



Song adjustments only partially restore effective communication among Baird's sparrows, *Centronyx bairdii*, exposed to oil well drilling noise

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Noise from oil and gas development is pervasive across many landscapes and creates a novel soundscape that wildlife must adapt to or avoid. In response to anthropogenic noise, many wildlife species alter their vocalizations. Some adjusted vocalizations may promote effective communication in the presence of noise by improving detection and preserving information about the sender's status. However, if adjusted vocalizations fail to improve communication in noise, both missed detections and misinterpretations of vocalizations could impact the fitness of individuals and ultimately contribute to population declines. Baird's sparrow is a species at risk in Canada that adjusts its songs in response to oil well drilling noise by altering whole-song elements such as decreasing the peak frequency of songs (Curry et al., 2017, *Bioacoustics*, 27(2), 105–130). We examined the efficacy of these adjusted songs in the mixed-grass prairies of southern Alberta, Canada during the Baird's sparrow breeding season (May–July 2018 and 2019) using a repeated measures study design ($N = 69$ dyads) in which we simulated territorial intrusions by broadcasting adjusted songs and unadjusted songs in the presence and absence of oil well drilling noise recordings. We found that focal male behaviour was mainly mediated by noise treatment when compared to song treatment. In noisy trials, males sang less, called more and performed more flybys, regardless of song treatment type. However, in noisy trials, males displayed longer song latency in response to unadjusted songs compared to adjusted songs. The results of our novel study suggest that the presence of oil well drilling noise elicits more aggressive territorial defence behaviour in Baird's sparrows or hinders the ability of individuals to locate or assess rivals. Additionally, our results suggest that adjusted songs only partially restore effective communication in noise.

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Anthropogenic noise can impact the ability of wildlife species to detect, identify and interpret acoustic signals used in social interactions such as predator avoidance, territorial defence and mate attraction through acoustic masking (Duquette et al., 2021; Roca et al., 2016). When acoustic masking occurs, the transmission distance of an acoustic signal, such as a vocalization, is shortened (Lohr et al., 2003); as a result, an acoustically masked signal may fail to elicit an appropriate behavioural response (Brenowitz, 1982; Dooling & Blumenrath, 2013). Acoustic masking can occur when acoustic signals and noise overlap in pitch (i.e. spectral frequency)

or when the amplitude of noise is greater than the amplitude of acoustic signals (Brenowitz, 1982; Dooling & Blumenrath, 2013). However, many wildlife groups, including birds, frogs, insects and bats respond to anthropogenic noise in ways that may lessen or entirely avoid the impacts of acoustic masking (Duquette et al., 2021; Roca et al., 2016). For example, as anthropogenic noise tends to be low in frequency (i.e. ≤ 4 kHz; Blickley & Patricelli, 2010; Gage & Axel, 2014; Luther & Gentry, 2013; Mullet et al., 2016; Pijanowski et al., 2011), several species increase the minimum frequencies of their vocalizations to avoid overlapping frequencies (Gross et al., 2010; Montague et al., 2013; Parris et al., 2009; Pytte et al., 2003). Other wildlife responses to anthropogenic noise include vocalizing louder (Brumm & Todt, 2002; Derryberry et al., 2017; Hardman et al., 2017; Kight & Swaddle, 2015; Lowry et al.,

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2012; Manabe et al., 1998; Pytte et al., 2003), increasing vocalization rate (Kaiser & Hammers, 2009; Penna et al., 2005; Sánchez et al., 2023), moving closer to the receiver (Kleist et al., 2016) or shifting vocalization behaviours to quieter periods (Dorado-Correa et al., 2016; Fuller et al., 2007; Gil et al., 2015; Nordt & Klenke, 2013).

Wildlife species can respond to anthropogenic disturbances in ways that are not adaptive (Sih, 2013; Sih et al., 2011; Wong & Candolin, 2015); likewise, the above responses to anthropogenic noise may not be adaptive if they fail to restore effective communication in noise. Indeed, noises that are acute, unpredictable and of high amplitude may be particularly hard to adapt to acoustically (Blickley, Blackwood, et al., 2012; Francis & Barber, 2013). For example, although great tits, *Parus major*, were found to increase the amplitude of alarm calls when exposed to traffic noise, these amplitude adjustments were not sufficient to improve acoustic detection in high-amplitude traffic noise (Templeton et al., 2016).

If adjusted vocalizations improve acoustic signal detection by receivers, then receivers may interpret or categorize adjusted vocalizations incorrectly (Halfwerk et al., 2011). Receivers, such as male oscine passerines (songbirds) defending their territories, attend to information encoded in rival males' songs and use this information to determine how to respond to potential rivals (Brumm & Ritschard, 2011; de Kort et al., 2009; Illes et al., 2006; Moseley et al., 2013). Features of oscine song, such as pitch, trill performance or number of syllables are theorized to contain a wealth of encoded information such as the singer's location (McGregor, 1993; McGregor & Falls, 1984; Naguib & Wiley, 2001), identity (Briefer et al., 2008; Falls & Brooks, 1975; Osiejuk & Manser, 2014), fighting ability (Linhart et al., 2012) or aggressive motivation (Ripmeester et al., 2007; Smith & Price, 1973). As such, noise-induced changes to these features may influence receiver perception and subsequent response. For example, a study on northern cardinals, *Cardinalis cardinalis*, found that the territorial response of focal males to shifted-frequency songs (i.e. adjusted) was significantly weaker than average-frequency songs (i.e. unadjusted) (Luther & Magnotti, 2014). Consequently, if adjusted songs in noisy environments result in missed detections or misinterpretations by focal males defending territories, then male fitness could be impacted through territorial take-overs or cuckoldry (Halfwerk et al., 2011; Kleist et al., 2016).

In North America, oil and gas production introduces anthropogenic noise and other forms of disturbance across vast swaths of grassland habitats (Barber et al., 2010; Francis, Ortega, et al., 2011; Francis, Paritsis, et al., 2011; Rosa & Koper, 2022). Noise generated by the construction and use of primary (e.g. well pads) and supporting infrastructure (e.g. roads) propagate over long distances; for example, the acoustic footprint of noise-generating compressor stations can elevate ambient noise conditions up to 650 m from their sources (Francis, Paritsis, et al., 2011). Functional habitat loss may occur when noise results in decreased habitat quality. Indeed, species have been found to avoid or leave noisy but otherwise suitable habitats (Bayne et al., 2008; Drolet et al., 2016; Francis et al., 2009; Rheindt, 2003) for reasons including acoustic masking (Mason et al., 2016) and noise-induced physiological stress responses (Blickley, Word, et al., 2012; Des Brisay et al., 2023; Kleist et al., 2018).

Noise generated by oil well drilling and the subsequent operation of oil wells are markedly different and these sources of anthropogenic noise may have different implications for wildlife species that rely on acoustic communication (Rosa & Koper, 2022). Noise generated by oil well drilling is sporadic, with random fluctuations in both frequency and amplitude. In comparison, noise generated by individual oil wells tends to be chronic, with less fluctuations in frequency and amplitude (Rosa & Koper, 2022). Oil

well drilling noise may have a more significant ecological footprint than predictable noise, even if it is present for only short periods, because it is more distracting and more likely to be perceived as a threat than chronic noise (Blickley, Blackwood, et al., 2012; Rosa & Koper, 2022). This hypothesis may help explain the negative impacts of well drilling activity on other wildlife as well, such as greater sage-grouse, *Centrocercus urophasianus* (Blickley, Blackwood, et al., 2012), and mule deer, *Odocoileus hemionus* (Northrup et al., 2015).

Baird's sparrow is a grassland-obligate songbird that breeds in a relatively restricted portion of mixed-grass prairies of south-western Canada and the north-central United States (Green et al., 2017; Youngberg et al., 2019). Oil and gas production is common throughout Baird's sparrows' breeding habitat (Askins et al., 2007), and male Baird's sparrows have been found to adjust their songs in response to oil well drilling noise (Curry et al., 2017), but the efficacy of these adjustments was previously unexplored. Understanding the efficacy of Baird's sparrow adjusted songs is important as their ability to adapt to increasingly human-modified grasslands of North America may have important conservation implications. Baird's sparrow populations have declined by 71% in the United States (Wilsey et al., 2019; Youngberg et al., 2019) and 74.4% in Canada (Smith et al., 2023) since 1966 and 1970, respectively. The decline of Baird's sparrow is mainly attributed to loss of physical habitat (Green et al., 2017; Jones & Green, 1998; Ludlow et al., 2015; Wiggins, 2006). However, the addition of anthropogenic noise to the remaining grasslands may contribute to further population declines if it reduces the quality of habitat for these grassland specialists.

We investigated the efficacy of Baird's sparrows adjusted songs to restore effective communication in noise by improving detection and preserving information about the sender's status in the presence of oil well drilling noise. We accomplished these research objectives by measuring the territorial defence behaviour of free-living male Baird's sparrow in response to simulated territorial intrusions using adjusted and unadjusted songs that we broadcast in both quiet (i.e. ambient noise conditions) and noisy trials (i.e. with experimentally introduced oil well drilling noise). We predicted that if adjusted songs improve acoustic detection in the presence of noise, then under noisy conditions, adjusted songs would elicit quicker and stronger responses when compared to unadjusted songs. Additionally, we predicted that if adjusted songs preserve signal content, then adjusted songs and unadjusted songs should elicit similar responses in quiet trials.

METHODS

Ethical Note

This research was conducted under University of Manitoba animal care protocols F15-005/1/2/3 (AC11301) (2018) and F19-003 (AC11449) (2019), Canadian bird banding permit 10840, Canadian Wildlife Service (CWS) permit 17-AB-SC001 and Alberta Environment and Sustainable Research Development Research Permits 18-347 (2018) and 19-258 (2019). To reduce stress in focal males, we processed and released birds at the location of their capture within 20 min. Our study design required the use of plastic colour bands to individually mark focal males. We minimized the chance of plastic colour bands reopening and snagging on vegetation by using a portable soldering iron to seal plastic bands shut. We reduced disturbance to individuals by performing a maximum of two playback trials on any individual per day. Additionally, to reduce disturbance to conspecifics, we did not conduct playback experiments on males in adjacent territories on the same day.

Species and Study Sites

In Baird's sparrows, only males engage in song behaviour (Green, 1992). During the breeding season, males sing from perches (i.e. grass stalks or small shrubs) and from the ground within their territories (Cartwright et al., 1937; Green et al., 2020). Currently, 13 song types have been described for Baird's sparrows (Green, 1992; Green et al., 2020). While individuals from other species may display repertoires of multiple song types, in which individuals sing with immediate or eventual variety, evidence suggests that male

Baird's sparrows only use one song type throughout their life span (Green, 1992). All song types of Baird's sparrows are of high frequency and typically contain two parts, introductory syllables and a trill (Fig. 1); occasionally song types include a terminal note or syllable (Green et al., 2020) (Fig. 1). While little is known about the function of song in this species, introductory notes may be important for species recognition (Green, 1992). Song dialects have not been observed in Baird's sparrows, suggesting that song types are not geographically constrained (Green, 1992; Green et al., 2020). It is possible that the lack of dialects in Baird's sparrows is a function

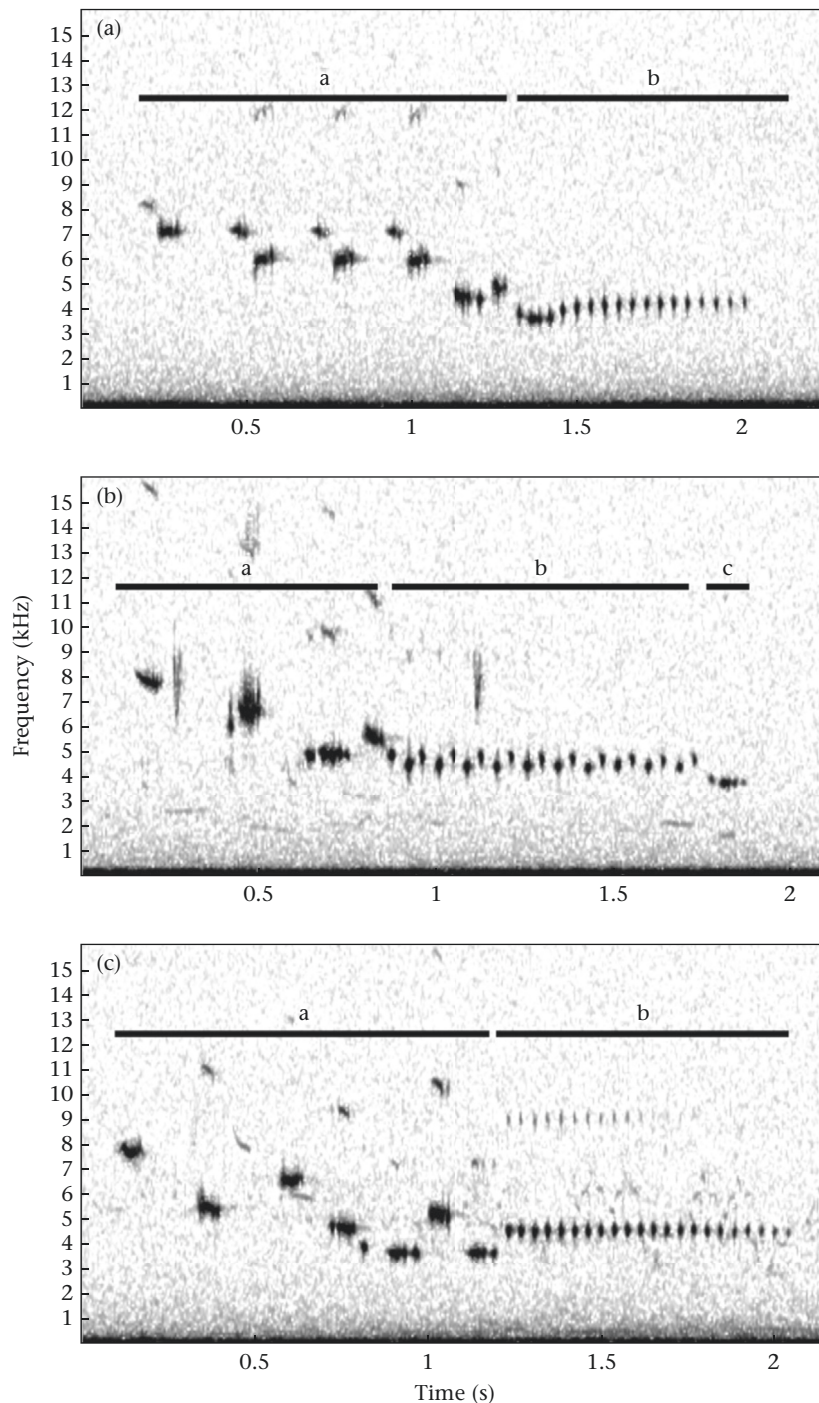


Figure 1. Spectrograms depicting three types of Baird's sparrow song: (a) introductory notes; (b) trill; (c) terminal notes. Spectrograms were generated in Raven Lite 2.0.4 using the spectrogram style, 'Grayscale', brightness 50, contrast 75 and a spectrogram window size of 512. Recordings were originally made by Curry et al. (2017).

of low site fidelity to breeding areas (Green, 1992; Green et al., 2020; Jones et al., 2007).

We conducted our study during the Baird's sparrow breeding season (May–July) over the course of two field seasons (2018 and 2019) in study sites (i.e. male territories) within a 50 km radius of Brooks, Alberta, Canada (50°33'51.012"N, 111°53'56.039"W, 760 m above sea level). This relatively flat area is located on the periphery of the prairie pothole region; as such, vegetation mostly included native mixed-grass prairie species such as western wheatgrass, *Pascopyrum smithii*, needle-and-thread, *Hesperostipa comata*, blue grama, *Bouteloua gracilis*, and Junegrass, *Koeleria macrantha*. Low abundances of exotic plant species, such as goatsbeard, *Tragopogon dubius*, and crested wheatgrass, *Agropyron cristatum*, were also present at our study sites.

Our focal males' territories were located on large tracts of native and improved pasture lands owned and managed by the Eastern Irrigation District (EID), an organization that primarily uses its land base for livestock production but also leases land for oil and gas production. As a result, both beef cattle and oil and gas infrastructure were present near our study sites. Local oil and gas infrastructure often included shallow gas well pads, pumpjacks (powered either via the provincial power grid or by a generator) and oil well drilling rigs. Shallow gas well pads have a spatial footprint of approximately 23 m², most of which is vegetated with native grasses and forbs, are approximately 1.44 m tall and emit no noise (Rodgers & Koper, 2017). Both types of pumpjacks have a footprint of 3787 m² on average (Bernath-Plaisted, 2015), are approximately 4.5 m tall and produce chronic noise (generator-powered pumpjacks 73 dB_C at 10 m, power grid pumpjacks 62 dB_C at 10 m; Rosa & Koper, 2022). Drilling rigs have a footprint of up to 10 000 m² (1 ha), a height of 20–25 m and produce unpredictable and variable noise that differs by production stage (e.g. casing, drilling, cementing) but ranges from 88.1 to 90.5 dB_C at 50 m (Rosa, 2019).

We selected study sites in which noise from active oil and gas infrastructure was not audible. Generally, we selected sites that were ≥600 m from noise-producing oil and gas infrastructure and major roads and ≥100 m from low-traffic dirt service roads. These distances ensured ambient noise was mostly generated by natural sources (e.g. wind, birdsong) and that ambient noise was similar across sites. These criteria helped us control the acoustic environment through our playback trials and ensure that our focal individuals responded to the experimentally introduced anthropogenic noise, rather than to other sources of anthropogenic noise. Within these sites we located, measured, banded and performed playback trials to Baird's sparrows (see [Playback Experiments](#)).

We used perching and singing behaviour to determine locations of male Baird's sparrows. We captured 90% of our focal males prior to conducting our playback experiments (see [Playback Experiments](#)); the remaining 10% were not banded ($N_{\text{colour-banded}} = 62$; $N_{\text{unbanded}} = 7$). To capture males, we used a 6 m mist net, a decoy and a small Bluetooth speaker broadcasting conspecific song. After extraction from the mist net, we verified each individual's sex (using cloacal protuberance) and age (Pyle et al., 2008). We took morphometric measurements (bill height, width, length, tarsus length, wing chord) and banded individuals with a Canadian Wildlife Service metal band and a unique combination of two or three plastic colour bands. To reduce the chance of colour bands reopening and injuring birds, we used a portable soldering iron to seal the plastic colour bands shut.

Playback Experiments

Our goal was to use field-based simulated territorial intrusions to determine whether the territory defence behaviour of focal males differed between song treatments (adjusted versus unadjusted

songs), noise treatments (quiet versus noise) and whether there were interactions between these treatments. To accomplish these research goals, we presented matched-stimuli playback experiments, or 'dyads' ($N_{\text{adjusted}} = 35$; $N_{\text{unadjusted}} = 34$) ([Appendix, Table A1](#)) to focal males. Dyad halves were ~17 min long and were separated by 1.3–2.2 h (median = 1.5 h) ([Fig. 2](#)). We ensured that the time between dyads was comparable to similar experiments (see [LaZerte et al., 2017](#)). Each dyad half consisted of three 5 min trials separated by approximately 1 min of no stimulus. We designed our study so that each focal male was exposed to a total of six trials ([Fig. 2](#)).

In priming trials (trials 1A and 2A), we broadcast a standardized conspecific song exemplar for 5 min to ensure that we had placed the speaker in the focal male's territory and to confirm the sex of unbanded individuals ([Fig. 2](#)). Approximately 1 min after the end of the priming trials, we initiated the noise-only trials (trials 1B and 2B), where we broadcast an oil well drilling noise exemplar (see [Noise exemplars](#)) to ensure the experimental noise would not cause the focal male to flee the experimental area. Approximately 1 min after the end of the noise-only trials, we initiated the main trials (trials 1C and 2C) ([Fig. 2](#)). In the main trials, we presented each focal male with a song exemplar (adjusted or unadjusted) in one of two noise treatments ('quiet', without broadcasted oil well drilling noise, and 'noise', with broadcasted oil well drilling noise). An individual's main trials were designed to be identical apart from the presence or absence of experimentally introduced oil well drilling noise ([Fig. 2](#)). In this way, we ensured that each focal male was only presented songs from a single individual (in both noisy and quiet conditions), and this component of our study design helped control for effects of individual variation in song exemplars ([Grava et al., 2013](#)).

We controlled for potential effects of pseudoreplication by using 66 unique playback treatment/stimulus sets ([Appendix, Table A1](#)). We randomly assigned each focal male a unique playback treatment/stimulus set ([Grava et al., 2013](#); [McGregor, 2000](#)) but ensured treatment order was balanced ([Milinski, 1997](#)). We played each unique playback treatment/stimulus set to a maximum of two focal males ([Appendix, Table A1](#)). We controlled for potential effects of seasonal variation by conducting each focal male's dyads on the same day. Playbacks of Baird's sparrow song may cause neighbouring males to sing ([Ahlering et al., 2006](#); [Green, 1992](#)). For this reason, and to avoid habituation of neighbours to exemplars, we did not conduct playback experiments on males with adjacent territories on the same day. We conducted all playbacks under standardized conditions (≤6 h after sunrise, temperature >0 °C and average wind speed ≤15 km/h). We specifically conducted all playbacks during times of low wind speed as wind is known to generate substantial environmental noise in natural open grassland habitats as it passes through vegetation ([Dodgin, 2018](#); [Green, 1992](#)). Additionally, wind can cause fluctuations in signal amplitude ([Rudnick, 1947](#)); as such, we wanted to limit variability in the amplitude of our exemplars used in our experiment (see [Song exemplars and Noise exemplars](#)).

Playback equipment, design and procedure

Our linear set-up for each playback experiment was approximately 70 m long and comprised three parts: the observer (at 0 m), the song speaker (at 20 m) and the noise speaker (at 70 m) ([Fig. 3](#)). As done in other conspecific playback experiments ([Kleist et al., 2016](#)), we placed both speakers at ground level where they were surrounded by natural vegetation (we did not use artificial camouflage to conceal the speakers) ([Fig. 3](#)). Speakers were oriented to face one another. To aid in distance estimates, we placed ropes marked at 5 m and 10 m intervals at the base of the song speaker in each cardinal direction ([Fig. 3](#)). We used the same location for each

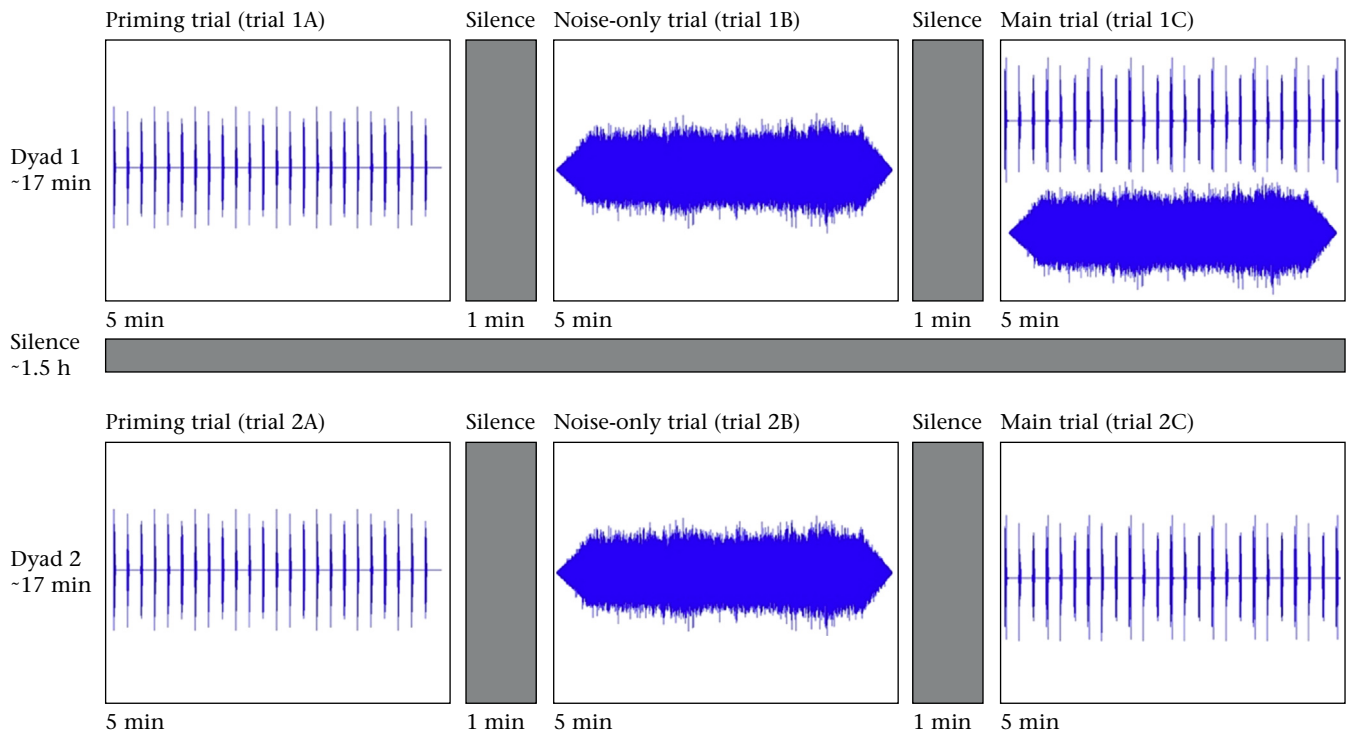


Figure 2. Experimental playback design showing an example of 'treatment order 1', where noise and song were presented in the main trial 1C and only song was presented in the main trial 2C.

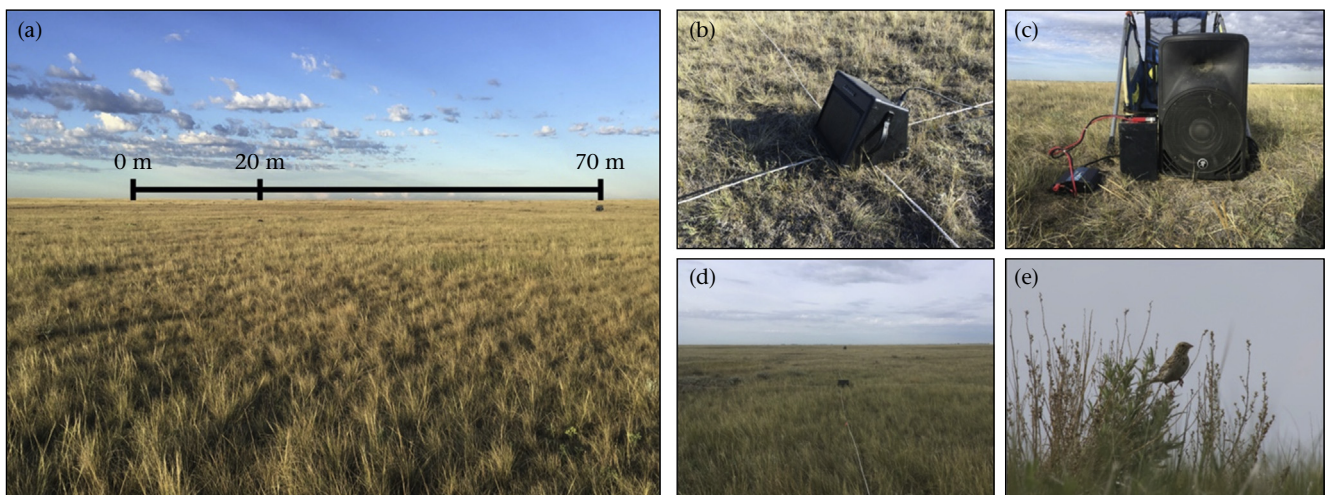


Figure 3. (a) The linear set-up for each playback experiment with the observer (0 m), the song speaker (20 m) and the noise speaker (70 m). (b) Song speaker with ropes. (c) Noise speaker with 12 V deep-cell battery and portable inverter. (d) Observer's point of view during trials. (e) Banded male Baird's sparrow.

focal male's dyads, as such we did not move the experimental equipment between dyads (Figs. 2, 3).

We simulated a male intruder by broadcasting song exemplars from a speaker (song speaker) in focal male territories. As done in other similar playback studies, we placed the song speaker near a song perch observed immediately prior to the initiation of dyad 1 for each focal male (Kleist et al., 2016; Reed et al., 2021; Zwart et al., 2016). We broadcast song exemplars at ~88 dB_C SPL at 1 m (reference level dB_C 34.2 SPL) from a Traynor TVM50 portable amplifier (Yorkville Sound, Pickering, ON, Canada) (Fig. 3). We used this amplitude because it is comparable to the natural amplitude of Baird's sparrow songs (Koper et al., 2016). We simulated anthropogenic noise on each focal male's territory by

broadcasting oil well drilling noise at ~87 dB_C SPL at 10 m (reference level dB_C 34.2 SPL) from a Mackie SRM350 v2 (LOUD Technologies, Woodinville, WA, U.S.A.) powered by a 12 V deep-cell battery and portable inverter (Fig. 3). This amplitude has been used in other studies (Curry et al., 2017) and is generally consistent with the amplitude of oil well drilling noise at a distance of approximately 50 m (Rosa, 2019). Both speakers were connected to an iPhone 5 s (Apple Inc., Cupertino, CA, U.S.A.) via XLR cables so we could control the devices and observe focal male responses from a crouched location (Fig. 3). During each playback experiment, we narrated the behaviours of focal males into a Zoom H4n Pro Digital Recorder (Zoom, Tokyo, Japan) which we later transcribed and tallied.

To characterize ambient noise levels at playback sites, we recorded ≥ 20 s of ambient noise using a Zoom H4n Pro Digital Recorder (Zoom, Tokyo, Japan) immediately after each main trial. We made these ambient noise recordings by orienting the recording device directly above the location of the song speaker. We ensured that the device microphones were angled 90° and that the maximal recording volume was used for each ambient noise recording. We made these ambient noise recordings as uncompressed audio files (WAV files at 48 kHz sampling rate, 16-bit resolution).

Noise exemplars

To create noise exemplars, we used existing high-quality audio files of oil well drilling noise recorded in September–October 2013 at three active drilling rigs located in Brooks, Alberta, Canada (Rosa, 2019). These three recordings were made in the same general area of our study using Zoom H4n Digital Recorders (Zoom, Tokyo, Japan; WAV files at 48 kHz sample rate, 24-bit resolution; Rosa, 2019). From these three recordings, we made three noise exemplars using Audacity (<https://audacityteam.org/>). As these three recordings featured occasional sudden or incidental noises (e.g. vehicle sounds, intercom communications), we selected 5 min of oil well drilling noise that excluded such noises. We edited the selections to create a 30 s fade-in to full volume, 4 min of full volume noise and a 30 s fade-out (Fig. 2), to preclude startling focal males with a sudden introduction of noise (LaZerte et al., 2017). To ensure that all noise exemplars had similar spectral properties, we created and compared noise spectra (Fig. 4) and we standardized the peak amplitude of each noise exemplar using the ‘amplify’ function in Audacity (did not allow clipping) (Grabarczyk et al., 2019).

Song exemplars

To create song exemplars, we used existing song recordings of free-living male Baird’s sparrow songs recorded in May–July 2014 in Brooks, Alberta, Canada (Curry et al., 2017). These recordings were made in the same general area of our study using Zoom H4n Digital Recorders (Zoom, Tokyo, Japan) with built-in stereo microphones angled at 90° at maximal recording volume (WAV files at 48 kHz sample rate, 16-bit resolution; Curry et al., 2017). Recordings were made by pointing the recording device directly at unbanded singing males who were perched 20–40 m from the observer until at least three sequential songs were recorded (Curry et al., 2017). Unadjusted Baird’s sparrow songs (Fig. 1) were recorded when background noise was limited to natural ambient sounds (e.g. wind, birdsong); adjusted Baird’s sparrow songs (Fig. 4) were recorded

within 400 m of experimental playback units broadcasting the above-mentioned oil well drilling noise (Rosa, 2019) at an average 88 dB_C SPL at 10 m (Fig. 5; Curry et al., 2017).

In response to noise, Baird’s sparrows decreased the pitch of their songs (for all song types), as measured by peak frequency (the frequency with maximum power) and 95% frequency (the frequency where 95% of the signal energy occurs, which is correlated with maximum frequency) (Charif et al., 2010; Curry et al., 2017). On average, adjusted song frequencies were lower (peak frequency = 4771 Hz; 95% frequency = 6953 Hz; Curry et al., 2017) than in unadjusted songs (peak frequency = 4978 Hz; 95% frequency = 6966 Hz; Curry et al., 2017). Baird’s sparrows also adjusted one introductory/final syllable (‘syllable b’), one introductory syllable (‘syllable k’) and one trill syllable (‘syllable p’) in song types where these were present (Curry et al., 2017). In response to noise, syllable b displayed a decrease in 95% frequency and syllable k displayed an increase in 5% frequency. Meanwhile, syllable p displayed a decrease in both time and average power in response to noise (Curry et al., 2017).

From these song recordings, we made 28 song exemplars ($N_{\text{adjusted}} = 14$, $N_{\text{unadjusted}} = 14$) using Audacity. These 28 song exemplars came from approximately 28 individuals; however, as individuals were unbanded and the study areas were resampled after the introduction of experimentally introduced oil well drilling noise, it is possible some individuals may have been sampled twice (Curry et al., 2017). To make a song exemplar, we selected three different sequential song recordings from one focal male and spaced the songs at ~ 10 s (natural spacing) for 5 min (~ 25 songs per song exemplar). We arranged song exemplars with immediate variety, after which we looped the songs (i.e. 1, 2, 3 ... 1, 2, 3). To ensure song exemplars were similar in quality, we reduced background and wind noise in song exemplars by filtering each exemplar below 1000 Hz with a roll-off of 48 dB. Additionally, we standardized the peak amplitude of each song exemplar using the ‘amplify’ function in Audacity (did not allow clipping) (Grabarczyk et al., 2019).

Statistical Analyses

We completed all analyses using R Statistical software (R Core Team, 2023). To develop generalized linear mixed-effects models, we used the package glmmTMB version 1.1.8 (Brooks et al., 2023). To compare model fit, we used Akaike’s information criterion corrected for small sample sizes (AIC_c) in the package bblme version 1.0.25 (Bolker, 2022). To graph focal male responses, we used the

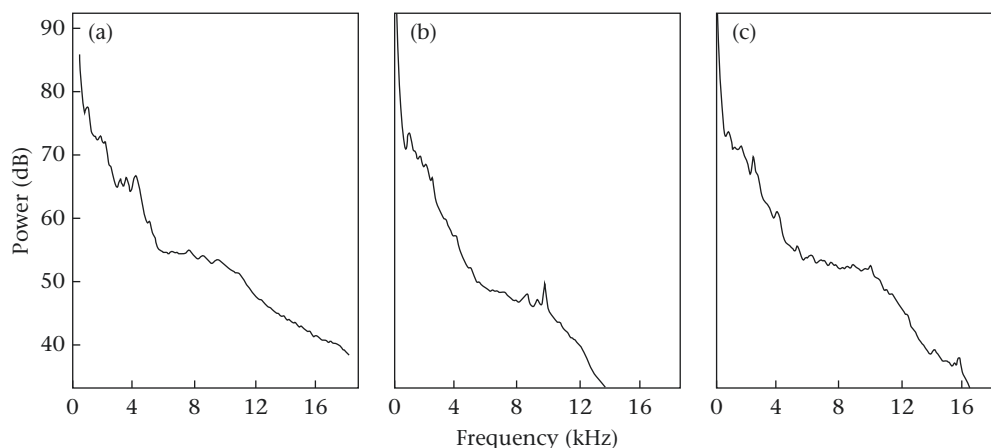


Figure 4. Power spectra of three noise exemplars used in our study: (a) noise exemplar 1; (b) noise exemplar 2; (c) noise exemplar 3. Power spectra were made in Raven Pro 1.4 using brightness = 50, contrast = 50, Hann window = 512 samples (135 Hz) and 3 dB bandwidth.

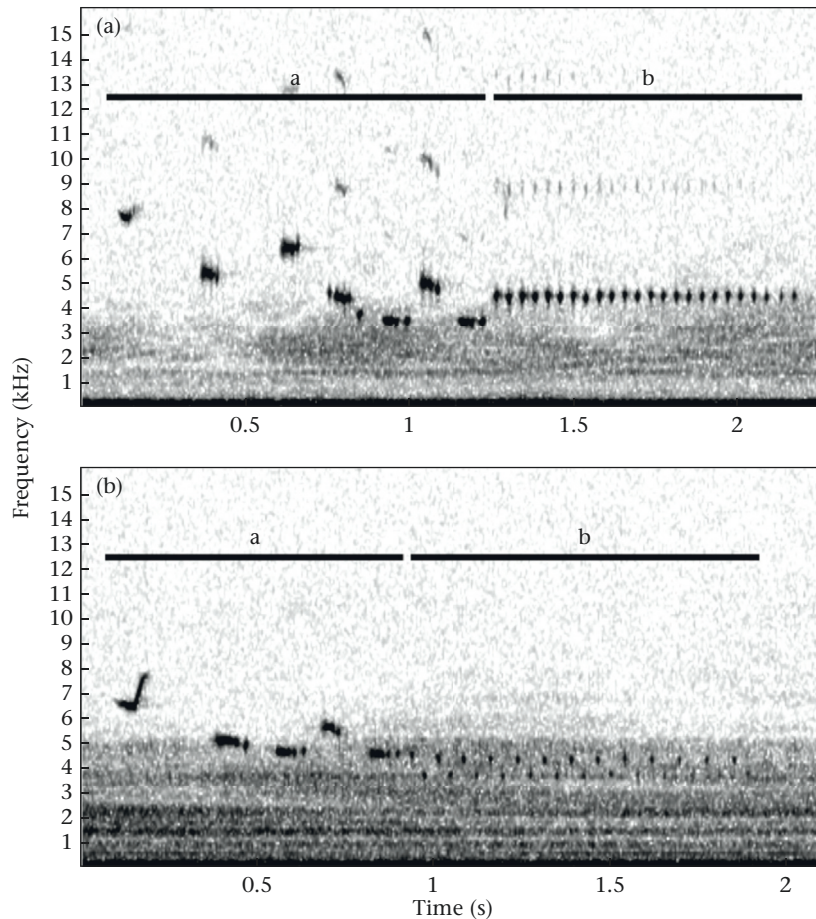


Figure 5. Spectrograms depicting two types of adjusted Baird's sparrow song (Curry et al., 2017): (a) introductory notes; (b) terminal notes. Spectrograms were generated in Raven Lite 2.0.4 using the spectrogram style, 'Grayscale', brightness = 50, contrast = 75 and spectrogram window size = 512. Recordings were originally made by Curry et al. (2017).

package *ggplot2* version 3.4.4 (Wickham, 2023). We considered variables to be significant using $\alpha = 0.05$.

Models

To explore the within-subject effect of noise treatment, the between-subject effect of song treatment and interactions between these treatments, we fitted generalized linear mixed-effects models analysing focal male responses observed during trials 1C and 2C (hereafter, 'trials') (Fig. 2). We analysed four focal male behavioural responses: (1) 'songs', total number of songs per trial; (2) 'calls', total number of agonistic calls (Green et al., 2020) per trial; (3) 'flybys', total number of times a male flew within ≤ 1 m of the song speaker per trial; (4) 'song latency', the time elapsed from the start of the trial until the focal male's first song.

As recommended by Mundry (2011), we used AIC_c to ensure our models used appropriate probability distributions and included influential random variables; however, we used null hypothesis significance testing (NHST) to assess the importance of our fixed variables around which we designed our study, as we had established a priori hypotheses regarding their influence. To account for concerns about pseudoreplication from our repeated measures design and the reuse of our exemplars, we included the following random effects in the majority of our models: focal male identity, song exemplar identity and noise exemplar identity (Appendix, Table A2). However, the inclusion of multiple random effects in a model can lead to overparameterization and convergence issues (Cheng et al., 2010; Thiele & Markussen, 2012). As such, we found that some of our models did not converge; when convergence

issues were a result of suspected overparameterization, which is often caused by correlation among random variables and thus redundancy among these variables, we attempted to resolve the issue by deleting noise exemplar as a random effect and rerunning the model (Cheng et al., 2010; Thiele & Markussen, 2012) (Appendix, Table A2).

We began our analyses by building a suite of preliminary models for each response variable to determine the probability distribution of the data and to explore the potential influence of six independent variables on focal male response (Appendix, Table A2). The preliminary models for each response variable generally only differed by the probability distribution specified (Poisson, *nbinom1* (negative binomial distribution, linear parameterization) and *nbinom2* (negative binomial distribution, quadratic parameterization)) (Brooks et al., 2023). However, in some instances, we deleted noise exemplar identity as a random effect when necessary to remedy model convergence issues (Appendix, Table A2). The preliminary models for each response variable included the following independent variables: (1) 'Julian date', Julian date of playback experiment; (2) 'start time', start time of the trial (min); (3) 'average wind speed', average wind speed recorded immediately after the trial (km/h); (4) 'starting distance', focal male's distance from the song speaker at the beginning of the trial (m); (5) 'treatment order', treatment order of noise presentation (quiet first or noise first); (6) 'trial identity', first or second main trial. We included both treatment order and trial identity to explore potential habituation in our study. We centred continuous variables around the mean and dummy-coded categorical variables where necessary. We compared model

fit between models for each response variable using AIC_c (Appendix, Table A3). We inspected the best fitting model (model with lowest AIC_c score) for significant independent variables on focal male response (Appendix, Table A4). We included significant variables identified in these preliminary models in subsequent models so that we could control for their effects (Appendix, Table A2).

We built a suite of subsequent models for each response variable using the identified probability distribution and significant variables (Appendix, Table A2). In these subsequent models, for each response variable, we also included the interaction of song and noise treatments as binary fixed effects (Appendix, Table A2). Additionally, as count data often include more zeros than what is expected for Poisson or negative binomial distributions (Heilbron, 1994), we assessed our relevant response variables (songs, calls and flybys) for zero inflation. We accomplished this by creating and using AIC_c to compare models that (1) did not model for zero inflation, (2) incorporated constant zero inflation (a single zero inflation parameter applying to all observations) and (3) incorporated complex zero inflation (zero inflation predicted by the interaction term; Brooks et al., 2017) (Appendix, Table A2). The subsequent models for each response variable generally only differed by whether and how zero inflation was specified and, as above, if the noise exemplar was included as a random effect (Appendix, Table A2).

To decrease overparameterization caused by collinearity associated with interaction terms (Quinn & Keough, 2002), we built an additional suite of models for each response variable if the interaction term in the above models was nonsignificant (Appendix, Table A2). As above, we created and compared models for each response variable that (1) did not model for zero inflation, (2) incorporated constant zero inflation (a single zero inflation parameter applying to all observations) and (3) incorporated complex zero inflation (zero inflation predicted by the fixed effects; Brooks et al., 2017) (Appendix, Table A2). The suite of models for each response variable generally only differed by whether and how zero inflation was specified and, as above, if noise exemplar was included as a random effect (Appendix, Table A2). For all model suites, with or without interaction terms, we compared model fit between models for each response variable using AIC_c (Appendix, Table A7), and we interpreted the importance of individual

variables within the best fitting model (model with lowest AIC_c score) using NHST (Mundry, 2011) (see Results).

Ambient noise

We used Raven Pro (version 1.5) to extract the average power (dB) and peak power (dB) of ambient noise recordings. We intended to use the extracted ambient noise values in the above analyses (see Models). However, we found that in 64% of trials, average wind speeds exceeded 5 km/h, which resulted in microphone ‘peaking’ (the sound level exceeded the maximum capacity of the microphone), leading to truncated measurements in Raven Pro. As such, we were unable to use ambient noise values in subsequent analyses. Given the distance of our experiments from noise-generating infrastructure, wind was by far the loudest source of noise in the environment after oil well drilling noise. We found that the amplitude of wind and environmental noise in the absence of our experimental trials were positively correlated (average wind speed and average power of frequency band 1 (0–24 kHz); Pearson correlation: $r_{133} = 0.82$, $P < 0.001$). As such, we used average wind speed as an index of the amplitude of environmental noise in our models (see Models).

RESULTS

Total songs by focal males ranged from 0 to 37 per trial (mean \pm SD = 11.59 ± 10.03 songs/trial; Fig. 6). There was no interaction between song treatment and noise treatment on the total songs ($P = 0.537$; Appendix, Table A6). Song treatment did not influence the total number of songs sung by focal males; however, focal males sang significantly less in noisy trials versus quiet trials (Fig. 6, Table 1).

Total calls by focal males ranged from 0 to 56 per trial (mean \pm SD = 6.79 ± 11.40 calls/trial; Fig. 7). There was no interaction between song treatment and noise treatment on total calls ($P = 0.686$; Appendix, Table A6). Song treatment did not influence the total number of calls by focal males; however, focal males called significantly more in noisy trials than in quiet trials (Fig. 7, Table 1).

Total flybys by focal males ranged from 0 to 15 per trial (mean \pm SD = 1.18 ± 2.28 flybys/trial; Fig. 8). There was no interaction between song treatment and noise treatment on the number

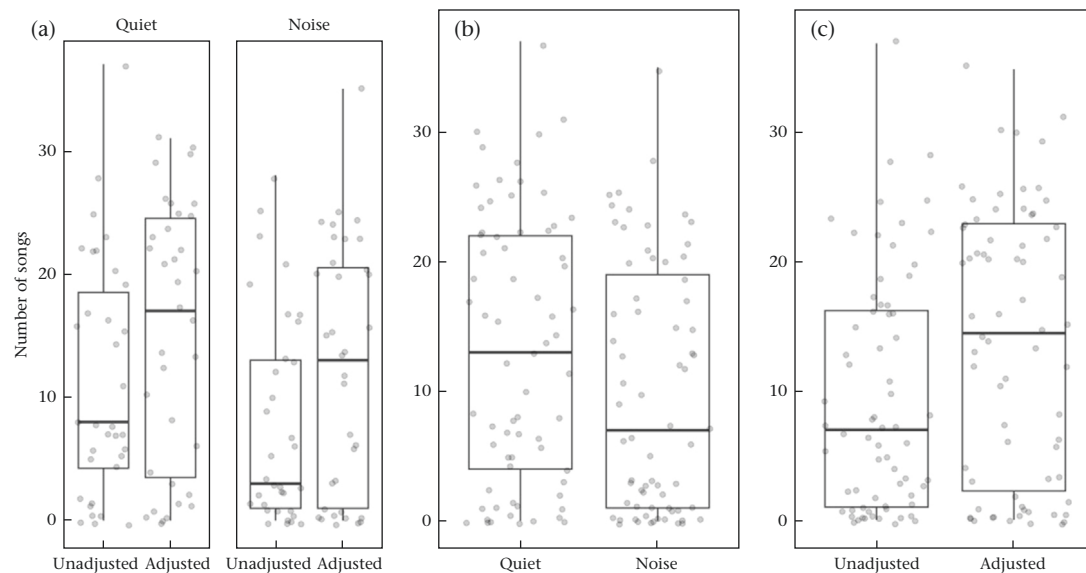


Figure 6. Number of songs by focal males ($N = 69$) in trials ($N = 138$). (a) Song treatment by noise treatment. (b) General response (song treatment pooled) to noise treatment. (c) General response (noise treatment pooled) to song treatment. Boxes represent the interquartile range (IQR), and horizontal lines within boxes represent medians. Vertical lines (whiskers) denote upper and lower quartile ranges. Dots represent individual data points. For statistical significance see Table 1.

Table 1
Final models of focal male responses to simulated territorial intrusion in sites with and without broadcasted oil well drilling noise

Analysis	Distribution	Parameter	Estimate	SE	P
Songs	Negative binomial (Nbinom1)	Intercept	2.09	0.19	<0.001
		Song treatment (1)	0.35	0.24	0.140
		Noise treatment (1)	-0.31	0.12	0.009
Calls	Negative Binomial (Nbinom1)	(Intercept)	1.75	0.28	<0.001
		Song treatment (1)	-0.10	0.32	0.766
		Noise treatment (1)	0.46	0.20	0.021
		Average wind speed	0.14	0.04	<0.001
		Trial identity (1)	-1.53	0.28	<0.001
Flybys	Poisson	(Intercept)	-0.46	0.38	0.230
		Song treatment (1)	0.15	0.39	0.707
		Noise treatment (1)	0.47	0.17	0.006
		Start time	-0.00	0.00	0.002
		Julian date	-0.04	0.01	0.003
		Starting distance	-0.02	0.01	0.003
		Treatment order (1)	-0.50	0.21	0.020
Song latency	Negative binomial (Nbinom2)	(Intercept)	4.10	0.21	<0.001
		Song treatment (1)	0.13	0.27	0.627
		Noise treatment (1)	0.70	0.24	0.003
		Treatment order (1)	-0.50	0.21	0.020
		Song treatment (1)*noise treatment (1)	-0.74	0.34	0.028

Dummy-coded categorical variables included song treatment (0 = unadjusted; 1 = adjusted), noise treatment (0 = quiet; 1 = noise), treatment order (0 = quiet, then noise; 1 = noise, then quiet) and trial identity (0 = trial 1C; 1 = trial 2C). Significant P values (<0.05) are shown in bold.

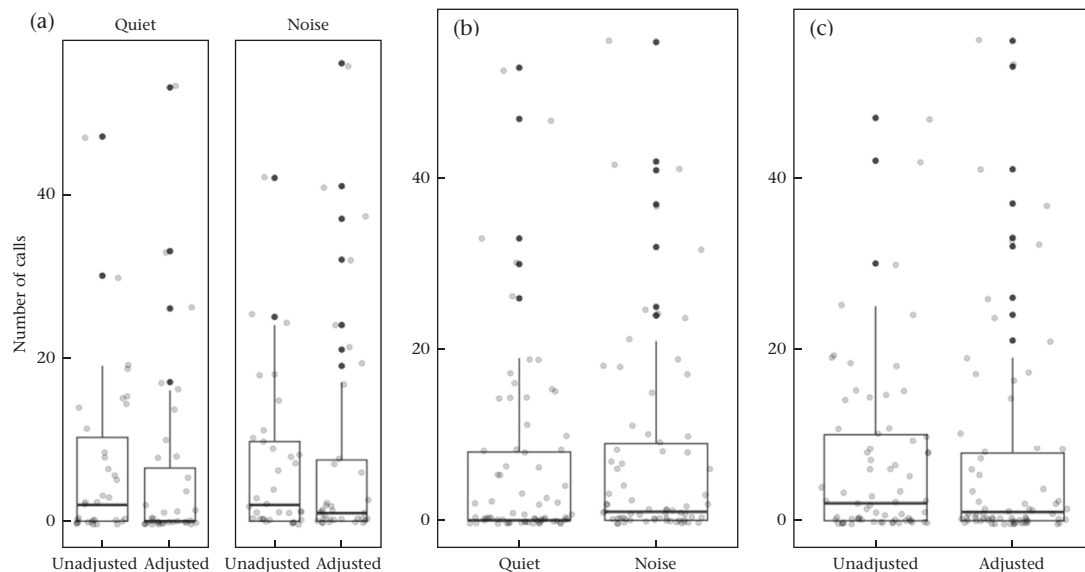


Figure 7. Number of calls by focal males ($N = 69$) in trials ($N = 138$). (a) Song treatment by noise treatment. (b) General response (song treatment pooled) to noise treatment. (c) General response (noise treatment pooled) to song treatment. Boxes represent the interquartile range (IQR), and horizontal lines within boxes represent medians. Vertical lines (whiskers) denote upper and lower quartile ranges. Dots represent individual data points. For statistical significance see Table 1.

of total flybys ($P = 0.344$; Appendix, Table A6). Song treatment did not influence the total number of flybys by focal males; however, focal males performed significantly more flybys during noisy trials than during quiet trials (Fig. 8, Table 1).

In 83% of trials, focal males responded by singing. Of these trials, song latency ranged from 10 to 300 s per trial (mean \pm SD = 71.36 ± 76.79 s/trial; Fig. 9). Unlike our other response variable models, there was a significant interaction between song type and noise treatment on song latency (Table 1). Noise treatment had an influence on song latency such that focal males took longer to begin singing in noisy trials (Fig. 9, Table 1). However, when main trials consisted of adjusted songs broadcast with noise, song latency was similar to unadjusted songs broadcast without noise (Fig. 9, Table 1).

DISCUSSION

We found that the behaviour of male Baird's sparrows was significantly impacted by the introduction of oil well drilling noise, with focal males performing more flybys, singing less and calling more in the presence of noise. Cumulatively, the behaviours we observed in noisy conditions might suggest that focal males became more aggressive or were more willing to escalate to physical conflict in the presence of oil well drilling noise (see also Grabarczyk et al., 2019; Phillips & Derryberry, 2018; Wolfenden et al., 2019). We found that focal males also sang fewer songs in noisy conditions and this result is contrary to similar research focused on Lincoln's sparrows, *Melospiza lincolni*, which found that individuals increased song rate in areas inundated with compressor

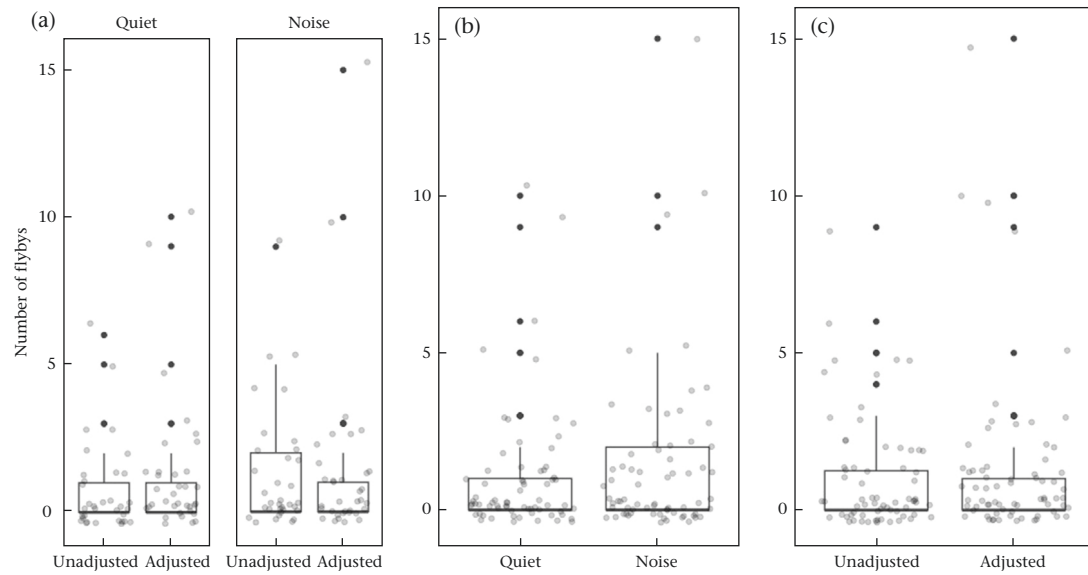


Figure 8. Number of flybys by focal males ($N = 69$) in trials ($N = 138$). (a) Song treatment by noise treatment. (b) General response (song treatment pooled) to noise treatment. (c) General response (noise treatment pooled) to song treatment. Boxes represent the interquartile range (IQR), and horizontal lines within boxes represent medians. Vertical lines (whiskers) denote upper and lower quartile ranges. Dots represent individual data points. For statistical significance see Table 1.

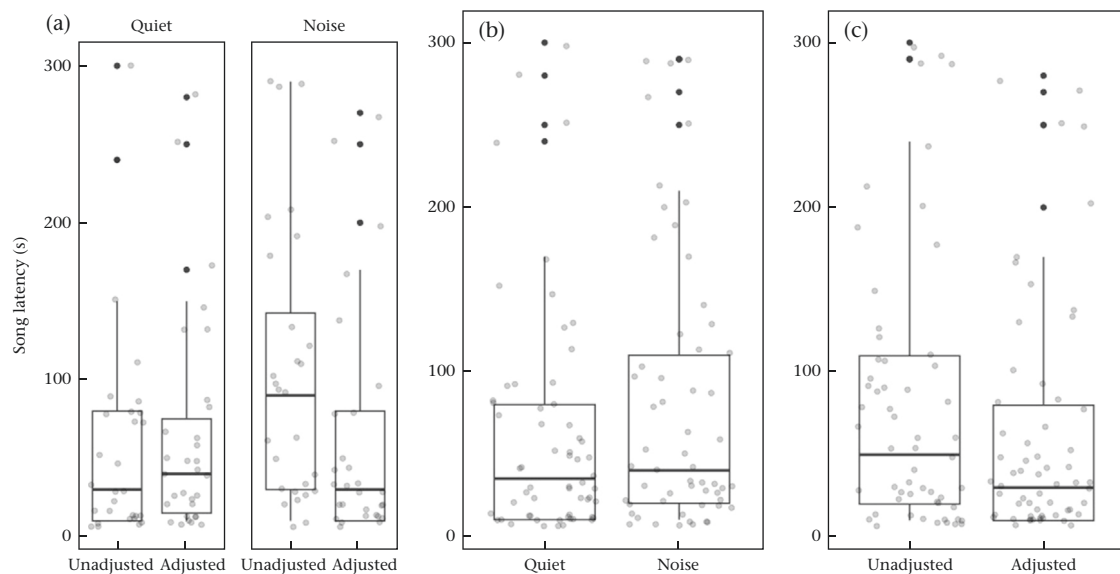


Figure 9. Song latency (s) of focal males ($N = 64$) in trials ($N = 117$). (a) Song treatment by noise treatment. (b) General response (song treatment pooled) to noise treatment. (c) General response (noise treatment pooled) to song treatment. Boxes represent the interquartile range (IQR), and horizontal lines within boxes represent medians. Vertical lines (whiskers) denote upper and lower quartile ranges. Dots represent individual data points. For statistical significance see Table 1.

station noise (Sánchez et al., 2023). However, while this result might seem contradictory to the above interpretation of our results, we note that song rate is a reliable predictor of aggression in some oscine species (Baker et al., 2012) but not in others (Akçay et al., 2013; Barnett et al., 2014). Additionally, other forms of song behaviour, such as song overlap (Dabelsteen et al., 1997) or low-amplitude soft songs (Searcy et al., 2006; Templeton et al., 2012) can convey aggressive motivation in other oscine species. In Baird's sparrows, it is possible that these other forms of song behaviour may be used to communicate aggressive motivation or intent to potential rivals. However, as our study did not measure these additional behaviours, we note the limitation of this interpretation of our results. Apart from songs, male oscines also produce other vocalizations during aggressive interactions. For example, calls

reliably predict attack in species like black-capped chickadees, *Poecile atricapillus* (Baker et al., 2012). If our results indeed represent increased aggressive behaviour, this may be a result of elevated corticosterone levels induced by noise (Blickley, Word, et al., 2012; Davies et al., 2017; Kleist et al., 2018). Indeed, altered corticosterone levels have been reported in grassland specialist species, including Baird's sparrows, dwelling in habitats impacted by oil and gas infrastructure and their associated noise (Curry et al., 2018; Des Brisay et al., 2023).

Alternatively, an increase in flybys past the song speaker and a decrease in the total number of songs might indicate that territorial males were seeking further information about simulated rivals (Grabarczyk et al., 2019; Phillips & Derryberry, 2018; Wolfenden et al., 2019), perhaps because the information from the songs

played in the presence of noise was unclear or degraded. In general, ambient background noise reduces the active space of acoustic signals and the listening area of receivers, so moving closer to the signal source through increased flybys would allow receivers to better attend to the encoded information in signals (Brenowitz, 1982; Kleist et al., 2016; Lohr et al., 2003), and visual information could be used to better understand the threat level posed by an intruder (Anderson et al., 2013; McGregor & Falls, 1984). Furthermore, by singing fewer songs in response to simulated territorial intrusions, focal males would prevent the creation of additional acoustic interference caused by their own signals (Akçay et al., 2020).

Interestingly, only our song latency results would suggest that adjusted songs may have improved communication effectiveness and enabled focal males to acoustically detect the presence of a rival in noisy conditions more quickly. Given this result, the increased song latency we observed in focal males responding to unadjusted songs played in noisy trials suggests that unadjusted songs, while still detectable, were potentially partially masked or degraded by noise, while adjusted songs were not. In a similar repeated measures study that examined male black-capped chickadees, a species that increases the pitch of its song in response to noise (LaZerte et al., 2016; Proppe et al., 2012), focal males responded (through song or by moving in the direction of the song speaker) faster to high-frequency conspecific songs when compared to low-frequency conspecific songs broadcast in conjunction with experimentally introduced low-frequency noise (LaZerte et al., 2017). Researchers concluded that high-frequency songs were more detectable in noisy conditions as a result of acoustic masking release.

However, given the general lack of differentiation we observed between song treatments in noisy trials and the acoustic properties of the noise exemplars (Fig. 4), it seems unlikely that the adjusted signals of Baird's sparrows used in this study provided complete release from acoustic masking. One way signal adjustments can theoretically accomplish masking release is when wildlife species increase the minimum frequency or decrease the maximum frequency of vocalizations; both of these responses can decrease a signal's bandwidth and more narrowband signals may be more detectable in the presence of noise (Duquette et al., 2021; Lohr et al., 2003; Roca et al., 2016). Yet, in the case of Baird's sparrows, individuals were found to respond to oil well drilling noise by decreasing the peak frequency of songs, but this did not result in more narrowband songs (Curry et al., 2017). While masking release did not likely occur, the decreased peak frequency of adjusted Baird's sparrows songs may have helped increase the active space (i.e. the transmission distance) of signals (Morton, 1986; Potvin et al., 2014).

We note that our study only measured latency to sing as opposed to latency to approach the song speaker. Evidence suggests that receivers can estimate the distance and directionality of signalers, such as conspecific rivals, by attending to the acoustic properties of a signal like frequency, degradation or amplitude; this acoustic information helps receivers determine how to appropriately respond (Morton, 1986; Naguib et al., 2000; Naguib & Wiley, 2001). In Baird's sparrows, playbacks of conspecific song can cause neighbouring males to sing (Ahlering et al., 2006). As such, it is possible that adjusted songs improved detection but acoustic information regarding the simulated male's location or directionality was distorted or degraded. As consequence, focal males may have failed to perceive song playbacks as simulated intrusions on their territories.

Based on our findings, adjusted and unadjusted songs may be functionally equivalent for male Baird's sparrows with respect to encoded information about male quality. If focal male responses

had consistently differed by song treatment, particularly during quiet trials, we could reasonably conclude that some aspect of noise-induced adjustments altered the encoded information of signals and influenced focal male motivation to respond. The lack of differentiation we observed is surprising because adjusted and unadjusted songs differed significantly across several acoustic parameters (Curry et al., 2017), and this result contrasts with research on other species that suggests information content is altered when songs are adjusted in response to ambient noise (Curry et al., 2018; Luther & Magnotti, 2014). For example, Savannah sparrows, *Passerculus sandwichensis*, are another species that adjusts its song in response to noise generated by different types of oil and gas infrastructure (Curry et al., 2017; Warrington et al., 2018). Acoustic adjustments of this species vary by noise source (Warrington et al., 2018), but in response to oil well drilling noise, Savannah sparrows generally increase the frequency of their songs (Curry et al., 2017). In a subsequent playback study, Savannah sparrow males, were found to display weaker responses (e.g. fewer attacks and wing flicks) to playbacks of adjusted songs when compared to unadjusted songs in quiet conditions, suggesting that encoded information within songs was altered (Curry et al., 2018), perhaps resulting in adjusted songs being perceived as less threatening.

Our study sought to determine whether adjusted songs of Baird's sparrows restore appropriate territorial responses in the face of anthropogenic noise. We note that our study design was limited to general whole-song measurements (i.e. peak frequency and 95% frequency). However, in some song types, the adjusted songs of Baird's sparrows displayed three altered syllables (Curry et al., 2017). As such, it is possible that some focal males in our study were presented song types (via our song exemplars) where a particular syllable was more or less audible in the presence of noise. Additionally, it is unknown whether some syllables influence behavioural responses more than others during intraspecific competition in male Baird's sparrows. Either of the above factors could have contributed to our observed responses and further studies would help us understand which signal features drive territorial behaviours in Baird's sparrows.

An alternative explanation of our results may be that male Baird's sparrows do not attend to the fine-scale acoustic features adjusted in response to noise. Instead, male Baird's sparrow may use alternative modalities to both convey information to and gain information from rivals. For example, in some species, higher song rate is linked to greater body condition (e.g. fat stores, body size, tarsus length) (Hofstad et al., 2002; Murphy et al., 2008), and body condition is believed to be an important variable in winning territorial fights (Jonart et al., 2007). Even if song rate is not costly to produce (i.e. linked intrinsically with body condition), song rate has been found to increase during agonistic interactions in several species (Beckett & Ritchison, 2010; Illes & Yunes-Jimenez, 2009) and is an important means of conveying aggressive motivation in other species (Baker et al., 2012). Curiously, we found that, in response to playbacks of oil well drilling noise, Baird's sparrows decreased song rate (Fig. 6, Table 1). If song rate is an important intrasexual signal in Baird's sparrows, this modality of communication may be disrupted by intermittent and unpredictable noise caused by oil well drilling and males may be less effective at deterring rivals. However, further studies examining broadscale or fine-scale acoustic behaviours may elucidate the potential impacts of anthropogenic noise on Baird's sparrows.

While this study only looked at the impacts of adjusted songs on male receiver behaviour, it is possible that intersexual interactions are also impacted by signals adjusted in response to noise (Halfwerk et al., 2011). In some avian species, song characteristics are honest signals of male quality, and thus females attend to males' acoustic information to select mates (Ballentine et al., 2004; Caro

et al., 2010). In theory, females may be equally if not more discriminating than male receivers with respect to attending to information encoded in song (Catchpole & Slater, 2008; Danner et al., 2011; Nelson & Soha, 2004). As such, song rate could be an important criterion that female Baird's sparrows use to select mates. However, additional research is required to determine what role song plays in mate selection in this species and the implications of adjusted songs and singing behaviour.

Alternatively, the lack of differentiation we observed between song treatments may be a result of a ceiling effect, whereby the focal males responded strongly to simulated territory intrusions at the centres of their territories, regardless of the content of encoded information within the broadcast song. As a result, the presence of any intruder in the centre of a male's territory would have elicited the same response. Indeed, several studies have found that speaker placement on the edge of a territory leads to less aggressive responses when compared to speakers placed at the centre of territories (Falls & Brooks, 1975; Stoddard et al., 1991). Perhaps the best form of addressing this concern in future studies would be the use of multiple song speakers placed both at the edge and centre of focal male territories, as this approach may better simulate real territorial intrusions (Akçay et al., 2013; Beecher et al., 2000; Hof & Podos, 2013). Despite this study design consideration, numerous studies have found that individuals discriminate between song treatments when only one speaker is used in the centre of a territory (LaZerte et al., 2017; Luther et al., 2016; Phillips & Derryberry, 2018; Ripmeester et al., 2010).

Ultimately, less effective communication among conspecifics in noisy landscapes could contribute to the decline of Baird's sparrows in a variety of ways. For example, males in noisy landscapes may need to leave their breeding territories and approach rivals within neighbouring territories to accurately assess threat levels. Increased proximity to rivals could heighten the potential for physical conflicts (Grabarczyk et al., 2019) and subsequent physical injuries (Clutton-Brock et al., 1979) that might make individuals more vulnerable to predation (Brick, 1998; Jakobsson et al., 1995). Furthermore, increased time spent on vigilance behaviours leaves less time for foraging and other fitness-related activities (Klett-Mingo et al., 2016; Quinn et al., 2006), ultimately leading to poor body condition (Huey et al., 2012; Kölzsch & Blasius, 2008; Ware et al., 2015) and decreased reproductive potential. Noise may have additional negative impacts on birds, such as decreased nesting success (Bernath-Plaisted & Koper, 2016) and decreased care of eggs and nestlings (Ng et al., 2019), and cumulatively these impacts may significantly affect populations that are vulnerable to anthropogenic development. This mechanism might help explain why Baird's sparrows are declining more rapidly than sympatric grassland songbirds such as the widely distributed Savannah sparrow, which effectively compensates for energy extraction noise through its song adjustments (Curry et al., 2018).

Conclusions

Our results demonstrate that the presence of anthropogenic noise significantly altered behaviour of Baird's sparrows in ways that could negatively impact the fitness of males living in noisy environments. These findings indicate that this species may experience functional loss of habitat quality in the vicinity of oil well drilling rigs. Well drilling noise negatively impacts many species (Blickley, Blackwood, et al., 2012; Northrup et al., 2015; Rosa & Koper, 2022), and our research suggests that this may be because the amplitude and unpredictability of drilling noise make it challenging to adapt to behaviourally. Unpredictable, variable anthropogenic noises in general may have particularly significant ecological impacts (e.g. roads; Blickley, Blackwood, et al., 2012;

Rosa & Koper, 2022), and given the pervasiveness of anthropogenic noise across modern landscapes, many individuals may be unable to fully compensate for noise through behavioural mechanisms.

Negative impacts of oil well drilling rigs could be reduced by decreasing their acoustic footprint. Acoustic footprints of infrastructure can be reduced by placing sound barrier walls around drilling rigs (Blickley & Patricelli, 2010; Francis, Paritsis, et al., 2011), or restricting drilling operations to months when migratory birds are not present (Blickley & Patricelli, 2010). We also emphasize landscape planning (Dumyahn & Pijanowski, 2011) to focus development in already degraded sites (Kight et al., 2012; Raynor et al., 2017; Thompson et al., 2015) while also decommissioning and reclaiming unused infrastructure and roads. The strength of landscape planning is that it addresses the cumulative impacts of oil and gas development (Daniel & Koper, 2019) while benefiting numerous species that co-occur with Baird's sparrows. At minimum, the negative impacts of oil well drilling noise on conspecific communication among Baird's sparrows must be recognized and considered in the development of mitigation strategies aimed at reducing the impacts of industrial development on this species.

Author Contributions

J. Waldinger collected and analysed the data and wrote most of the text. N. Koper supervised the research and data analysis, contributed to writing and editing and obtained nonscholarship funding. M. H. Warrington advised on data analysis and interpretation. K. Ellison supervised field methods and contributed to interpretation of results. J. Waldinger and N. Koper led conceptualization and study design.

Data Availability

Data are available as [Supplementary material](#).

Declarations of Interest

We declare no competing interests.

Acknowledgments

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2024.02.010>.

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Appendix

Table A1
 Unique treatment/stimulus sets ($N = 66$) assigned to focal males ($N = 69$)

Bird ID	Treatment order	Song treatment	Song exemplar	Noise exemplar
Unbanded 1	2	Unadjusted	16	2
Unbanded 2	1	Adjusted	20	1
Unbanded 3	2	Unadjusted	14	3
Unbanded 4	2	Adjusted	9	3
Unbanded 5	2	Adjusted	9	3
Unbanded 6	2	Unadjusted	12	2
208118807	1	Adjusted	6	2
208118809	1	Unadjusted	25	3
208118810	1	Adjusted	22	1
208118811	2	Unadjusted	27	3
208118818	1	Adjusted	5	2
208118821	2	Unadjusted	11	2
208118853	1	Unadjusted	26	3
208118867	2	Unadjusted	12	1
208118868	1	Unadjusted	13	3
208118869	1	Adjusted	8	3
208118870	2	Unadjusted	18	2
208118871	2	Adjusted	6	1
208118872	1	Adjusted	4	2
208118887	2	Adjusted	19	3
208118888	2	Unadjusted	28	3
208118896	2	Adjusted	10	2
208118898	2	Unadjusted	17	2
208118899	1	Unadjusted	24	1
208118931	1	Unadjusted	17	2
208118932	2	Unadjusted	15	3
208118934	2	Adjusted	22	1
208118935	1	Adjusted	19	1
208118936	2	Adjusted	6	3
263175475	2	Unadjusted	26	2
263175736	1	Adjusted	21	3
263175801	1	Adjusted	8	1
263175803	2	Unadjusted	14	1
263175804	1	Unadjusted	17	3
263175806	2	Unadjusted	18	1
263175809	2	Adjusted	4	1
263175811	1	Unadjusted	15	1
263175812	2	Adjusted	8	3
263175813	1	Unadjusted	15	2
263175814	2	Adjusted	1	1
263175815	2	Adjusted	10	1
263175816	2	Unadjusted	17	1
263175823	1	Adjusted	19	3
263175824	2	Unadjusted	27	1
263175826	1	Unadjusted	23	2
263175828	1	Adjusted	21	2
263175829	1	Unadjusted	28	2
263175830	1	Adjusted	5	3
263175831	2	Adjusted	10	1
263175833	2	Unadjusted	11	1
263175839	2	Adjusted	2	1
263175841	1	Adjusted	7	2
263175842	1	Unadjusted	13	2
263175843	2	Adjusted	20	1
263175865	2	Unadjusted	24	3
263175866	1	Adjusted	6	3
263175868	2	Adjusted	9	1
263175869	1	Unadjusted	25	2
263176048	2	Adjusted	3	3
263176050	1	Adjusted	22	3
263176051	1	Unadjusted	16	1
263176053	2	Adjusted	1	2
263176089	2	Unadjusted	23	3
263176090	1	Unadjusted	25	1
263176091	1	Adjusted	3	2
263176092	2	Unadjusted	28	2
263176093	2	Adjusted	7	2
263176094	1	Unadjusted	24	2
263176099	2	Adjusted	2	2

Unique treatment/stimulus sets comprised one treatment order, one song exemplar and one noise exemplar.

Table A2
All models created during analysis and their respective convergence outcomes

Model number	Model	Convergence outcome
1	glmmTMB(songs ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=poisson)	Converged
2	glmmTMB(songs ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom1)	Converged
3	glmmTMB(songs ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom2)	Converged
4	glmmTMB(songs ~ song.dum * noise.dum + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom1)	Converged
5	glmmTMB(songs ~ song.dum*noise.dum + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), zi=-1, pbms, family=nbinom1)	Error; did not converge
6	glmmTMB(songs ~ song.dum*noise.dum + (1 band.num) + (1 song.exemplar), zi=-1, pbms, family=nbinom1)	Converged
7	glmmTMB(songs ~ song.dum*noise.dum + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), zi=-song.dum*noise.dum, pbms, family=nbinom1)	Error; did not converge
8	glmmTMB(songs ~ song.dum*noise.dum + (1 band.num) + (1 song.exemplar), zi=-song.dum*noise.dum, pbms, family=nbinom1)	Error; did not converge
9 ^a	glmmTMB(songs ~ song.dum + noise.dum + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom1)	Converged
10	glmmTMB(songs ~ song.dum + noise.dum + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), zi=-1, pbms, family=nbinom1)	Error; did not converge
11	glmmTMB(songs ~ song.dum + noise.dum + (1 band.num) + (1 song.exemplar), zi=-1, pbms, family=nbinom1)	Converged
12	glmmTMB(songs ~ song.dum + noise.dum + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), zi= -song.dum + noise.dum, pbms, family=nbinom1)	Error; did not converge
13	glmmTMB(songs ~ song.dum + noise.dum + (1 band.num) + (1 song.exemplar), zi= -song.dum + noise.dum, pbms, family=nbinom1)	Converged
14	glmmTMB(calls ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=poisson)	Converged
15	glmmTMB(calls ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom1)	Converged
16	glmmTMB(calls ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom2)	Error; did not converge
17	glmmTMB(calls ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar), pbms, family=nbinom2)	Converged
18	glmmTMB(calls ~ song.dum*noise.dum + average.wind.speed.mc + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom1)	Converged
19	glmmTMB(calls ~ song.dum*noise.dum + average.wind.speed.mc + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), zi=-1, pbms, family=nbinom1)	Error; did not converge
20	glmmTMB(calls ~ song.dum*noise.dum + average.wind.speed.mc + trial.code + (1 band.num) + (1 song.exemplar), zi=-1, pbms, family=nbinom1)	Converged
21	glmmTMB(calls ~ song.dum*noise.dum + average.wind.speed.mc + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), zi=-song.dum*noise.dum, pbms, family=nbinom1)	Error; did not converge
22	glmmTMB(calls ~ song.dum*noise.dum + average.wind.speed.mc + trial.code + (1 band.num) + (1 song.exemplar), zi=-song.dum*noise.dum, pbms, family=nbinom1)	Error; did not converge
23 ^a	glmmTMB(calls ~ song.dum + noise.dum + average.wind.speed.mc + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom1)	Converged
24	glmmTMB(calls ~ song.dum + noise.dum + average.wind.speed.mc + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), zi=-1, pbms, family=nbinom1)	Converged
25	glmmTMB(calls ~ song.dum + noise.dum + average.wind.speed.mc + trial.code + (1 band.num) + (1 song.exemplar), zi=-1, pbms, family=nbinom1)	Error; did not converge
26	glmmTMB(calls ~ song.dum + noise.dum + average.wind.speed.mc + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), zi=-song.dum + noise.dum, pbms, family=nbinom1)	Error; did not converge
27	glmmTMB(flybys ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=poisson)	Converged
28	glmmTMB(flybys ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom1)	Error; did not converge
29	glmmTMB(flybys ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar), pbms, family=nbinom1)	Converged
30	glmmTMB(flybys ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom2)	Error; did not converge
31	glmmTMB(flybys ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar), pbms, family=nbinom2)	Converged
32	glmmTMB(flybys ~ song.dum*noise.dum + start.time.min.mc + pb.date.julian.mc + start.dist.song + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=poisson)	Converged
33	glmmTMB(flybys ~ song.dum*noise.dum + start.time.min.mc + pb.date.julian.mc + start.dist.song + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), zi=-1, pbms, family=poisson)	Error; did not converge
34	glmmTMB(flybys ~ song.dum*noise.dum + start.time.min.mc + pb.date.julian.mc + start.dist.song + (1 band.num) + (1 song.exemplar), zi=-1, pbms, family=poisson)	Converged
35	glmmTMB(flybys ~ song.dum*noise.dum + start.time.min.mc + pb.date.julian.mc + start.dist.song + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), zi=-song.dum*noise.dum, pbms, family=poisson)	Error; did not converge
36	glmmTMB(flybys ~ song.dum*noise.dum + start.time.min.mc + pb.date.julian.mc + start.dist.song + (1 band.num) + (1 song.exemplar), zi=-song.dum*noise.dum, pbms, family=poisson)	Error; did not converge
37 ^a	glmmTMB(flybys ~ song.dum + noise.dum + start.time.min.mc + pb.date.julian.mc + start.dist.song + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=poisson)	Converged

(continued on next page)

Table A2 (continued)

Model number	Model	Convergence outcome
38	glmmTMB (flybys ~ song.dum + noise.dum + start.time.min.mc + pb.date.julian.mc + start.time.min.mc + start.dist.song + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), zi=~1, pbms, family=poisson)	Error; did not converge
39	glmmTMB(flybys~ soing.dum + noise.dum + start.time.min.mc + pb.date.julian.mc + start.time.min.mc + start.dist.song + (1 band.num) + (1 song.exemplar), zi=~1, pbms, family=poisson)	Error; did not converge
40	glmmTMB(flybys ~ song.dum + noise.dum + start.time.min.mc + pb.date.julian.mc + start.dist.song + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), zi=~song.dum + noise.dum, pbms, family=poisson)	Converged
41	glmmTMB (lat.song ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=poisson)	Converged
42	glmmTMB (lat.song ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom1)	Error; did not converge
43	glmmTMB (lat.song ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar), pbms, family=nbinom1)	Converged
44	glmmTMB (lat.song ~ start.time.min.mc + pb.date.julian.mc + average.wind.speed.mc + start.dist.song + treatment.dum + trial.code + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom2)	Converged
45	glmmTMB (lat.song ~ song.dum*noise.dum + treatment.dum + (1 band.num) + (1 song.exemplar) + (1 noise.exemplar), pbms, family=nbinom2)	Error; did not converge
46 ^a	glmmTMB (lat.song ~ song.dum*noise.dum + treatment.dum + (1 band.num) + (1 song.exemplar), pbms, family=nbinom2)	Converged

Mean-centred variables include the following: 'start.time.min.mc': start time of the trial; 'pb.date.julian.mc': Julian date of playback experiment; 'average.wind.speed.mc': average wind speed recorded immediately after the trial. Dummy-coded variables include: 'treatment.dum': treatment order of noise presentation (0 = quiet, then noise; 1 = noise, then quiet); 'trial.code': first or second main trial (0 = first; 1 = second); 'song.dum': (0 = unadjusted; 1 = adjusted); 'noise.dum': (0 = quiet; 1 = noise). All other variables include: 'start.dist.song': focal male's distance from the song speaker at the beginning of the trial; 'band.num': focal male identity (69 categorical levels); 'song.exemplar': song exemplar identity (28 categorical levels); 'noise.exemplar': noise exemplar identity (4 categorical levels, including no noise).

^a Final models selected for interpretation.

Table A3

AIC_c selection results from preliminary models of independent variables (Table A4)

Analysis	Model	ΔAIC _c	AIC _c	df
Songs	Negative binomial (Nbinom1)	939.9	0.0	11
	Negative binomial (Nbinom2)	970.0	30.1	11
	Poisson	1058.2	118.3	10
Calls	Negative binomial (Nbinom1)	696.8	0	11
	Poisson	871.1	174.2	10
Flybys	Poisson	360.2	0.0	10
	Negative binomial (Nbinom2)	364.0	3.8	10
	Negative binomial (Nbinom1)	364.1	3.9	10
Song latency	Negative binomial (Nbinom2)	1245.5	0	11
	Negative binomial (Nbinom1)	1250.1	4.5	10
	Poisson	3223.0	1977.5	10

Selection occurred between nbinom1, nbinom2 and Poisson distributions. Models that failed to converge were not compared and are not displayed but are summarized in Table A1.

Table A4

Preliminary models of independent variables inspected for significance

Analysis	Distribution	Parameter	Estimate	SE	P
Songs	Negative binomial (Nbinom1)	(Intercept)	2.12	0.24	<0.001
		Start time	0.00	0.00	0.843
		Julian date	0.00	0.01	0.811
		Average wind speed	-0.04	0.03	0.154
		Starting distance	-0.01	0.00	0.076
		Treatment order (1)	0.29	0.23	0.212
		Trial identity (1)	0.15	0.22	0.478
		(Intercept)	2.13	0.36	<0.001
Calls	Negative binomial (Nbinom1)	Start time	-0.00	0.00	0.062
		Julian date	-0.00	0.001	0.610
		Average wind speed	0.14	0.04	<0.001
		Starting distance	-0.01	0.01	0.267
		Treatment order (1)	-0.20	0.32	0.529
		Trial identity (1)	-1.08	0.34	0.002
		(Intercept)	-0.03	0.44	0.953
		Start time	-0.01	0.00	0.024
Flybys	Poisson	Julian date	-0.03	0.01	0.004
		Average wind speed	-0.01	0.04	0.731
		Starting distance	-0.02	0.01	0.005
		Treatment order (1)	-0.56	0.39	0.152
		Trial identity (1)	0.38	0.37	0.314

Table A4 (continued)

Analysis	Distribution	Parameter	Estimate	SE	P
Song latency	Negative binomial (Nbinom2)	(Intercept)	4.69	0.25	<0.001
		Start time	0.00	0.00	0.322
		Julian date	0.01	0.01	0.371
		Average wind speed	0.04	0.03	0.186
		Starting distance	0.00	0.00	0.651
		Treatment order (1)	-0.46	0.21	0.029
		Trial identity (1)	-0.42	0.25	0.085

All categorical variables were dummy-coded: treatment order (0 = quiet, then noise; 1 = noise, then quiet) and trial identity (0 = first trial (1C); 1 = second trial (2C)). Significant P values (<0.05) are shown in bold.

Table A5

AICc selection results of preliminary models inspected for significant interactions

Model	AIC _c	ΔAIC _c	df
Song (1)	932.8	0.0	8
Song (2)	932.8	0.0	8
Call (1)	694.8	0.0	10
Call (2)	694.8	0.0	10
Flyby (2)	357.2	0.0	10
Flyby (1)	357.4	0.1	10

Selection occurred between (1) nonzero inflated models, (2) zero-inflated models with constant inflation and (3) zero-inflated models with complex zero inflation. Models that failed to converge were not compared and are not displayed but are summarized in Table A1.

Table A7

AICc selection results of preliminary main effects models

Model	AIC _c	ΔAIC _c	df
Song (1)	931.0	0.0	7
Song (2)	931.0	0.0	7
Song (3)	935.5	4.5	9
Call (1)	692.6	0.0	9
Call (2)	695.0	2.3	10
Flyby (1)	357.2	0.0	9
Flyby (3)	359.8	2.6	12

Selection occurred between (1) nonzero inflated models, (2) zero-inflated models with constant inflation and (3) zero-inflated models with complex zero inflation. Models that failed to converge were not compared and are not displayed but are summarized in Table A1.

Table A6

Preliminary models inspected for significant interactions

Analysis	Distribution	Parameter	Estimate	SE	P	
Songs	Negative binomial (Nbinom1)	(Intercept)	2.13	0.2	<0.001	
		Song treatment (1)	0.29	0.26	0.266	
		Noise treatment (1)	-0.39	0.18	0.032	
		Song treatment (1)*noise Treatment (1)	0.146	0.24	0.537	
Calls	Negative binomial (Nbinom1)	(Intercept)	1.79	0.30	<0.001	
		Song treatment (1)	-0.19	0.39	0.636	
		Noise treatment (1)	0.38	0.28	0.181	
		Average wind speed	0.14	0.04	<0.001	
		Trial identity (1)	-1.52	0.28	<0.001	
		Song treatment (1)*noise treatment (1)	0.16	0.39	0.686	
Flybys	Zero-inflated Poisson with constant zero inflation	(Intercept)	-0.44	0.39	0.264	
		Song treatment (1)	0.30	0.44	0.500	
		Noise treatment (1)	0.60	0.25	0.018	
		Start time	0.00	0.00	0.003	
		Julian date	-0.04	0.01	0.003	
		Starting distance	-0.02	0.01	0.002	
		Song treatment (1)*noise treatment (1)	-0.31	0.33	0.344	
		Zero-inflated model				
		(Intercept)	-3.84	-3.68	0.000	

Models selected for interpretation (see Table 1) and models that failed to converge are not displayed. All categorical variables were dummy-coded: treatment order (0 = quiet, then noise; 1 = noise, then quiet) and trial identity (0 = trial 1C; 1 = trial 2C). Significant P values (<0.05) are shown in bold.