancement strategies could be based on signalling constraints (such as body size affecting frequency production) or their differing natural histories. Baird’s sparrow songs tend to be lower than Savannah sparrow songs (Figure 5), which may make it more difficult to compensate for noise by increasing frequencies; however, Baird’s sparrow’s adjustment strategy of lowering frequency for improved transmission might not gain as much distance as required in the presence of loud low-frequency noise such as that created by oil-well drilling. Perhaps more importantly, Baird’s sparrow has lower territory densities than Savannah sparrow throughout their range (Green et al. 2002; Wheelwright & Rising 2008). Any gain in transmission distance from lowering the frequency in Baird’s sparrow might be offset by the fact that their population densities are already lower, and thus receivers of the signal are further away. Such differences in natural history and population densities result in a larger distance over which any given Baird’s sparrow needs to transmit its song compared to a Savannah sparrow.

Signalling also may be constrained by which parts of the song are important for recognition or detection of quality by conspecifics. Altering an important component of the song could ensure that conspecifics receive an important signal. However, if the adjustment alters the content, it could change the ability of conspecifics to recognize the song as that of a conspecific, or change their ability to evaluate its attractiveness. Alternatively, species markers may be under selection to stay stable (Williams et al. 2013), in which case either option could result in poor communication in a noisy environment. Most changes to Baird’s sparrows song frequencies occurred in the introduction, which is the more important part of their song for species recognition (Green 1992). In Savannah sparrows, almost all syllables were altered, even those that are considered to be species or population markers such as the buzzes (Williams et al. 2013). Together, our data suggest that altering signals to improve transmission in noisy environments is possible for both species, and is occurring. An increasing number of studies are now examining whether alterations for effective transmission through noise alter attractiveness of signals (Mockford & Marshall 2009; Luther & Derryberry 2012; Cunnington & Fahrig 2013; Luther et al. 2016), so additional work is needed to determine the consequences of song alterations in this system.

We know little about why only some species that persist in noisy environments are able to change their behaviours (Francis, Ortega, et al. 2011b). At least in our study system, the species’ ability to adjust to noise does not appear to be related to variability in song features, so we speculate instead that it could be tied to the acoustic environment in which the species evolved. Both study species appear to have comparable local levels of population variation despite species-level differences in temporal and geographic variation. Species where individuals frequently encounter and adjust to natural noise may also be more likely to adjust to anthropogenic noise (e.g., Gough et al. 2014). Baird’s and Savannah sparrows both live in an environment with strong and variable winds (Environment Canada 2015), which strongly alter sound transmission. Previous work on Baird’s sparrow found that their song is well-suited for transmission and recognition in this acoustically heterogeneous environment (Green 1992). Baird’s sparrows can recognize and respond to any part of the song even after artificial modifications to imitate wind distortion of the signal (Green 1992). Thus, our study species may both show high song plasticity because they have evolved in the acoustically heterogeneous grasslands. More comparisons of additional species with varying levels of song plasticity are needed to determine the mechanism.

Our unexpected finding that seasonal, population, and individual variability were unrelated to the ability to adjust songs suggests that many species that evolved in acoustically variable environments, such as grasslands, may be capable of adjusting their vocal signals in the presence of anthropogenic noise. If this is true, other factors must explain negative effects such as noise avoidance and behavioral changes (Habib et al. 2006; Francis, Paritsis, et al. 2011; Blickley et al. 2012). For example, altering songs to increase sound propagation may not be sufficient to ensure signal transmission, or may alter the meaning of signals such that they are no longer attractive to potential mates. We recommend additional research into the plasticity of animal communication in the presence of noise, as understanding these mechanisms should allow us to target our conservation and mitigation efforts more effectively to ultimately help conserve species at risk.

# Acknowledgements

We thank Eastern Irrigation District of Newell County, Alberta, for land access. M. Fenton, C. Swider, and W.T. Honeycutt assisted with calculating predicted noise. Volunteers and technicians N. Abbott, M.-È. Cyr, E. Geurts, J. Horvat, S. Orue, L. Parker, J. Roy, S. Sibler, and C. Swider assisted with noise playback and song measurements.

# References

Alberta Government. 2012. Alberta’s energy development: An overview. Edmonton, Alberta, Canada: Energy Resources Conservation Board.

Askins RA, Chávez-Ramírez F, Dale BC, Haas CA, Herkert JR, Knopf FL, Vickery PD. 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions. Ornithol Monogr.:iii–46.

Bailey RC, Byrnes J. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. Syst Biol. 39:124–130.

Bartoń K. 2009. MuMIn: multi-model inference. Available from: https://cran.r-project.org/package=MuMIn

Bates D, Maechler M, Bolker B. 2011. lme4: Linear mixed-effects models using S4 classes. Available from: http://CRAN.R-project.org/package=lme4

Bayne EM, Habib L, Boutin S. 2008. Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conserv Biol. 22:1186–1193.

Bermudez-Cuamatzin E, Rios-Chelen AA, Gil D, Garcia CM. 2011. Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. Biol Lett. 7:36–38.

Bioacoustics Research Program. 2014. Raven Pro: Interactive Sound Analysis Software (Version 1.5). Ithaca, NY: Cornell Laboratory of Ornithology.

Blickley JL, Blackwood D, Patricelli GL. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of Greater Sage-Grouse at leks. Conserv Biol. 26:461–471.

Borror DJ. 1961. Songs of finches (Fringillidae) of eastern North America. Ohio J Sci. 61:161–174.

Bradbury JW, Vehrencamp SL. 1998. Principles of Animal Communication. Sunderland, MA: Sinauer Associates, Inc.

Bradley RA. 1977. Geographic variation in the song of Belding’s Savannah Sparrow (*Passerculus sandwichensis beldingi*). Bull Fla State Mus Biol Sci. 22:57–100.

Bradley RA. 1994. Cultural change and geographic variation in the songs of the Belding’s Savannah Sparrow (*Passerculus sandwichensis beldingi*). Bull South Calif Acad Sci. 93:91–109.

Brumm H. 2004. The impact of environmental noise on song amplitude in a territorial bird. J Anim Ecol. 73:434–440.

Burnell K. 1998. Cultural variation in savannah sparrow, *Passerculus sandwichensis*, songs: an analysis using the meme concept. Anim Behav. 56:995–1003.

Byers, B. 1995. Song types, repertoires and song variability in a population of chestnut-sided warblers. Condor 97:390–401.

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

Charif RA, Strickman LM, Waack. 2010. Raven Pro 1.4 User’s Manual. Ithaca, NY: Cornell Laboratory of Ornithology.

Chew L. 1981. Geographic and individual variation in the morphology and sequential organization of the song of the Savannah Sparrow (*Passerculus sandwichensis*). Can J Zool. 59:702–713.

COSEWIC. 2012. COSEWIC assessment and status report on the Baird’s Sparrow *Ammodramus bairdii* in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada. Available from: www.registrelep-sararegistry.gc.ca/default\_e.cfm

Cunnington GM, Fahrig L. 2013. Mate attraction by male anurans in the presence of traffic noise: Anuran mate attraction and traffic noise. Anim Conserv. 16:275–285.

Derryberry EP. 2007. Evolution of bird song affects signal efficacy: an experimental test using historical and current signals. Evolution. 61:1938–1945.

Environment Canada. 2015. Precipitation Chart for 1981 to 2010 Canadian Climate Normals for Brooks, AB. [cited 2015 Oct 16]. Available from: http://climate.weather.gc.ca/climate\_normals/results\_1981\_2010\_e.html?stnID=2197&lang=e&province=AB&provSubmit=go&dCode=0

Ey E, Fischer J. 2009. The “acoustic adaptation hypothesis”—A review of the evidence from birds, anurans, and mammals. Bioacoustics Int J Anim Sound Its Rec. 19:21–48.

Fox J, Weisberg S, Bates D, Fox MJ. 2012. Package “car”. Available from: http://cran.ma.imperial.ac.uk/web/packages/car/car.pdf

Francis CD. 2015. Vocal traits and diet explain avian sensitivities to anthropogenic noise. Glob Change Biol. 21:1809–1820.

Francis CD, Kleist NJ, Ortega CP, Cruz A. 2012. Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal. Proc R Soc B Biol Sci. 279:2727–2735.

Francis CD, Ortega CP, Cruz A. 2011a. Noise pollution filters bird communities based on vocal frequency. PLoS One. 6:e27052.

Francis CD, Ortega CP, Cruz A. 2011b. Different behavioural responses to anthropogenic noise by two closely related passerine birds. Biol Lett. 7:850–852.

Francis CD, Paritsis J, Ortega CP, Cruz A. 2011. Landscape patterns of avian habitat use and nest success are affected by chronic gas well compressor noise. Landsc Ecol. 26:1269–1280.

Garcia CM, Bermúdez-Cuamatzin E, Ríos-Chelén AA, Gil D. 2009. Strategies of song adaptation to urban noise in the house finch: syllable pitch plasticity or differential syllable use? Behaviour. 146:1269–1286.

Gough DC, Mennill DJ, Nol E. 2014. Singing seaside: Pacific Wrens ( *Troglodytes pacificus* ) change their songs in the presence of natural and anthropogenic noise. Wilson J Ornithol. 126:269–278.

Green MT. 1992. Adaptations of Baird’s Sparrows (*Ammodramus bairdsii*) to grasslands: acoustic communication and nomadism [Ph.D. dissertation]. Chapel Hill: University of North Carolina.

Green MT, Lowther PE, Jones SL, Davis SK, Dale BC. 2002. Baird’s Sparrow (*Ammodramus bairdii*). In: Poole A, editor. Birds N Am Online No 638. Ithaca: Cornell Lab of Ornithology.

Habib L, Bayne EM, Boutin S. 2006. Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*: Chronic noise and ovenbird pairing success. J Appl Ecol. 44:176–184.

Halfwerk W, Slabbekoorn H. 2009. A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. Anim Behav. 78:1301–1307.

International Standards Organization. 1993. ISO 9613-1:1993 Attenuation of sound during propagation outdoors -- Part 1: Calculation of the absorption of sound by the atmosphere. Geneva, Switzerland: International Standards Organization.

International Standards Organization. 1996. ISO 9613-2:1996 Attenuation of sound during propagation outdoors -- Part 2: General method of calculation. Geneva, Switzerland: International Standards Organization.

Jakes A. 2015. Factors influencing seasonal migrations of pronghorn across the northern sagebrush steppe [Ph.D. dissertation]. Calgary, AB, Canada: University of Calgary.

Kirschel ANG, Blumstein DT, Cohen RE, Buermann W, Smith TB, Slabbekoorn H. 2009. Birdsong tuned to the environment: green hylia song varies with elevation, tree cover, and noise. Behav Ecol. 20:1089–1095.

Kuznetsova A, Brockhoff PB, Christensen RHB. 2015. lmerTest: tests in linear mixed effects models. Available from: http://CRAN.R-project.org/package=lmerTest

Lackey MA, Morrison ML, Loman ZG, Collier BA, Wilkins RN. 2012. Experimental determination of the response of Golden-cheeked Warblers ( *Setophaga chrysoparia* ) to road construction noise. Ornithol Monogr. 74:91–100.

Laiolo P. 2011. The Rufous-Collared Sparrow Zonotrichia capensis utters higher frequency songs in urban habitats. Rev Catalana D’Ornitologia. 27:25–30.

Lampe HM, Espmark YO. 1987. Singing activity and song pattern of the redwing *Turdus iliacus* during the breeding season. Ornis Scand. 18:179–185.

Lampe U, Schmoll T, Franzke A, Reinhold K. 2012. Staying tuned: grasshoppers from noisy roadside habitats produce courtship signals with elevated frequency components. Funct Ecol. 26:1348–1354.

Lessells CM, Boag PT. 1987. Unrepeatable repeatabilities: a common mistake. Auk. 104:116–121.

Ludlow SM, Brigham RM, Davis SK. 2015. Oil and natural gas development has mixed effects on the density and reproductive success of grassland songbirds. Condor. 117:64–75.

Luther DA, Derryberry EP. 2012. Birdsongs keep pace with city life: changes in song over time in an urban songbird affects communication. Anim Behav. 83:1059–1066.

Luther DA, Phillips J, Derryberry EP. 2016. Not so sexy in the city: urban birds adjust songs to noise but compromise vocal performance. Behav Ecol. 27:332–340.

Marten K, Quine D, Marler P. 1977. Sound transmission and its significance for animal vocalization. Behav Ecol Sociobiol. 2:291–302.

McClure CJW, Ware HE, Carlisle J, Kaltenecker G, Barber JR. 2013. An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proc R Soc Lond B Biol Sci. 280:20132290.

Mockford EJ, Marshall RC. 2009. Effects of urban noise on song and response behaviour in great tits. Proc R Soc B Biol Sci. 276:2979–2985.

Morton ES. 1975. Ecological sources of selection on avian sounds. Am Nat. 109:17–34.

Nenninger HR. 2016. The effects of conventional oil wells and associated infrastructure on the abundances of five grassland songbird species in Alberta’s mixed-grass prairie [Master of Natural Resource Management]. Winnipeg, MB, Canada: University of Manitoba.

Northrup JM, Wittemyer G. 2013. Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. Ecol Lett. 16:112–125.

Parris KM, McCarthy MA. 2013. Predicting the effect of urban noise on the active space of avian vocal signals. Am Nat. 182:452–464.

Parris KM, Schneider A. 2009. Impacts of traffic noise and traffic volume on birds of roadside habitats. Ecol Soc. 14:29.

Patricelli GL, Blickley JL. 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. Auk. 123:639–649.

Pitocchelli J. 1981. Song dialects, and vocal development of Savannah sparrows (*Passerculus sandwichensis labradorius*, Howe) breeding in Newfoundland and the St. Pierre et Miquelon islands [M.Sc. thesis]. St. John’s, Newfoundland, Canada: Memorial University of Newfoundland.

Podos J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). Evolution. 51:537–551.

Pohl NU, Slabbekoorn H, Klump GM, Langemann U. 2009. Effects of signal features and environmental noise on signal detection in the great tit, *Parus major*. Anim Behav. 78:1293–1300.

Potvin DA, Mulder RA, Parris KM. 2014. Silvereyes decrease acoustic frequency but increase efficacy of alarm calls in urban noise. Anim Behav. 98:27–33.

R Core Team. 2015. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: http://www.R-project.org/

Rheindt FE. 2003. The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? J Für Ornithol. 144:295–306.

Ripmeester EAP, Kok JS, van Rijssel JC, Slabbekoorn H. 2010. Habitat-related birdsong divergence: a multi-level study on the influence of territory density and ambient noise in European blackbirds. Behav Ecol Sociobiol. 64:409–418.

Rosa P, Swider CR, Leston L, Koper N. 2015. Disentangling effects of noise from presence of anthropogenic infrastructure: Design and testing of system for large-scale playback experiments. Wildl Soc Bull. 39:364–372.

Sauer JR, Hines JE, Fallon JE, Pardieck KL, Ziolkowski, Jr. DJ, Link WA. 2014. The North American Breeding Bird Survey, Results and Analysis 1966 – 2013, version 01.30.2015. Laurel, MD: USGS Patuxent Wildlife Research Center.

Shannon G, Angeloni LM, Wittemyer G, Fristrup KM, Crooks KR. 2014. Road traffic noise modifies behaviour of a keystone species. Anim Behav. 94:135–141.

Slabbekoorn H, Bouton N, van Opzeeland I, Coers A, Cate C ten, Popper AN. 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. Trends Ecol Evol. 25:419–427.

Slabbekoorn H, Ripmeester EAP. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Mol Ecol. 17:72–83.

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

Smith GT, Brenowitz EA, Wingfield JC. 1997. Roles of photoperiod and testosterone in seasonal plasticity of the avian song control system. J Neurobiol. 32:426–442.

Smith GT, Brenowitz EA, Wingfield JC, Beecher MD. 1997. Seasonal changes in testosterone, neural attributes of song control nuclei, and song structure in wild songbirds. J Neurosci. 17:6001–6010.

Snell-Rood EC. 2012. The effect of climate on acoustic signals: does atmospheric sound absorption matter for bird song and bat echolocation? J Acoust Soc Am. 131:1650–1658.

Sokal RR, Rohlf FJ. 2012. Biometry. 4th ed. New York: W.H. Freeman and Company.

Sung H-C, Handford P. 2006. Songs of the Savannah Sparrow: structure and geographic variation. Can J Zool. 84:1637–1646.

Tumer EC, Brainard MS. 2007. Performance variability enables adaptive plasticity of “crystallized” adult birdsong. Nature. 450:1240–1244.

Verzijden MN, Ripmeester EAP, Ohms VR, Snelderwaard P, Slabbekoorn H. 2010. Immediate spectral flexibility in singing chiffchaffs during experimental exposure to highway noise. J Exp Biol. 213:2575–2581.

Ware HE, McClure CJW, Carlisle JD, Barber JR. 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. Proc Natl Acad Sci. 112:12105–12109.

Wheelwright NT, Rising JD. 2008. Savannah Sparrow (*Passerculus sandwichensis*). In: Poole A, editor. Birds N Am Online No 045. Ithaca: Cornell Lab of Ornithology.

Wheelwright NT, Swett MB, Levin II, Kroodsma DE, Freeman-Gallant CR, Williams H. 2008. The influence of different tutor types on song learning in a natural bird population. Anim Behav. 75:1479–1493.

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

Van Wilgenburg SL, Hobson KA, Bayne EM, Koper N. 2013. Estimated avian nest loss associated with oil and gas exploration and extraction in the western Canadian sedimentary basin. Avian Conserv Ecol 8:9.

Williams H, Levin II, Norris DR, Newman AEM, Wheelwright NT. 2013. Three decades of cultural evolution in Savannah sparrow songs. Anim Behav. 85:213–223.

Wolak ME, Fairbairn DJ, Paulsen YR. 2012. Guidelines for estimating repeatability. Methods Ecol Evol. 3:129–137.

# Tables

Table 1. Song and syllable repeatability and model parameters for Baird’s sparrows and Savannah sparrows in southern Alberta,, from May-July 2014, testing whether song and syllable parameters change in response to experimental noise playback. Repeatability calculated using only non-treatment time periods (before and after noise). Model parameters significant at p<0.05 in bold.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  |  | Coefficient of variation | Whole-season model |  |  | During noise model |  |
|  |  |  |  |  |  |  |  | Ambient noise |  | Relative date |  |  |  |  |  | Ambient noise |  |  |  |  |
| Species | Section | Parameter | CV (%) | N | Nobs | Nindividuals | Intercept (SE) | β (SE) | p | β (SE) | p | Marginal R2 | Conditional R2 | Nobs | Nindividuals | Intercept (SE) | β (SE) | p | Marginal R2 | Conditional R2 |
| Baird's Sparrow | songs | Peak.Freq | 16.9 | 16 | 86 | 29 | 5600.124 (966.961) | -9.19 (14.252) | 0.525 | -3.38 (7.423) | 0.653 | 0.013 | 0.572 | 37 | 13 | 7041.416 (839.854) | **-34.648 (12.635)** | **0.021** | 0.194 | 0.519 |
|  | Freq95 | 10.7 | 16 | 86 | 29 | 8432.855 (871.243) | -20.503 (12.678) | 0.119 | -4.875 (6.726) | 0.475 | 0.052 | 0.438 | 37 | 13 | 10647.882 (1056.886) | **-56.723 (16.185)** | **0.005** | 0.323 | 0.481 |
|  | Freq5 | 11.1 | 16 | 86 | 29 | 4276.273 (594.747) | -4.669 (8.787) | 0.6 | 1.942 (4.593) | 0.676 | 0.015 | 0.737 | 37 | 13 | 5377.62 (745.507) | -21.212 (11.444) | 0.089 | 0.161 | 0.66 |
|  | Freq.BW90 | 27.1 | 16 | 86 | 29 | 4167.32 (892.114) | -15.898 (13.117) | 0.236 | -7.093 (6.802) | 0.307 | 0.044 | 0.435 | 37 | 13 | 5272.145 (1143.401) | -35.48 (17.52) | 0.066 | 0.147 | 0.401 |
|  | Delta.Time | 10.6 | 16 | 86 | 29 | 1.682 (0.255) | 0.003 (0.004) | 0.44 | -0.001 (0.002) | 0.668 | 0.02 | 0.435 | 37 | 13 | 1.79 (0.45) | 0.002 (0.007) | 0.82 | 0.003 | 0.513 |
|  | Avg.Power | 7.8 | 16 | 86 | 29 | 80.899 (7.028) | -0.086 (0.104) | 0.414 | **0.152 (0.054)** | **0.01** | 0.22 | 0.809 | 37 | 13 | 79.954 (10.424) | -0.015 (0.159) | 0.929 | 0 | 0.718 |
|  | Agg.Entropy | 10.1 | 16 | 86 | 29 | 4.477 (0.437) | -0.007 (0.006) | 0.305 | -0.004 (0.003) | 0.203 | 0.057 | 0.618 | 37 | 13 | 4.448 (0.487) | -0.007 (0.007) | 0.338 | 0.044 | 0.415 |
| syllables.a | Peak.Freq | 8.5 | 6 | 48 | 15 | 6112.492 (1282.861) | 9.791 (19.311) | 0.623 | 4.529 (13.195) | 0.739 | 0.021 | 0.998 | 28 | 9 | 8011.449 (1883.076) | -16.78 (29.799) | 0.59 | 0.035 | 0.997 |
|  | Freq95 | 8.9 | 6 | 48 | 15 | 5396.111 (1289.012) | 31.699 (19.526) | 0.13 | -4.373 (12.095) | 0.724 | 0.159 | 0.976 | 28 | 9 | 6859.811 (2069.563) | 7.918 (32.733) | 0.816 | 0.007 | 0.979 |
|  | Freq5 | 8.7 | 6 | 48 | 15 | 5882.173 (1296.436) | 11.565 (19.508) | 0.566 | 5.177 (13.375) | 0.707 | 0.028 | 0.997 | 28 | 9 | 7812.632 (1924.917) | -15.173 (30.461) | 0.633 | 0.028 | 0.997 |
|  | Freq.BW90 | 58.6 | 6 | 48 | 15 | -529.633 (533.351) | **18.688 (7.975)** | **0.04** | -4.368 (5.684) | 0.458 | 0.238 | 0.889 | 28 | 9 | -970.377 (801.902) | 23.422 (12.687) | 0.107 | 0.258 | 0.88 |
|  | Delta.Time | 19.2 | 6 | 48 | 15 | 0.077 (0.031) | 0.0003 (0.0004) | 0.527 | -0.0004 (0.0003) | 0.185 | 0.136 | 0.857 | 28 | 9 | 0.116 (0.047) | <-0.001 (0.001) | 0.553 | 0.035 | 0.848 |
|  | Avg.Power | 4.7 | 6 | 48 | 15 | 96.943 (13.115) | -0.168 (0.199) | 0.413 | 0.142 (0.123) | 0.272 | 0.11 | 0.758 | 28 | 9 | 105.621 (22.388) | -0.274 (0.354) | 0.465 | 0.056 | 0.817 |
|  | Agg.Entropy | 21.4 | 6 | 48 | 15 | 0.521 (0.91) | **0.033 (0.014)** | **0.035** | -0.008 (0.01) | 0.423 | 0.262 | 0.898 | 28 | 9 | -0.346 (1.451) | 0.043 (0.023) | 0.104 | 0.266 | 0.903 |
| syllables.b | Peak.Freq | 25.2 | 16 | 399 | 29 | 6108.509 (591.756) | -13.221 (8.48) | 0.12 | -1.998 (4.122) | 0.628 | 0.006 | 0.006 | 175 | 13 | 6758.28 (827.031) | -23.85 (12.473) | 0.058 | 0.021 | 0.021 |
|  | Freq95 | 25.4 | 16 | 399 | 29 | 6553.072 (614.692) | **-17.094 (8.809)** | **0.053** | -3.42 (4.282) | 0.425 | 0.01 | 0.01 | 175 | 13 | 7395.944 (897.077) | **-30.885 (13.492)** | **0.046** | 0.031 | 0.046 |
|  | Freq5 | 26.2 | 16 | 399 | 29 | 5669.014 (592.023) | -9.533 (8.484) | 0.262 | -1.34 (4.124) | 0.745 | 0.003 | 0.003 | 175 | 13 | 6085.52 (820.411) | -16.814 (12.373) | 0.177 | 0.011 | 0.011 |
|  | Freq.BW90 | 66.4 | 16 | 399 | 29 | 966.455 (254.275) | **-7.848 (3.666)** | **0.043** | **-3.615 (1.979)** | **0.08** | 0.066 | 0.416 | 175 | 13 | 1358.521 (464.175) | -14.67 (7.072) | 0.067 | 0.109 | 0.491 |
|  | Delta.Time | 29.5 | 16 | 399 | 29 | 0.126 (0.027) | -0.001 (<0.001) | 0.258 | **<-0.001 (<0.001)** | **0.041** | 0.07 | 0.509 | 175 | 13 | 0.145 (0.041) | -0.001 (0.001) | 0.176 | 0.069 | 0.5 |
|  | Avg.Power | 8.9 | 16 | 399 | 29 | 89.948 (7.78) | -0.066 (0.115) | 0.567 | **0.156 (0.06)** | **0.015** | 0.131 | 0.562 | 175 | 13 | 84.329 (8.458) | 0.076 (0.127) | 0.563 | 0.007 | 0.393 |
|  | Agg.Entropy | 22.2 | 16 | 399 | 29 | 3.051 (0.44) | **-0.015 (0.006)** | **0.03** | -0.006 (0.003) | 0.104 | 0.067 | 0.461 | 175 | 13 | 3.421 (0.759) | -0.022 (0.012) | 0.084 | 0.108 | 0.544 |
| syllables.j | Peak.Freq | 7.8 | 3 | 28 | 3 | -690592.284 (969912.174) | 13479.181 (18766.714) | 0.557 | -4432.844 (6176.452) | 0.557 | 0.115 | 0.656 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Freq95 | 7.7 | 3 | 28 | 3 | -608292.142 (1590114.747) | 11895.46 (30766.922) | 0.705 | -3903.796 (10125.687) | 0.705 | 0.1 | 0.833 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Freq5 | 2.5 | 3 | 28 | 3 | -121813.294 (149307.982) | 2471.473 (2888.952) | 0.739 | -814.535 (950.952) | 0.739 | 0.065 | 0.229 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Freq.BW90 | 49.5 | 3 | 28 | 3 | -486476.951 (1694086.172) | 9423.95 (32778.649) | 0.777 | -3089.248 (10787.733) | 0.778 | 0.088 | 0.861 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Delta.Time | 7.6 | 3 | 28 | 3 | -12.64 (14.455) | 0.247 (0.28) | 0.415 | -0.081 (0.092) | 0.417 | 0.38 | 0.8 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Avg.Power | 8.1 | 3 | 28 | 3 | 5856.65 (9407.728) | -111.89 (182.029) | 0.561 | 37.098 (59.908) | 0.558 | 0.431 | 0.813 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Agg.Entropy | 18 | 3 | 28 | 3 | -652.294 (724.285) | 12.659 (14.014) | 0.399 | -4.156 (4.612) | 0.4 | 0.298 | 0.766 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
| syllables.k | Peak.Freq | 13.5 | 3 | 87 | 6 | 5180.761 (533.751) | 2.121 (7.077) | 0.765 | 1.426 (4.088) | 0.728 | 0.002 | 0.498 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Freq95 | 10.6 | 3 | 87 | 6 | 6235.833 (724.888) | -2.735 (10.293) | 0.791 | 8.654 (5.995) | 0.152 | 0.016 | 0.376 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Freq5 | 11.9 | 3 | 87 | 6 | 5038.654 (371.7) | 5.023 (4.688) | 0.468 | -22.093 (2.837) | 0.162 | 0.278 | 0.752 | 51 | 3 | 4128.667 (149.084) | **9.391 (2.52)** | **0.001** | 0.217 | 0.217 |
|  | Freq.BW90 | 82.6 | 3 | 87 | 6 | 1295.325 (749.596) | -9.251 (10.959) | 0.401 | **30.622 (6.43)** | **<0.001** | 0.162 | 0.409 | 51 | 3 | 2185.641 (2043.292) | -13.235 (33.846) | 1 | 0.008 | 0.373 |
|  | Delta.Time | 28.1 | 3 | 87 | 6 | 0.096 (0.022) | <0.001 (<0.001) | 0.683 | **0.002 (<0.001)** | **0.07** | 0.299 | 0.975 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Avg.Power | 6.2 | 3 | 87 | 6 | 78.607 (15.962) | 0.077 (0.257) | 0.785 | -0.097 (0.198) | 0.657 | 0.033 | 0.757 | 51 | 3 | 43.045 (19.016) | 0.652 (0.32) | 0.985 | 0.391 | 0.751 |
|  | Agg.Entropy | 18.7 | 3 | 87 | 6 | 2.46 (0.371) | -0.005 (0.006) | 0.511 | 0.011 (0.004) | 0.206 | 0.148 | 0.286 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
| syllables.m | Peak.Freq | 4.1 | 10 | 750 | 16 | 4036.347 (418.885) | 5.124 (6.152) | 0.42 | -1.626 (3.347) | 0.635 | 0.063 | 0.939 | 238 | 6 | 3444.142 (669.04) | 12.446 (10.121) | 0.286 | 0.138 | 0.934 |
|  | Freq95 | 4 | 10 | 750 | 16 | 4141.829 (419.085) | 5.47 (6.155) | 0.39 | -1.575 (3.349) | 0.646 | 0.066 | 0.931 | 238 | 6 | 3584.651 (643.328) | 12.136 (9.733) | 0.281 | 0.142 | 0.94 |
|  | Freq5 | 4.5 | 10 | 750 | 16 | 3931.276 (436.877) | 4.764 (6.417) | 0.471 | -1.968 (3.491) | 0.583 | 0.062 | 0.937 | 238 | 6 | 3347.093 (694.1) | 11.856 (10.501) | 0.322 | 0.119 | 0.934 |
|  | Freq.BW90 | 24.9 | 10 | 750 | 16 | 254.196 (47.228) | 0.117 (0.633) | 0.857 | 0.297 (0.335) | 0.396 | 0.006 | 0.282 | 238 | 6 | 254.761 (75.956) | 0.034 (1.116) | 0.978 | 0 | 0.206 |
|  | Delta.Time | 22.9 | 10 | 750 | 16 | 0.02 (0.003) | 0 (<0.001) | 0.938 | 0 (<0.001) | 0.366 | 0.009 | 0.149 | 238 | 6 | 0.022 (0.007) | 0 (0<0.001) | 0.781 | 0.003 | 0.248 |
|  | Avg.Power | 10.1 | 10 | 750 | 16 | 77.527 (11.558) | 0.045 (0.169) | 0.794 | 0.145 (0.092) | 0.139 | 0.082 | 0.589 | 238 | 6 | 54.6 (12.351) | 0.45 (0.179) | 0.079 | 0.175 | 0.545 |
|  | Agg.Entropy | 9.7 | 10 | 750 | 16 | 1.943 (0.176) | -0.001 (0.002) | 0.628 | 0.001 (0.001) | 0.57 | 0.009 | 0.581 | 238 | 6 | 1.84 (0.27) | 0 (0.004) | 0.994 | 0 | 0.434 |
| syllables.o | Peak.Freq | 6.7 | 2 | 153 | 4 | 6005.499 (2492.938) | -28.874 (34.117) | 0.999 | 3.123 (3.874) | 0.999 | 0.036 | 0.426 | 72 | 2 | -227.552 (5795.561) | 58.446 (80.54) | 0.999 | 0.078 | 0.355 |
|  | Freq95 | 1.4 | 2 | 153 | 4 | 4075.211 (1423.396) | 3.877 (19.567) | 0.932 | 1.057 (2.175) | 0.882 | 0.026 | 0.52 | 72 | 2 | 5981.323 (1995.625) | -22.203 (27.733) | 0.999 | 0.094 | 0.366 |
|  | Freq5 | 2.1 | 2 | 153 | 4 | 5406.824 (763.572) | -24.555 (10.42) | 0.999 | 0.555 (1.198) | 0.999 | 0.112 | 0.742 | 72 | 2 | 2892.771 (1185.356) | 10.503 (16.472) | 0.998 | 0.07 | 0.398 |
|  | Freq.BW90 | 15.4 | 2 | 153 | 4 | 506.082 (2288.586) | 3.514 (31.785) | 0.98 | -2.525 (3.299) | 0.964 | 0.079 | 0.607 | 72 | 2 | 3089.966 (3198.284) | -32.726 (44.443) | 0.991 | 0.127 | 0.58 |
|  | Delta.Time | 7.7 | 2 | 153 | 4 | 0.097 (0.017) | -0.001 (<0.001) | 0.999 | -0.001 (<0.001) | 1 | 0.121 | 0.124 | 72 | 2 | 0.092 (0.045) | -0.001 (0.001) | 1 | 0.045 | 0.139 |
|  | Avg.Power | 6.5 | 2 | 153 | 4 | 227.456 (154.757) | -2.079 (2.137) | 0.665 | 0.171 (0.231) | 0.824 | 0.159 | 0.836 | 72 | 2 | 27.18 (82.18) | 0.731 (1.142) | 0.999 | 0.047 | 0.257 |
|  | Agg.Entropy | 5.1 | 2 | 153 | 4 | 2.387 (0.608) | 0.005 (0.009) | 0.586 | **-0.003 (0.001)** | **<0.001** | 0.101 | 0.101 | 72 | 2 | 2.431 (0.92) | 0.003 (0.013) | 1 | 0.001 | 0.002 |
| syllables.p | Peak.Freq | NA | NA | NA | NA | NA (NA) | NA (NA) | NA | NA (NA) | NA | NA | NA | 146 | 4 | 4438.149 (138.376) | 0.086 (2.031) | 0.966 | 0 | 0.647 |
|  | Freq95 | NA | NA | NA | NA | NA (NA) | NA (NA) | NA | NA (NA) | NA | NA | NA | 146 | 4 | 5112.046 (237.024) | -5.443 (3.793) | 0.156 | 0.031 | 0.249 |
|  | Freq5 | NA | NA | NA | NA | NA (NA) | NA (NA) | NA | NA (NA) | NA | NA | NA | 146 | 4 | 4339.33 (145.235) | -0.281 (2.147) | 0.896 | 0 | 0.629 |
|  | Freq.BW90 | NA | NA | NA | NA | NA (NA) | NA (NA) | NA | NA (NA) | NA | NA | NA | 146 | 4 | 664.599 (233.752) | -3.396 (3.814) | 0.75 | 0.019 | 0.136 |
|  | Delta.Time | NA | NA | NA | NA | NA (NA) | NA (NA) | NA | NA (NA) | NA | NA | NA | 146 | 4 | 0.066 (0.006) | **<-0.001 (<0.001)** | **0.038** | 0.04 | 0.588 |
|  | Avg.Power | NA | NA | NA | NA | NA (NA) | NA (NA) | NA | NA (NA) | NA | NA | NA | 146 | 4 | 94.354 (2.962) | **-0.119 (0.049)** | **0.015** | 0.04 | 0.04 |
|  | Agg.Entropy | NA | NA | NA | NA | NA (NA) | NA (NA) | NA | NA (NA) | NA | NA | NA | 146 | 4 | 2.248 (0.737) | 0.002 (0.012) | 0.909 | 0.001 | 0.223 |
| Savannah Sparrow | songs | Peak.Freq | 19.9 | 21 | 86 | 29 | 7694.593 (1165.569) | -13.173 (19.798) | 0.512 | -11.777 (11.032) | 0.295 | 0.037 | 0.401 | 24 | 8 | 5876.974 (1632.95) | 10.088 (27.344) | 0.725 | 0.006 | 0.035 |
|  | Freq95 | 2.5 | 21 | 86 | 29 | 8325.346 (167.298) | 3.682 (2.842) | 0.207 | **-6.449 (1.58)** | **<0.001** | 0.296 | 0.696 | 24 | 8 | 7822.147 (293.593) | 9.89 (4.916) | 0.091 | 0.302 | 0.81 |
|  | Freq5 | 13.5 | 21 | 86 | 29 | 3229.846 (597.452) | **21.551 (10.15)** | **0.043** | -9.193 (5.626) | 0.114 | 0.161 | 0.858 | 24 | 8 | 2861.791 (509.01) | 18.271 (8.523) | 0.076 | 0.221 | 0.383 |
|  | Freq.BW90 | 13.8 | 21 | 86 | 29 | 5081.091 (560.601) | -17.425 (9.483) | 0.078 | 2.551 (5.27) | 0.632 | 0.091 | 0.803 | 24 | 8 | 4965.1 (537.297) | -8.594 (8.997) | 0.376 | 0.053 | 0.242 |
|  | Delta.Time | 17 | 21 | 86 | 29 | 2.324 (0.442) | 0 (0.008) | 0.96 | 0.003 (0.004) | 0.431 | 0.02 | 0.819 | 24 | 8 | 2.072 (0.777) | 0.008 (0.013) | 0.57 | 0.042 | 0.885 |
|  | Avg.Power | 4.8 | 18 | 76 | 25 | 68.024 (3.581) | 0.081 (0.06) | 0.193 | 0.018 (0.036) | 0.615 | 0.066 | 0.716 | 21 | 7 | 63.386 (3.945) | 0.151 (0.058) | 0.085 | 0.183 | 0.879 |
|  | Agg.Entropy | 6.9 | 21 | 86 | 29 | 4.55 (0.299) | 0 (0.005) | 0.981 | 0.002 (0.003) | 0.485 | 0.013 | 0.623 | 24 | 8 | 4.186 (0.285) | 0.008 (0.005) | 0.098 | 0.095 | 0.292 |
| syllables.A | Peak.Freq | 4.6 | 21 | 371 | 29 | 8047.258 (158.585) | 2.549 (2.688) | 0.352 | **-5.061 (1.52)** | **0.002** | 0.061 | 0.147 | 102 | 8 | 7534.381 (171.588) | **9.005 (2.754)** | **0.001** | 0.093 | 0.131 |
|  | Freq95 | 3.9 | 21 | 371 | 29 | 8577.954 (155.437) | 1.946 (2.636) | 0.467 | **-5.164 (1.485)** | **0.002** | 0.08 | 0.206 | 102 | 8 | 8206.544 (215.593) | 6.461 (3.608) | 0.137 | 0.065 | 0.143 |
|  | Freq5 | 5 | 21 | 371 | 29 | 7938.195 (152.976) | 1.422 (2.592) | 0.588 | **-4.776 (1.468)** | **0.003** | 0.051 | 0.12 | 102 | 8 | 7410.568 (153.869) | **8.561 (2.457)** | **0.001** | 0.104 | 0.147 |
|  | Freq.BW90 | 45.4 | 21 | 371 | 29 | 634.664 (105.167) | 0.876 (1.733) | 0.618 | -0.625 (0.984) | 0.531 | 0.002 | 0.067 | 102 | 8 | 764.957 (196.554) | -1.718 (3.241) | 0.623 | 0.016 | 0.436 |
|  | Delta.Time | 14.9 | 21 | 371 | 29 | 0.058 (0.005) | 0 (<0.001) | 0.277 | 0 (<0.001) | 0.97 | 0.011 | 0.186 | 102 | 8 | 0.071 (0.009) | 0 (<0.001) | 0.353 | 0.035 | 0.209 |
|  | Avg.Power | 10.2 | 18 | 330 | 25 | 78.398 (4.176) | 0.047 (0.07) | 0.506 | 0.061 (0.042) | 0.162 | 0.022 | 0.148 | 91 | 7 | 68.83 (3.733) | **0.219 (0.063)** | **0.001** | 0.119 | 0.119 |
|  | Agg.Entropy | 11.4 | 21 | 371 | 29 | 2.872 (0.216) | 0.002 (0.004) | 0.624 | -0.001 (0.002) | 0.697 | 0.004 | 0.295 | 102 | 8 | 3.236 (0.436) | -0.005 (0.007) | 0.559 | 0.028 | 0.544 |
| syllables.B | Peak.Freq | 6.8 | 17 | 84 | 25 | 8943.401 (477.335) | -0.963 (7.936) | 0.904 | -1.882 (4.356) | 0.67 | 0.003 | 0.12 | 20 | 8 | 8147.677 (577.239) | 15.34 (9.878) | 0.138 | 0.113 | 0.113 |
|  | Freq95 | 6.6 | 17 | 84 | 25 | 9541.659 (561.014) | 0.235 (9.326) | 0.98 | -4.936 (5.217) | 0.356 | 0.019 | 0.319 | 20 | 8 | 9257.196 (928.761) | 7.138 (15.609) | 0.667 | 0.023 | 0.543 |
|  | Freq5 | 17.6 | 17 | 84 | 25 | 6348.851 (1195.585) | 6.377 (19.879) | 0.751 | 11.875 (11.197) | 0.3 | 0.03 | 0.424 | 20 | 8 | 6945.464 (1721.326) | 12.359 (28.966) | 0.69 | 0.018 | 0.442 |
|  | Freq.BW90 | 42.9 | 17 | 84 | 25 | 3210.784 (1145.72) | -6.32 (19.049) | 0.743 | -16.881 (10.721) | 0.129 | 0.06 | 0.429 | 20 | 8 | 2373.019 (2004.938) | -5.552 (33.675) | 0.877 | 0.003 | 0.596 |
|  | Delta.Time | 85.2 | 17 | 84 | 25 | 0.062 (0.061) | 0.001 (0.001) | 0.516 | 0 (0.001) | 0.589 | 0.008 | 0.008 | 20 | 8 | 0.143 (0.045) | -0.002 (0.001) | 0.052 | 0.181 | 0.223 |
|  | Avg.Power | 5.6 | 15 | 77 | 22 | 52.68 (3.142) | **0.21 (0.052)** | **0.001** | 0.04 (0.03) | 0.211 | 0.238 | 0.339 | 19 | 7 | 44.719 (5.524) | **0.345 (0.085)** | **0.037** | 0.438 | 0.834 |
|  | Agg.Entropy | 12.5 | 17 | 84 | 25 | 4.537 (0.541) | -0.005 (0.009) | 0.583 | -0.003 (0.005) | 0.532 | 0.015 | 0.285 | 20 | 8 | 4.556 (1.009) | -0.011 (0.017) | 0.572 | 0.036 | 0.374 |
| syllables.C | Peak.Freq | 15.9 | 20 | 85 | 28 | 4734.32 (1009.727) | 16.619 (17.214) | 0.344 | -7.175 (9.65) | 0.464 | 0.04 | 0.99 | 23 | 8 | 3402.501 (1606.856) | 32.424 (25.516) | 0.269 | 0.087 | 0.999 |
|  | Freq95 | 17.5 | 20 | 85 | 28 | 5220.06 (1184.878) | 11.263 (20.2) | 0.582 | -1.551 (11.324) | 0.892 | 0.01 | 0.991 | 23 | 8 | 3833.745 (2020.095) | 31.641 (33.114) | 0.407 | 0.075 | 0.993 |
|  | Freq5 | 16 | 20 | 85 | 28 | 4260.532 (985.77) | 20.338 (16.76) | 0.236 | -5.676 (9.404) | 0.552 | 0.05 | 0.987 | 23 | 8 | 2979.65 (1483.871) | 36.22 (23.313) | 0.2 | 0.112 | 0.993 |
|  | Freq.BW90 | 63.7 | 20 | 85 | 28 | 938.226 (349.214) | -9.086 (5.957) | 0.14 | 4.511 (3.342) | 0.189 | 0.094 | 0.839 | 23 | 8 | 702.565 (691.593) | -4.508 (11.598) | 0.711 | 0.016 | 0.831 |
|  | Delta.Time | 38.7 | 20 | 85 | 28 | 0.121 (0.032) | -0.001 (0.001) | 0.245 | 0 (<0.001) | 0.826 | 0.046 | 0.99 | 23 | 8 | 0.167 (0.053) | -0.001 (0.001) | 0.213 | 0.184 | 0.989 |
|  | Avg.Power | 7.4 | 17 | 71 | 24 | 70.619 (6.996) | **0.25 (0.118)** | **0.046** | -0.011 (0.072) | 0.884 | 0.139 | 0.818 | 20 | 7 | 61.823 (12.643) | 0.415 (0.214) | 0.108 | 0.296 | 0.808 |
|  | Agg.Entropy | 30.3 | 20 | 85 | 28 | 3.183 (0.787) | -0.017 (0.013) | 0.214 | 0.008 (0.007) | 0.285 | 0.065 | 0.888 | 23 | 8 | 2.737 (1.521) | -0.011 (0.026) | 0.686 | 0.019 | 0.834 |
| syllables.D | Peak.Freq | 10.9 | 17 | 61 | 23 | 6392.71 (840.088) | -4.774 (14.204) | 0.74 | -3.575 (7.953) | 0.658 | 0.015 | 0.901 | 13 | 6 | 6079.929 (647.591) | -4.543 (3.104) | 0.4 | 0.002 | 0.991 |
|  | Freq95 | 8.4 | 17 | 61 | 23 | 7442.673 (732.442) | -6.565 (12.614) | 0.608 | -9.173 (6.992) | 0.204 | 0.1 | 0.986 | 13 | 6 | 6741.811 (627.48) | -3.797 (3.731) | 0.381 | 0.001 | 0.987 |
|  | Freq5 | 7.3 | 17 | 61 | 23 | 5219.79 (625.952) | 3.283 (10.782) | 0.764 | -3.476 (5.973) | 0.567 | 0.016 | 0.972 | 13 | 6 | 3952.39 (779.685) | 22.85 (10.645) | 0.162 | 0.078 | 0.996 |
|  | Freq.BW90 | 24.9 | 17 | 61 | 23 | 2219.082 (498.568) | -9.739 (8.594) | 0.271 | -5.773 (4.754) | 0.239 | 0.134 | 0.943 | 13 | 6 | 2762.315 (565.233) | -25.551 (8.434) | 0.09 | 0.23 | 0.958 |
|  | Delta.Time | 21.8 | 17 | 61 | 23 | 0.657 (0.13) | -0.003 (0.002) | 0.203 | **0.004 (0.001)** | **0.003** | 0.253 | 0.942 | 13 | 6 | 0.598 (0.102) | 0.001 (0.001) | 0.687 | 0.001 | 0.91 |
|  | Avg.Power | 5.8 | 15 | 56 | 21 | 66.946 (5.232) | 0.067 (0.089) | 0.463 | 0.091 (0.052) | 0.098 | 0.161 | 0.857 | 13 | 6 | 60.353 (7.763) | 0.241 (0.108) | 0.175 | 0.088 | 0.975 |
|  | Agg.Entropy | 9.9 | 17 | 61 | 23 | 4.66 (0.521) | -0.007 (0.009) | 0.459 | -0.006 (0.005) | 0.252 | 0.099 | 0.949 | 13 | 6 | 5.103 (0.457) | **-0.022 (0.006)** | **0.05** | 0.144 | 0.967 |
| syllables.E | Peak.Freq | 7.7 | 20 | 136 | 26 | 7525.58 (638.908) | 7.283 (10.907) | 0.511 | -6.997 (5.819) | 0.241 | 0.041 | 0.642 | 35 | 6 | 5904.741 (1864.23) | 29.963 (30.236) | 0.378 | 0.129 | 0.93 |
|  | Freq95 | 7.6 | 20 | 136 | 26 | 7754.561 (654.54) | 13.176 (11.176) | 0.251 | -6.21 (5.968) | 0.309 | 0.05 | 0.619 | 35 | 6 | 5913.511 (1793.664) | 37.852 (29.089) | 0.263 | 0.212 | 0.98 |
|  | Freq5 | 10.6 | 20 | 136 | 26 | 7740.69 (895.153) | -4.734 (15.267) | 0.759 | -12.991 (8.119) | 0.123 | 0.089 | 0.789 | 35 | 6 | 5487.906 (1521.461) | 15.89 (23.439) | 0.567 | 0.023 | 0.986 |
|  | Freq.BW90 | 35.1 | 20 | 136 | 26 | 28.478 (656.351) | 17.692 (11.186) | 0.127 | 6.639 (5.931) | 0.274 | 0.155 | 0.935 | 35 | 6 | 535.288 (2657.87) | 15.933 (43.104) | 0.73 | 0.021 | 0.977 |
|  | Delta.Time | 45.9 | 20 | 136 | 26 | 0.049 (0.025) | 0 (<0.001) | 0.991 | 0 (<0.001) | 0.829 | 0.002 | 0.744 | 35 | 6 | 0.08 (0.024) | -0.001 (<0.001) | 0.176 | 0.169 | 0.465 |
|  | Avg.Power | 6 | 17 | 125 | 23 | 87.054 (5.527) | -0.099 (0.091) | 0.292 | -0.104 (0.052) | 0.059 | 0.142 | 0.707 | 35 | 6 | 90.797 (12.757) | -0.247 (0.207) | 0.298 | 0.148 | 0.741 |
|  | Agg.Entropy | 16 | 20 | 136 | 26 | 1.792 (0.618) | **0.026 (0.011)** | **0.022** | 0.008 (0.006) | 0.145 | 0.277 | 0.903 | 35 | 6 | 1.665 (1.769) | 0.033 (0.029) | 0.317 | 0.162 | 0.912 |
| syllables.F | Peak.Freq | 15.9 | 19 | 73 | 25 | 2871.234 (748.995) | 25.55 (13.13) | 0.065 | -10.105 (6.861) | 0.155 | 0.168 | 0.993 | 16 | 6 | 3553.592 (1045.288) | 0.845 (18.064) | 0.966 | 0 | 0.993 |
|  | Freq95 | 12.5 | 19 | 73 | 25 | 3361.282 (673.949) | 21.706 (11.814) | 0.08 | -9.219 (6.173) | 0.15 | 0.159 | 0.991 | 16 | 6 | 4045.904 (1214.06) | -2.869 (21.135) | 0.901 | 0.002 | 0.968 |
|  | Freq5 | 16.2 | 19 | 73 | 25 | 2734.539 (756.853) | 24.316 (13.267) | 0.08 | -9.732 (6.933) | 0.174 | 0.153 | 0.993 | 16 | 6 | 3538.618 (1009.686) | -3.683 (16.785) | 0.845 | 0.003 | 0.997 |
|  | Freq.BW90 | 30.6 | 19 | 73 | 25 | 662.683 (181.66) | -2.935 (3.106) | 0.355 | 0.18 (1.615) | 0.912 | 0.028 | 0.781 | 16 | 6 | 196.321 (524.311) | 5.121 (9.459) | 0.617 | 0.045 | 0.777 |
|  | Delta.Time | 38.6 | 19 | 73 | 25 | 0.396 (0.162) | 0 (0.003) | 0.914 | -0.002 (0.001) | 0.317 | 0.045 | 0.977 | 16 | 6 | 0.413 (0.114) | -0.003 (0.001) | 0.223 | 0.025 | 0.973 |
|  | Avg.Power | 5.7 | 16 | 62 | 21 | 70.749 (4.82) | 0.139 (0.082) | 0.107 | 0.003 (0.045) | 0.956 | 0.096 | 0.768 | 13 | 5 | 87.095 (12.415) | -0.208 (0.229) | 0.479 | 0.205 | 0.832 |
|  | Agg.Entropy | 12.2 | 19 | 73 | 25 | 2.94 (0.392) | -0.006 (0.007) | 0.37 | 0.002 (0.003) | 0.662 | 0.028 | 0.806 | 16 | 6 | 2.437 (1.17) | 0.004 (0.021) | 0.866 | 0.005 | 0.835 |
| syllables.G | Peak.Freq | 4.3 | 5 | 14 | 5 | 5275.379 (2734.911) | 26.72 (38.594) | 0.56 | -2.472 (47.623) | 0.97 | 0.008 | 0.999 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Freq95 | 4.9 | 5 | 14 | 5 | 5448.003 (2734.731) | 29.405 (47.007) | 0.595 | -6.965 (15.697) | 0.922 | 0.079 | 0.967 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Freq5 | 5.9 | 5 | 14 | 5 | 5349.739 (4949.772) | 21.534 (54.165) | 0.728 | 0.44 (113.523) | 0.997 | 0.001 | 1 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Freq.BW90 | 33.3 | 5 | 14 | 5 | 98.154 (888.397) | 7.873 (15.189) | 0.656 | -7.405 (5.805) | 0.999 | 0.212 | 0.784 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Delta.Time | 15.3 | 5 | 14 | 5 | 0.035 (0.095) | 0.001 (0.002) | 0.675 | 0 (0.001) | 0.991 | 0.057 | 0.898 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
| syllables.I | Peak.Freq | 16.9 | 9 | 46 | 11 | -41.782 (1701.824) | 56.656 (26.37) | 0.066 | -5.698 (9.002) | 0.545 | 0.312 | 0.879 | 7 | 2 | -1474.827 (843.633) | 75.919 (11.959) | 1 | 0.948 | 0.985 |
|  | Freq95 | 12.8 | 9 | 46 | 11 | 559.907 (1216.482) | **51.695 (18.85)** | **0.026** | -3.482 (6.434) | 0.603 | 0.41 | 0.898 | 7 | 2 | 483.363 (728.695) | 52.527 (10.33) | 1 | 0.922 | 0.978 |
|  | Freq5 | 20.8 | 9 | 46 | 11 | -942.718 (1615.182) | **67.51 (25.029)** | **0.028** | -8.982 (8.543) | 0.324 | 0.435 | 0.905 | 7 | 2 | -1420.05 (909.255) | 71.947 (12.89) | 1 | 0.934 | 0.981 |
|  | Freq.BW90 | 39.4 | 9 | 46 | 11 | 1494.774 (558.742) | -15.731 (8.654) | 0.109 | 5.558 (2.957) | 0.099 | 0.383 | 0.859 | 7 | 2 | 1903.437 (1150.183) | -19.421 (16.305) | 1 | 0.392 | 0.823 |
|  | Delta.Time | 32.5 | 9 | 46 | 11 | 0.07 (0.048) | 0 (0.001) | 0.614 | 0 (<0.001) | 0.586 | 0.041 | 0.701 | 7 | 2 | -0.026 (0.023) | 0.001 (<0.001) | 1 | 0.746 | 0.926 |
|  | Avg.Power | 9.5 | 9 | 46 | 11 | 34.772 (17.974) | 0.637 (0.278) | 0.057 | -0.036 (0.095) | 0.714 | 0.287 | 0.75 | 7 | 2 | 28.124 (30.211) | 0.684 (0.428) | 1 | 0.536 | 0.865 |
|  | Agg.Entropy | 21.3 | 9 | 46 | 11 | 4.825 (1.66) | -0.035 (0.026) | 0.212 | 0.012 (0.009) | 0.217 | 0.266 | 0.91 | 7 | 2 | 5.713 (2.064) | -0.043 (0.029) | 1 | 0.494 | 0.853 |
| syllables.J | Peak.Freq | 1.4 | 2 | 15 | 3 | 4134.335 (2819.384) | 14.099 (42.485) | 1 | 6.403 (17.785) | 1 | 0.012 | 0.033 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Freq95 | 1 | 2 | 15 | 3 | 5207.864 (2628.448) | 0.12 (39.608) | 1 | 0.856 (16.299) | 0.998 | 0 | 0.001 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Freq5 | 2.7 | 2 | 15 | 3 | 2730.137 (3001.211) | 32.443 (45.269) | 1 | 11.515 (19.005) | 1 | 0.048 | 0.128 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Delta.Time | 7.2 | 2 | 15 | 3 | 0.036 (0.04) | 0 (0.001) | 1 | 0 (<0.001) | 1 | 0.022 | 0.105 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  | Agg.Entropy | 27.6 | 2 | 15 | 3 | 11.26 (2.417) | -0.139 (0.037) | 0.998 | -0.032 (0.015) | 0.998 | 0.71 | 0.917 | NA | NA | NA (NA) | NA (NA) | NA | NA | NA |
|  |  |  |  |  |

# Figure captions

Figure 1. Average sound pressure levels (SPL; Z-weighted time-average value of SPL, in decibels; LZeq) of midpoint frequencies of one-third-octave frequency bands from 40 Hz - 20 kHz, measured at three drilling playback sites (n=36 sound measurements) and background noise at 35 sites in our study area (including background sound measurements from the three drilling playback sites while noise was not being broadcast) (n=50 background sound measurements). Multiple sites were used to show that drilling playback is louder than representative background noise in the region when playback was not being broadcast. Shaded areas represent 95% confidence intervals.

Figure 2. Savannah Sparrow syllable classifications used in this paper, shown with two songs that contain all syllables (A, B, C, D, E, F, G, I, and J). Syllables A and B occur both together (in variable numbers of repeats) and separately. The “AB” combination was counted together for purposes of classifying song types, but otherwise analyzed separately. Spectrograms generated in Raven Pro at brightness 50, contrast 90, and spectrogram window size 512.

Figure 3. Baird’s Sparrow syllable classifications used in the paper, shown with six songs that contain all syllables: a (upward sloping introductory syllable), b (flat or downward sloping introductory or final syllable), j (two-note two-frequency introductory syllable), k (two-note two-frequency introductory syllable), l, (three note two-frequency introductory syllable), m (single frequency trill syllable), n (clustered single frequency trill syllable), o (alternating frequency trill syllable with higher start note), and p (alternating frequency trill syllable with lower start note). Syllable n was only found in a unique song type (not shown in Green’s classification and only found in one individual). Syllable b, while often very different in these songs, contained a continuous range of frequency and duration that could not be classified graphically by eye or by clustering algorithms. Spectrograms generated in Raven Pro at brightness 50, contrast 90, and spectrogram window size 512.

Figure 4 ISO-predicted dBC (noise from playback) has a positive relationship with the ambient noise recorded at male perch sites for Baird’s Sparrows (“B”) and Savannah Sparrows (“S”) in southern Alberta, from May-July 2014, at experimental noise playback.

Figure 5. Box-and-whisker plots show median (centre line), quartiles (lower and upper edges of box), sample minima and maxima (lower and upper bars), and outliers (dots) for Baird’s Sparrow (BAIS) and Savannah Sparrow (SAVS) for seven whole-song parameters in southern Alberta, May-July 2014, samples pooled from before and after noise treatments (not during).