

NATURAL AND EXPERIMENTAL NOISE AFFECTS ACOUSTIC
COMMUNICATION IN SONGBIRDS

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ABSTRACT

Natural and Experimental Noise Affects Acoustic Communication in Songbirds

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Background noise is ubiquitous and can impair acoustic communication and influence signaling behavior in animals. Despite evidence demonstrating myriad effects of anthropogenic noise on animal communication, precisely how natural background noise influences communication and behavior remains unclear. Yet, natural sources of background noise, such as rushing rivers or crashing ocean surf, share similar power spectra to sources of anthropogenic noise and can occur at high amplitudes, potentially masking acoustic signals.

To investigate the effects of water-generated noise on songbird behavior, we experimentally broadcast landscape-level playbacks of ocean surf and river noise in coastal California, USA, and riparian habitat in Idaho, USA, respectively. In Chapter 1, we conducted a conspecific playback experiment examining how territorial defense behaviors of lazuli buntings (*Passerina amoena*) and spotted towhees (*Pipilo maculatus*) vary in response to broadcast water noise. We also incorporated cicada noise from a serendipitous *Okanagana* spp. emergence as a biotic source influencing lazuli bunting behavior. Both species produce songs that share substantial spectral overlap with low-frequency, water-generated noise, and lazuli bunting song shares an additional high-frequency overlap with cicada calls. Thus, there is potential for background acoustic conditions to mask conspecific signals. We found that detection and discrimination of conspecific playback occurred more slowly for both species as sound level increased.

Lazuli buntings also exhibited divergent flight behaviors in response to high- and low-frequency acoustic sources, both dependent and independent of sound level.

In Chapter 2, we investigated how amplitude and frequency of water-generated noise influences spectral and temporal song characteristics in six songbird species. We recorded individuals defending territories across 37 sites, with each site representing one of four acoustic environments: naturally quiet ‘controls’, naturally noisy ‘positive controls’ adjacent to the ocean or a whitewater river, ‘phantom’ playback sites with continuous broadcast of low-frequency water noise, and ‘shifted’ playback sites with continuous broadcast of high-frequency water noise. We predicted that all individuals exposed to ‘positive control’, ‘phantom’, or ‘shifted’ noise would adjust song structure, but the magnitude of signal modification would be larger in noisier locations and the type of modification would depend on the spectral profile of the acoustic environment. No two species altered songs in precisely the same way. However, song structure of all six species varied with amplitude and/or frequency of background noise.

Together our results demonstrate that natural noise can impair agonistic behaviors and influence vocal structure. These findings suggest that the natural acoustic environment shapes acoustic communication, highlighting natural soundscapes as an under-appreciated axis of the environment.

Keywords: Acoustic communication, acoustic masking, natural sound, ambient noise, territorial behavior, vocal behavior, songbird

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CHAPTER 1

NATURAL AND EXPERIMENTALLY BROADCAST NOISE AFFECTS
CONSPECIFIC SIGNAL DETECTION AND TERRITORIAL DEFENSE BEHAVIOR
IN SONGBIRDS

1.1 Introduction

Countless animals rely upon the acoustic environment to interact with their surroundings (Bradbury and Vehrencamp 2011). Biotic and abiotic sounds are omnipresent and influence an individual's ability to successfully detect and discriminate various sensory signals. When acoustic signals and cues are interrupted or degraded via shifts in ambient noise conditions, a phenomenon known as masking can occur (Luther and Gentry 2013). Masking may be exacerbated depending on the overlap of frequency, amplitude, timing, or duration of imposing noise relative to the acoustic space used by a species and can cause a listener to miss relevant stimuli (Ortega 2012; Francis and Barber 2013; Shannon et al. 2016).

Recent research suggests that anthropogenic noise can present especially challenging listening conditions in which missed signals and cues can have wide-ranging consequences for both signalers and receivers (e.g., Halfwerk et al. 2011; Kleist et al. 2016; Lucass et al. 2016; Mason et al. 2016). For example, ovenbirds (*Seiurus aurocapilla*) that occupy noise-polluted areas exhibit reduced pairing success, suggesting that chronic noise impairs their ability to attract and find a mate (Habib et al. 2007). Despite an expansive body of research examining the behavioral implications of anthropogenic noise exposure (e.g., Slabbekoorn and Peet 2003; Fuller et al. 2007; Habib

et al. 2007; Francis et al. 2012; Luther et al. 2016; for reviews, see Francis and Barber 2013; Shannon et al. 2016), comparatively few studies have attempted to quantify the effects of natural noise on behavior (e.g., Dubois and Martens 1984; Slabbekoorn and Hunt 2007; Davidson et al. 2017; Gentry and Luther 2017; reviewed in Ortega 2012). Yet natural, abiotic sources of ambient noise, such as rushing white-water rivers or crashing ocean surf, typically occupy low acoustic frequencies and share similar power spectra to sources of chronic anthropogenic noise (Ortega 2012; Davidson et al. 2017; Halfwerk et al. 2018), such as traffic or urban sounds (Blickley and Patricelli 2012; Luther and Gentry 2013).

Birds are reliant upon the acoustic landscape for extracting biologically relevant signals and cues to successfully communicate with conspecifics and detect predators and prey (e.g., Montgomerie and Weatherhead 1997; Mennill et al. 2002; Templeton et al. 2005). As such, they are often used as a model taxon for examining the effects of acoustic masking. The influence of anthropogenic noise on various stages of bird life history has been well documented for dozens of species, showing a reduced ability to detect (discern a signal from irrelevant sound [i.e., noise]; Luther and Gentry 2013; e.g., Lucass et al. 2016), discriminate (differentiate one signal from another, e.g., intruder song from neighbor song; Luther and Gentry 2013; e.g., Pohl et al. 2012), and localize signals (identify the location of the signal source; Senzaki et al. 2018; e.g., Mason et al. 2016) within noise-polluted environments. Recent evidence indicates that avian signalers respond to both anthropogenic and natural noise exposure by adjusting song performance (Davidson et al. 2017) and vocal activity (Gentry and Luther 2017) under more intense ambient conditions. These comparable reactions to different noise sources suggest that

masking from ambient noise could be a prevailing evolutionary force imposing strong selection on acoustic signals (Luther and Gentry 2013; Davidson et al. 2017). Whether natural noise presents similar challenges for receivers, and whether receiver responses mirror those documented for anthropogenic noise remains a critical gap in our knowledge of soundscapes and behavioral processes.

Here, we tackle this gap with a conspecific playback experiment exploring the effects of natural noise conditions on the territorial defense behaviors of lazuli buntings (*Passerina amoena*; hereafter bunting[s]) in Idaho and spotted towhees (*Pipilo maculatus*; hereafter towhee[s]) in California and Idaho, USA. These species possess songs that heavily overlap with the spectral profiles of low-frequency water-generated noise (Figure 1.1), thus, there is potential for acoustic masking to interfere with conspecific detection. To assess this, we experimentally broadcast white-water river noise across riparian zones in Idaho and ocean surf noise across coastal sage scrublands in California, allowing us to test the influence of these sounds across a noise gradient on organisms that have evolved with them. We employed a modified BACI/repeated measures design and exposed free-living territorial males on acoustically manipulated treatment sites to conspecific song with treatment playbacks turned on and off in comparison to males exposed to conspecific song on nearby control sites. We also incorporated high-frequency cicada (*Okanagana* spp.) chorus noise in our observations of buntings as a serendipitous emergence occurred in Idaho during our study and this biotic noise overlaps strongly with components of bunting song (Figure 1.1).

Large-scale soundscape manipulation experiments are an underused method that can allow us to alter acoustic conditions across entire territories and simultaneously

control for potentially confounding factors that may covary with the noise sources (Blickley et al. 2012a; McClure et al. 2013; Shannon et al. 2016). Studies broadcasting anthropogenic noise have been paramount in the corroboration of natural experiments (e.g., Habib et al. 2007; Goodwin and Shriver 2010) by showing that noise alone directly affects stop-over efficiency (Ware et al. 2015), avoidance behavior (McClure et al. 2013) and habitat quality (Blickley et al. 2012a; Blickley et al. 2012b). To our knowledge this is the first large-scale playback experiment aimed at investigating the effects of natural noise.

Our species-specific objectives for this study were to test whether (i) buntings exhibit divergent behavioral responses to high- and low-frequency acoustic sources, and (ii) whether riparian and coastal sage scrub towhee populations respond differentially to habitat-specific, low-frequency water noise. We hypothesized that natural noise impairs signal detection and agonistic behaviors, predicting that both species would respond to intruder song along a behavioral gradient, with increasingly delayed detection and an overall weaker agonistic response as background sound levels intensified. We further anticipated that buntings would exhibit divergent responses to river versus cicada chorus noise due to spectral differences in source noise and frequency overlap with bunting song. Finally, because riparian sites were collectively characterized by higher sound levels than coastal sites (regardless of the experimental addition of noise), we predicted that if riparian sound levels were consistently above the threshold necessary to impair behavior, then Idaho towhees would show less of a behavioral distinction between sound level and acoustic condition (treatment-on, treatment-off, control) compared to California spotted towhees.

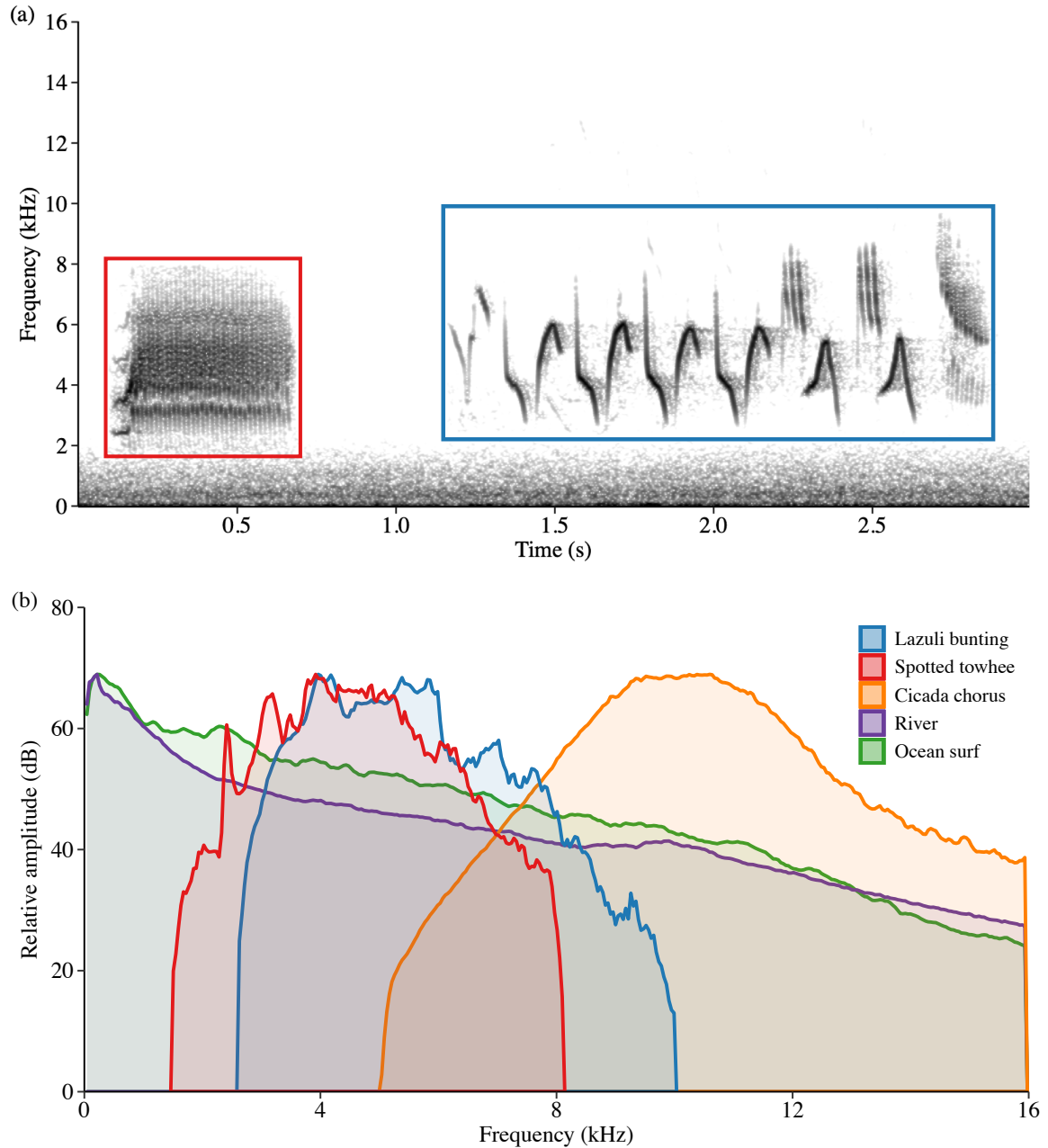


Figure 1.1 Spectrograms (a) of spotted towhee song (left) and lazuli bunting song (right) under control conditions. (b) Power spectra (distribution of acoustic power [energy per unit time] in waveform) of songs and each noise condition. Power spectra are normalized to the same peak frequency for each acoustic source illustrating substantial spectral overlap between natural noise sources and species song.

1.2 Methods

1.2.1 Study areas

We conducted conspecific playback experiments with buntings in Idaho and towhees in Idaho and California. We performed all trials on private lands in riparian drainages on Lava Lake Ranch in the Pioneer Mountains, Idaho (between 43°33'N and 43°26'N latitude and 113°44'W and 113°38'W longitude), and in coastal sage scrub habitat on Vandenberg Air Force Base (VAFB), California (between 34°39'N and 34°46'N latitude and 120°36'W and 120°30'W longitude). The timing of playback trials was selected to coincide with the breeding season at each location: between June 6 – June 19, 2017 and April 23 – June 19, 2018 in California, and June 26 – July 2, 2017 and June 27 – July 1, 2018 in Idaho.

The riparian sites in Idaho are uninhabited, with periodic use by outdoor recreationists and livestock. We selected treatment and control sites (≥ 1.08 km apart) along riparian corridors with seasonal creeks running through them, dominated by quaking aspen (*Populus tremuloides*), black cottonwood (*Populus trichocarpa*), willows (*Salix* spp.), and gray alder (*Alnus incana*). VAFB is largely undeveloped, containing over 70 km of protected coastal habitat. The ~ 57 km² base primarily functions as a satellite launch and missile-testing facility, with few annual launches and infrequent air traffic. We selected sites (≥ 0.89 km apart) at varying distances from the coastline, with dominant coastal sage scrub species including coyote brush (*Baccharis pilularis*), California sagebrush (*Artemisia californica*), black sage (*Salvia mellifera*), and non-native grasses.

1.2.2 River and ocean surf stimuli and playback design

We constructed river and ocean surf playbacks using three 45 min recordings obtained from three separate locations near our study sites adjacent to whitewater rapids in Idaho, and the ocean in California. We recorded river noise with a Zoom H4N Pro recorder connected to a Rode NT-1A microphone, and ocean surf noise with Roland R-05 recorders and custom windscreens, all at 48.0 kHz sampling rate in uncompressed WAV format. All recordings were screened for non-relevant sounds and amplified in Audacity 2.1.3 (Audacity Team 2017) to -2 dB of the maximum amplitude before clipping. We then constructed separate, composite river and ocean surf playbacks with each 45 min file linearly combined in random order, creating a total playback length of 4.5 h. We applied a 7 s fade in/out to each file and a 5 s crossfade to avoid clipping between appended files and when the playback looped.

We continuously broadcast river and ocean surf playbacks from two solar-powered loudspeakers (Octasound SP820A 360° × 180° Central Speaker, 35 Hz-20 kHz; Appendix A Figure S1.1) per treatment site (4 treatments per location), each connected to an amplifier (Lepai LP-2020TI Mini Amp or PRV Audio AD1200.1-2 Amplifier) and an audio recorder (Roland R-05 or R-09). We placed river loudspeakers ~100 m apart, adjacent to the creek running through each site in Idaho, and ocean surf loudspeakers ~85 m apart in the California coastal scrub. Control sites (3 controls per location) mirrored treatment site layout with mock loudspeaker and solar panel set-ups that did not broadcast noise to control for any effect of infrastructure presence. We calibrated loudspeakers at 2 m so the average sound level (LA_{eq} , 3 min [continuous level A-weighted decibel equivalent re 20 μ Pa]; Larson Davis 824 Sound Level Meter [SLM])

was ~95 dBA in Idaho and ~91 dBA in California. At these levels, noise has the potential to propagate to ≥ 1.0 km in Idaho and ≥ 550 m in California before reaching the minimum levels shown to cause responses to anthropogenic noise (40-45 dBA; Shannon et al. 2016).

1.2.3 Study species and conspecific stimuli

Buntings and towhees are conspicuous, prolific singers and possess songs that may be differentially masked by background noise. Male buntings have one individually unique, complex song (Greene et al. 2014) encompassing low and high frequencies (1.6-11.0 kHz; Thompson 1968), whereas songs of both Idaho and California spotted towhee populations consist of a single broadband trill (1.5-8.0 kHz; Figure 1.1a; Greenlaw 1996; Francis et al. 2012; Smith and Greenlaw 2015). Towhees also sing shorter songs at a faster rate than buntings (Thompson 1968; Greenlaw 1996; Kleist et al. 2016), resulting in a more redundant signal, which may increase the likelihood of successful cue detection under chronic, acoustically intense conditions (Brumm and Slater 2006).

We created five conspecific playback stimuli per species. All five bunting stimuli were created from recordings downloaded from Xeno-canto. We used files that were originally recorded in or near Idaho (see Appendix B Table S1.1 for Xeno-canto recording details). However, the same song syllables are shared throughout the bunting geographic range, with each individual possessing a unique syllable combination (Greene et al. 2014), thus, sampling from within the study population was not deemed necessary. We recorded territorial towhees on VAFB in Spring 2017 using a Marantz PMD 660 digital recorder with an Audio-Technica AT815 directional shotgun microphone or using

the TwistedWave Recorder iPhone/iPad application with a MicW iShotgun microphone with a sampling rate of 44.1 kHz. We then selected five high-quality files to create playback stimuli. The primary difference between regional towhee song dialects is the presence of a unique introductory phrase before the trill, a characteristic absent from both populations tested here (Smith and Greenlaw 2015). Due to the similarity in song structure between California and Idaho towhees, we chose to use the same playback stimuli for both populations. Pilot trials in Idaho further demonstrated that territorial males respond strongly to California songs.

We edited all playback stimuli using Audacity 2.1.3 (Audacity Team 2017) and Raven Pro 1.4 (Bioacoustics Research Program 2011). Each playback stimulus consisted of 4-9 songs from a single song bout looped over 3 min. Bunting songs were separated by ~ 8.25 s for a rate of 6 songs min^{-1} (Baker 1991), and towhee songs were separated by ~ 5.5 s (Kleist et al. 2016) for a rate of 9.3 songs min^{-1} , within range of the natural singing rate for each respective species (Greene et al. 2014; Smith and Greenlaw 2015). We removed background noise between and during songs and standardized peak amplitude across playback files using the Band Pass and Amplify tools in Raven Pro 1.4 (Bioacoustics Research Program 2011), respectively. The particular song frequency range for bunting playback stimuli was 2.6-8.7 kHz and the range for towhee stimuli was 2.3-7.7 kHz.

1.2.4 Conspecific playback design

We targeted singing males actively defending territories within a gradient of ambient and experimentally manipulated natural noise, with individuals averaging a

distance of 237.92 ± 186.72 SD m from the nearest treatment/mock loudspeaker. We carried out all trials between 0600 and 1400 h and tested each male twice from the same conspecific playback speaker location (hereafter “speaker” refers to the conspecific playback speaker only). To prevent habituation and eavesdropping, trials were separated by at least 24 h for a given male and neighboring territories were not tested under the same acoustic conditions on the same day. Territories located on treatment sites received one trial with river/ocean surf loudspeakers on (treatment-on), and one trial with loudspeakers off (treatment-off), in random order. Ten buntings and four towhees were only tested once because either the individual could not be relocated for a second trial, or one trial was excluded post hoc due to equipment malfunction or poor recording conditions (e.g., focal bird was inaudible over background noise).

We conducted conspecific playbacks using a directional speaker (either SME-AFS Model No. 7-100R or Motorola X Sol Republic Deck controlled by an Olympus LS-P2 Linear PCM Recorder, or FOXPRO Wildfire 2 Predator Call controlled via proprietary controller) with playbacks normalized to 85 dBA peak SPL at 1 m (SLM, fast response), reflective of natural song amplitudes for both species. After brief territory monitoring (~30 min, or as needed), we placed the speaker at or near a landmark location within the subject’s territory at an average distance of 29.71 ± 10.01 SD m from the bird (measured via rangefinder). One observer stood ≥ 5 m from the speaker and 20-50 m from the subject in a location with high visibility of the focal bird. When a subject was in view and not actively engaged in territorial disputes, we initiated playback by randomly selecting a stimulus and broadcasting it through the speaker. Trials lasted 6 min, with a 3 min playback followed by a 3 min observation period. Immediately following each trial,

we measured sound level (LA_{eq} , 2 min) at the bird's initial location using either the SLM or a MicWi436 microphone with the SPLnFFT Sound Meter v6.2 iPhone/iPad application. We verbally recorded all relevant behavioral observations using an Olympus LS-P2 Linear PCM Recorder.

A large cicada emergence occurred across our sites in Idaho during the 2017 field season. Several species of the *Okanagana* genus are thought to exhibit a protoperiodical life cycle, in which explosive population years are tied to annual variation in weather conditions (Williams and Simon 1995). Cicadas are the loudest insect group known (Hart et al. 2015), and background sound levels on our sites reached > 90 dBA while cicadas were chorusing, often overpowering all other sound, including treatment playbacks. Chorus intensity is largely dependent on temporal and climatic conditions (e.g., temperature, sunlight; Stölting et al. 2004), and most cicada singing occurred between 0800 and 1400 h. We took advantage of the acoustic conditions created by cicadas ad hoc by conducting playbacks when cicadas were and were not singing, providing a unique high-frequency (~ 6 -14 kHz), high amplitude acoustic condition that differed from the low-frequency river noise and ambient conditions (Figure 1.1b). Though initially tested, we later excluded cicada trials from towhee analysis due to small sample size ($n = 7$).

1.2.5 Response measures

We measured six behavioral variables to assess responses to conspecific playback under different acoustic conditions: closest approach (m) to the speaker, approach latency (s), number of flights, number of flights within 5 m of the speaker, song latency (s), and number of songs. These variables are reliable indicators of aggression and signaling

behavior and have been used in previous studies on our focal species and closely related allies (lazuli bunting, Baker 1991; song sparrow [*Melospiza melodia*], Akçay et al. 2010; northern cardinal [*Cardinalis cardinalis*], Luther and Magnotti 2014; spotted towhee, Kleist et al. 2016). Specifically, reduced latency time indicates faster signal detection and discrimination, increased number of flights and closer approach suggest aggressive intent, and more songs indicate aggressive signaling and territorial ownership (Akçay et al. 2014). We defined approach latency as the first flight toward the speaker and song latency as the first song sung after playback initiation. If a focal male did not fly toward the speaker or sing during playback, then we recorded latency for that respective measure as 180 s, i.e., the length of the playback period (e.g., Akçay et al. 2010; Kleist et al. 2016). We defined closest approach as the bird's closest Euclidian distance (m) to the speaker by flight or perch. If an individual did not approach the speaker, then we reported the measure as the bird's distance at the start of the trial. Though we continued to monitor behavior for 3 min following playback, we only included responses from the playback period for analysis.

1.2.6 Data analysis

All data analyses were completed in R (R Core Team 2018). We performed species-specific principal component analysis (PCA) with varimax rotation using the *psych* package (Revelle 2017) to reduce dimensionality and potential multicollinearity of behavioral response measures. We ran PCAs for both species separately and reduced the six response measures into three principal components (PC[s]) for both species, yielding PCs that loaded well with approach, flight, and song behavior (axes denoted PC_{approach},

PC_{fly}, and PC_{song}; see Table 1.1 for variable loadings).

We built linear mixed effect models to describe each species-specific response component using the *lme4* package (Bates et al. 2015). Our species-specific global models included parameters for dBA (i.e., 2 min LA_{eq} from bird's initial location), trial type (categorical: control, treatment-off, or treatment-on), initial bird-to-speaker distance (hereafter distance), cicada chorus noise (no or yes; buntings only; hereafter cicadas), year (2017 or 2018), and location (California or Idaho; towhees only). We also included interactions for cicadas*dBA (buntings only) and location*trial type (towhees only). We investigated the effects of noise on a fine and coarse scale (Ware et al. 2015) through covariates representing different hypotheses. The continuous dBA variable examined whether birds responded linearly to increasing sound levels, and the interaction cicadas*dBA parsed whether buntings differentially responded in a gradient to high-frequency cicada versus low-frequency background sound levels. Alternatively, the categorical parameters cicadas, trial type, and the interaction location*trial type tested whether the presence of noise invoked a response, independent of sound level. We controlled for repeated measures and individual variation by adding playback stimulus I.D., observer, and territory I.D. nested within site as random effects for all models, including the null (intercept-only). Following recommendations of Bates et al. (2015), we systematically dropped random effects if they led to model singularity or accounted for zero variance, however, all models included territory I.D. as a random intercept.

We transformed species-specific response components that deviated from normality using Tukey's Ladder of Powers transformations to normalize residual variance (Tukey 1977). To reduce collinearity for bunting models, we scaled and

centered dBA with a z-transformation. Unless otherwise indicated, reference conditions for categorical variables were alphabetically and chronologically selected through the “lmer” function (*lme4* package, Bates et al. 2015; reference conditions: cicadas = no cicada chorus, location = California, trial type = control, year = 2017). For the trial type covariate and location*trial type interaction, we rotated reference conditions as needed and reran each model to identify all pairwise relationships. To characterize variation in sound level across trial type by species, we built separate models for both bunting trial years and towhee trial locations. We then examined dBA in response to trial type, with territory I.D. nested within site as random effects.

We ranked and compared models using Akaike’s Information Criterion (Akaike 1974) corrected for small sample size (AIC_c ; Hurvich and Tsai 1989) and considered competitive models with $\Delta AIC_c \leq 2$ from the highest-ranked model equivalent (Burnham and Anderson 2002). We performed model selection using the *MuMIn* package (Barton 2019). Individual predictors within each model were deemed to have a strong effect if the 95% confidence interval (CI) did not overlap zero. For simplicity, we present and discuss outcomes from the highest-ranked bunting and towhee models.

Table 1.1 Loading coefficients for species-specific principal component analyses and responses to conspecific playback.

Response variable	Loadings			Raw response (mean \pm SD)	
	PC1	PC2	PC3	Idaho	California
Spotted towhee				Idaho	California
Total no. flights	-0.34	0.84	0.20	4.40 \pm 2.95	8.17 \pm 4.88
No. flights \leq 5 m	-0.20	0.93	-0.04	1.33 \pm 2.18	2.36 \pm 3.28
Closest approach (m)	0.84	-0.34	-0.02	10.60 \pm 10.72	8.75 \pm 9.76
Approach latency (s)	0.91	-0.20	-0.05	47.78 \pm 59.44	34.44 \pm 51.86
Song latency (s)	-0.25	-0.04	0.87	20.93 \pm 30.57	75.72 \pm 102.20
Total no. songs	-0.16	-0.16	-0.88	20.85 \pm 11.06	13.22 \pm 10.02
Eigenvalue	1.79	1.75	1.59		
Proportion of variance	0.30	0.29	0.27		
Lazuli bunting				Idaho	
Total no. flights	0.92	0.16	-0.25	4.53 \pm 3.55	
No. flights \leq 5 m	0.94	0.09	-0.20	1.44 \pm 2.94	
Closest approach (m)	-0.28	0.05	0.83	11.06 \pm 11.18	
Approach latency (s)	-0.14	-0.08	0.89	56.70 \pm 63.21	
Song latency (s)	0.19	0.87	0.06	35.72 \pm 53.20	
Total no. songs	-0.02	-0.90	0.10	8.98 \pm 5.38	
Eigenvalue	1.86	1.61	1.60		
Proportion of variance	0.31	0.27	0.27		

Response variable loadings interpreted for each PC are in bold.

1.3 Results

1.3.1 Lazuli buntings

We performed 64 trials on 37 buntings in Idaho ($n = 22$ in 2017, $n = 42$ in 2018), including 19 individuals tested twice on treatment sites with river loudspeakers on and off and 8 birds tested twice on control sites. We conducted trials when cicadas were singing, regardless of the trial type, for a total of 16 trials on 11 individuals in the presence of cicada noise. Acoustic conditions across all bunting trials ranged from 32.8 to

82.8 dBA with an average sound level of 50.9 ± 12.5 SD dBA. Sound levels for treatment-on trials were significantly more intense than those for treatment-off (effect size $[\beta] \pm \text{SE}$; $\beta = 9.17 \pm 1.98$, 95% CI [5.30, 13.05]) and control trials during 2018 ($\beta = 6.97 \pm 3.43$, 95% CI [0.24, 13.69]), and there was no difference between sound levels for treatment-off and controls ($\beta = -2.21 \pm 3.46$, 95% CI [-8.98, 4.56]; trial type means \pm SD: treatment-on = 51.3 ± 6.2 dBA, treatment-off = 42.0 ± 6.6 dBA, control = 43.7 ± 8.0 dBA). However, the 2017 cicada emergence resulted in an overall increase in amplitude across sites, such that there was no difference in sound levels between treatment-on and -off trials ($\beta = 2.51 \pm 4.38$, 95% CI [-6.07, 11.10]), and sound levels on both treatment-on and treatment-off trials were significantly lower in intensity than controls ($\beta_{\text{treatment-on}} = -16.00 \pm 6.35$, 95% CI [-28.44, -3.56]; $\beta_{\text{treatment-off}} = -18.52 \pm 6.35$, 95% CI [-30.95, -6.08]; trial type means \pm SD: treatment-on = 56.8 ± 11.6 dBA, treatment-off = 55.3 ± 12.8 dBA, control = 74.3 ± 7.1 dBA).

Bunting flight behavior (PC1_{fly}) was influenced by the presence and amplitude of chorusing cicada noise, with the highest-ranked model including cicadas, dBA, and their interaction as strong effects (Table 1.2; $\beta_{\text{cicadas}} = 0.22 \pm 0.09$, 95% CI [0.04, 0.40]; $\beta_{\text{dBA}} = -0.14 \pm 0.05$, 95% CI [-0.23, -0.05]; $\beta_{\text{cicadas*dBA}} = 0.20 \pm 0.07$, 95% CI [0.06, 0.35]; see Appendix B Table S1.2 for additional parameter estimate details for highest-ranked bunting models). Specifically, buntings flew more frequently in the presence of chorusing cicadas, both independent of sound level, and along an increasing noise gradient. Conversely, in the absence of cicadas, buntings flew less, also independent of sound level and as low-frequency noise (river treatment or ambient) increased (Figure 1.2a). A model including trial type and the cicadas*dBA interaction term was also among those receiving

strong support ($\Delta AIC_c \leq 2$; Table 1.2). Buntings flew more during treatment-off trials compared to controls ($\beta = 0.15 \pm 0.07$, 95% CI [0.02, 0.29]) and more during treatment-on trials compared to controls ($\beta = 0.14 \pm 0.07$, 85% CI [0.04, 0.24]), though the precision of the latter estimated effect was lower.

The highest-ranked model for song behavior (PC2_{song}) included the distance parameter only. However, the null received the same support in model weight and no parameters in the candidate model set strongly predicted bunting song behavior (Table 1.2). Song latency for buntings ranged from 2 s to no response (scored as 180 s; 9.4% of bunting trials; see Table 1.1 for response variable averages).

The top model predicting speaker approach behavior (PC3_{approach}) included dBA and distance as strong effects (Table 1.2; Figure 1.2b). Specifically, as sound level and initial distance to speaker increased, buntings approached the speaker more slowly and maintained a greater overall distance from it ($\beta_{\text{dBA}} = 0.08 \pm 0.02$, 95% CI [0.03, 0.12]; $\beta_{\text{distance}} = 0.01 \pm 0.002$, 95% CI [0.001, 0.01]). Approach latency for buntings ranged from 2 s to no approach (180 s; 14.1% of bunting trials).

Table 1.2 Lazuli bunting model selection results for principal components explaining flight, song, and approach behavior.

Lazuli bunting model	K	$\log(\mathcal{L})$	AIC_c	Δ	w_i
PC1_{fly}					
Cicadas (+), dBA (-), Cicadas*dBA (+)	7	7.12	1.77	0.00	0.45
Cicadas (+), dBA (-), Distance (-), Cicadas*dBA (+)	8	7.93	2.76	0.99	0.28
Cicadas (+), dBA (-), Trial type (+), Cicadas*dBA (+)	9	9.27	2.80	1.03	0.27
Null _{ID+Obs}	4	-2.47	13.61	11.85	-
PC2_{song}					
Distance (-)	4	-88.73	186.13	0.00	0.35
Null _{ID}	3	-89.87	186.15	0.02	0.35
dBA (+)	4	-89.52	187.72	1.59	0.16
Cicadas (+)	4	-89.69	188.06	1.93	0.13
PC3_{approach}					
dBA (+), Distance (+)	7	11.04	-6.07	0.00	0.39
dBA (+), Distance (+), Year (+)	8	11.86	-5.11	0.97	0.24
dBA (+), Year (+)	7	10.43	-4.85	1.22	0.21
dBA (+)	6	8.86	-4.25	1.82	0.16
Null _{ID+Obs+Stim}	5	5.57	-0.11	5.96	-

Flight, song, and approach components denoted PC1_{fly}, PC2_{song}, and PC3_{approach}. Models with $\Delta AIC_c \leq 2.00$ and the null (intercept-only) are reported. K is the number of model parameters, $\log(\mathcal{L})$ is the maximized log-likelihood, AIC_c is the Akaike Information Criterion corrected for small sample size, Δ is the change in AIC_c from the top model (0.00), w_i is the Akaike weight for all strong supporting models. Parameters with 95% CIs that do not include zero are in bold. Parenthesized positive/negative signs (+/-) indicate the direction of parameter influence. Null (intercept-only) subscripts denote the random effects structure of all models for each principal component; e.g., ID+Obs+Stim = territory I.D., observer, and stimulus random intercepts. $n = 64$ trials.

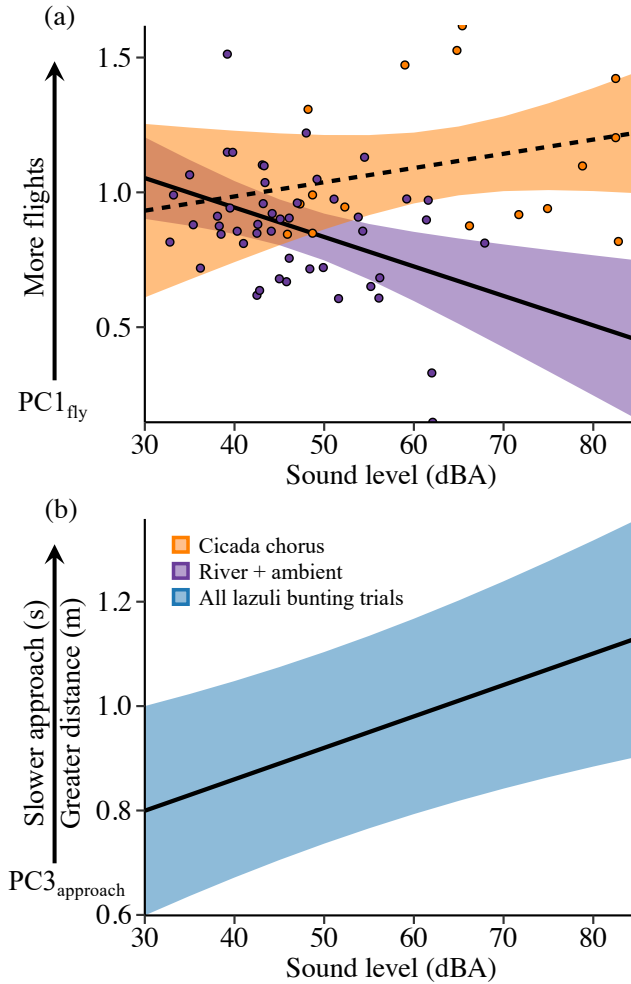


Figure 1.2 Lazuli bunting predictors from the AIC_c top model for PC1_{fly} (a) and PC3_{approach} (b) response variables. (a) Buntings fly more with increasing cicada chorus noise (dashed line) and fly less as low-frequency noise (either river treatment or ambient) increases in the absence of cicada noise (solid line). Points denote individual trials differentiated by presence/absence of cicadas (see [b] for color legend). (b) As sound level increases, buntings approach the speaker more slowly and maintain a greater distance from it. (a & b) Shaded bands denote 95% CIs.

1.3.2 Spotted towhees

We conducted 40 trials on 21 towhees in Idaho ($n = 4$ in 2017, $n = 36$ in 2018) and tested 9 individuals twice on control sites and 10 individuals twice on river treatment sites with loudspeakers on and off. Sound levels ranged from 34.3 to 83.3 dBA, with an average of 44.5 ± 9.1 SD dBA across all Idaho towhee trials. Unlike bunting trials, sound

levels on treatment-on trials were significantly more intense than treatment-off ($\beta = 16.42 \pm 2.48$ SE, 95% CI [11.56, 21.27]) and control trials for towhees across years ($\beta = 12.63 \pm 2.44$ SE, 95% CI [7.83, 17.42]). There was no difference between treatment-off and controls ($\beta = -3.79 \pm 2.44$, 95% CI [-8.59, 1.00]; trial type means \pm SD: treatment-on = 54.8 ± 10.5 dBA, treatment-off = 38.2 ± 2.6 dBA, control = 42.2 ± 4.7 dBA).

We completed 36 trials on 19 individuals in California ($n = 7$ in 2017, $n = 29$ in 2018). We tested 5 individuals twice on control sites and 12 individuals twice on ocean surf treatment sites with loudspeakers on and off. California trials ranged from 24.4 to 61.4 dBA with an average of 39.6 ± 9.0 SD dBA across trials. Sound levels on treatment-on trials were significantly more intense than those on treatment-off ($\beta = 15.70 \pm 1.90$, 95% CI [11.98, 19.42]) and control trials across years ($\beta = 10.66 \pm 2.76$, 95% CI [5.26, 16.06]). There was no difference between sound levels on treatment-off and control trials ($\beta = -5.04 \pm 2.72$, 95% CI [-10.38, 0.29]; trial type means \pm SD: treatment-on = 48.2 ± 7.3 dBA, treatment-off = 32.9 ± 5.2 dBA, control = 38.1 ± 6.4 dBA).

Approach behavior ($PC1_{\text{approach}}$) was strongly affected by sound level for towhees; the highest-ranked model included dBA and distance, both with 95% CIs that did not overlap zero (Table 1.3). Towhees in both populations maintained a greater distance from the speaker and approached it more slowly as sound level and initial distance from the speaker increased (Figure 1.3a; $\beta_{\text{dBA}} = 0.01 \pm 0.003$, 95% CI [0.01, 0.02]; $\beta_{\text{distance}} = 0.01 \pm 0.003$, 95% CI [0.001, 0.01]; see Appendix B Table S1.3 for additional parameter estimate details for highest-ranked towhee models). Latency to approach ranged from 1 s in California and 2 s in Idaho, to no response in both locations (180 s; 9.2% of all towhee trials; see Table 1.1 for response variable averages by population).

The model that best explained flight behavior ($PC2_{fly}$) included the variables location, trial type, and their interaction as strong effects (Table 1.3). Specifically, towhees flew more frequently on control trials in California than all other trials in both locations (Figure 1.3b; $\beta_{location} = -1.85 \pm 0.35$, 95% CI [-2.53, -1.16]; $\beta_{treatment-off} = -1.31 \pm 0.35$, 95% CI [-1.99, -0.63]; $\beta_{treatment-on} = -1.79 \pm 0.35$, 95% CI [-2.48, -1.11]; $\beta_{location*treatment-off} = 1.82 \pm 0.47$, 95% CI [0.90, 2.74]; $\beta_{location*treatment-on} = 2.07 \pm 0.47$, 95% CI [1.15, 2.99]). Towhees in Idaho did not exhibit a strong difference in flight activity between trial types (Appendix B Table S1.3).

The top model for song behavior ($PC3_{song}$) included the parameters location, trial type, their interaction, and distance (Table 1.3). Trial type did not strongly influence song behavior among towhees in Idaho (Appendix B Table S1.3). California spotted towhees had a weaker song response on treatment-off trials compared to all other trials in both locations (Figure 1.3c; with treatment-off as the trial type reference condition: $\beta_{location} = -1.77 \pm 0.50$, 95% CI [-2.75, -0.79]; $\beta_{control} = -1.49 \pm 0.49$, 95% CI [-2.46, -0.52]; $\beta_{treatment-on} = -0.78 \pm 0.29$, 95% CI [-1.35, -0.21]; $\beta_{location*control} = 1.79 \pm 0.69$, 95% CI [0.43, 3.15]; $\beta_{location*treatment-on} = 1.28 \pm 0.42$, 95% CI [0.45, 2.11]). Across populations, towhees collectively sang more songs sooner as initial distance from the conspecific speaker increased ($\beta_{distance} = -0.02 \pm 0.01$, 95% CI [-0.05, -0.003]). All Idaho towhees responded with song to playback with a latency range of 2 to 133 s, while song latency for California birds ranged from 1 s to no response (180 s; 5.3% of all towhee trials).

Table 1.3 Spotted towhee model selection results for principal components explaining approach, flight, and song behavior.

Spotted towhee model	K	$\log(\mathcal{L})$	AIC_c	Δ	w_i
PC1_{approach}					
dBA (+), Distance (+)	5	6.96	-3.06	0.00	0.50
dBA (+), Distance (+), Location (-)	6	7.64	-2.07	0.99	0.30
dBA (+), Distance (+), Year (+)	6	7.21	-1.21	1.85	0.20
Null _{ID}	3	-2.66	11.65	14.71	-
PC2_{fly}					
Location (-), Trial type (-), Location*Trial type	9	-87.76	196.25	0.00	0.71
dBA (-), Location (-), Trial type (-), Location*Trial type	10	-87.35	198.08	1.83	0.29
Null _{ID+Stim}	4	- 101.21	210.99	14.74	-
PC3_{song}					
Distance (-), Location (-), Trial type (-), Location*Trial type	10	-90.28	203.95	0.00	0.72
Location (-), Trial type (-), Location*Trial type	9	-92.55	205.83	1.88	0.28
Null _{Site/ID}	4	- 100.10	208.77	4.82	-

Approach, flight, and song components denoted PC1_{approach}, PC2_{fly}, and PC3_{song}. For PC3_{song} the relevant reference condition for trial type is treatment-off. Null (intercept-only) subscripts denote the random effects structure of all models for each principal component; e.g., Site/ID = territory I.D. nested within site, ID+Stim = territory I.D. and stimulus random intercepts. See text and figure 1.3b-c for contrasts among Location*Trial type interactions. See Table 1.2 description for additional table detail. $n = 76$ trials.

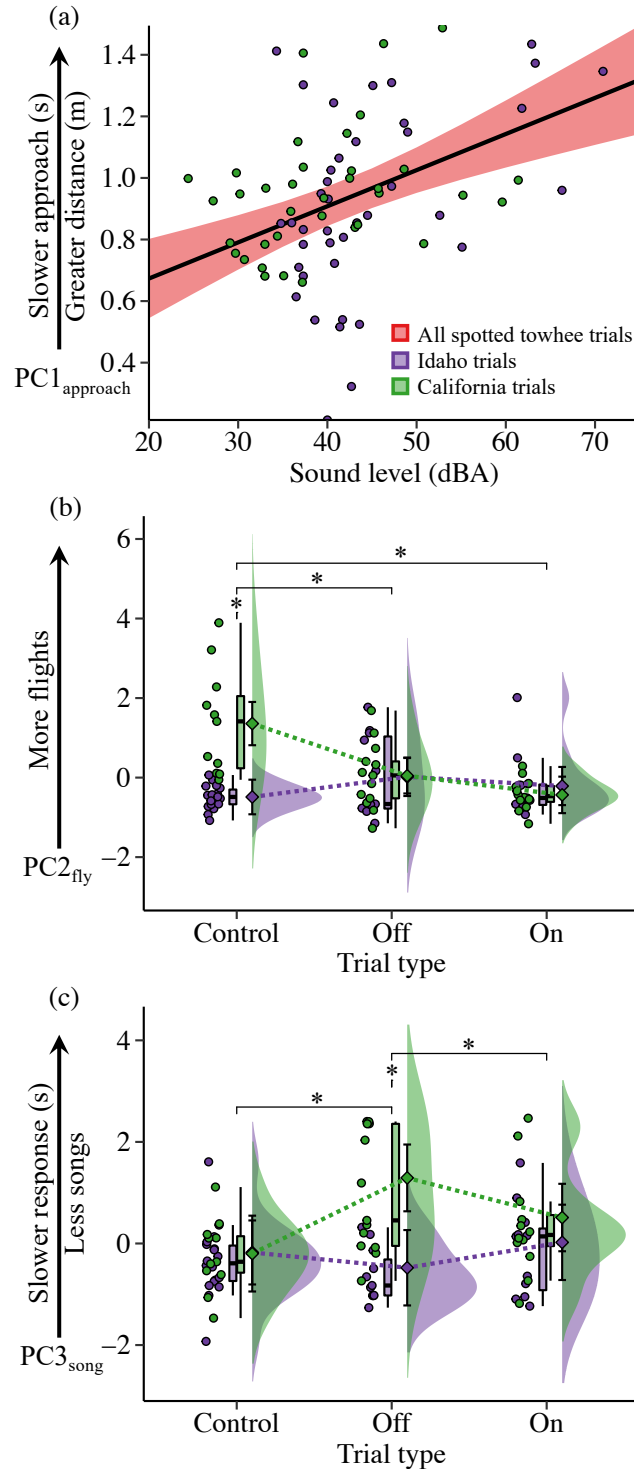


Figure 1.3 Spotted towhee predictors from the AIC_c top model for PC1_{approach} (a), PC2_{fly} (b), and PC3_{song} (c). (a) Towhees approach more slowly and maintain a greater distance from the speaker as sound level increases. Shading represents 95% CI and points denote individual trials. California spotted towhees fly more frequently on control trials (b) and display a weaker song response during treatment-off trials (c) than on all other trials, between and among populations (see [a] for color legend). (b-c) Violins denote kernel

density probabilities differentiated by trial type (x-axis) and population (color), with means (± 1 SE) connected by dotted line. Boxplots denote median and quartiles, and whiskers show 1.5 times the interquartile range. Asterisks denote significant contrasts corresponding to 95% CIs (see Appendix B Table S1.3 for values).

1.4 Discussion

Our results demonstrate that natural noise can interfere with acoustic communication in lazuli buntings and spotted towhees with a differential effect on towhee behavior between our study locations. To our knowledge, this is the first study to show that changes in natural biotic and abiotic acoustic conditions impair territorial defense behaviors of signal receivers; with elevated sound levels, both species were slower to orient toward intruder stimuli and buntings exhibited contrasting flight patterns in the presence of high-frequency cicada calls versus low-frequency background noise. These findings support the hypothesis that natural sound levels can obstruct the detection and discrimination of conspecific signals via acoustic masking. Nevertheless, receiver responses to background acoustic conditions are not clearly predictable and may vary, not only at the species or population level but by the frequency or intensity of ambient noise and other external factors (Francis and Barber 2013; Luther and Gentry 2013; Shannon et al. 2016).

Individuals of both species responded to conspecific song during playback in approach, song, or both in all but two trials (from two different buntings) indicating that signal detection was possible in acoustic conditions spanning 24.4-83.3 dBA. However, buntings and towhees showed a diminished approach response in conditions with elevated sound levels compared to quieter trials, suggesting that detectability and discrimination were nevertheless impaired. The exhibited response latency corroborates

previous anthropogenic noise research where birds responded more slowly to conspecific signals and cues under noisy conditions (Kleist et al. 2016; Lucass et al. 2016). These findings additionally suggest that serial redundancy may improve signal transmission when ambient noise might otherwise impair vocal communication (Brumm and Slater 2006). If we had truncated our response period to a single playback song, only 20.3% of bunting and 19.7% of towhee trials would have had an approach response compared to 85.9% of bunting and 90.8% of towhee trials that approached during the full 3 min playback. Although redundancy of song may ensure eventual detection when signaling pathways are impaired (Bradbury and Vehrencamp 2011), a listener's failure to quickly detect and discriminate other acoustic cues and signals, such as predator and prey sounds or conspecific alarm calls could have wide-ranging fitness consequences for an individual.

While the spectral properties of cicada calls and/or water-generated noise heavily overlap with the acoustic profiles of both species' songs, indicative of high masking potential, it is possible that the behavioral responses demonstrated may be an effect of distraction (although the two are not mutually exclusive). Irrelevant stimuli can cause a signal receiver to involuntarily divert its limited attention away from responding to relevant signals and cues (Chan et al. 2010), such as a conspecific intruder. Attributing a specific mechanism – namely acoustic masking or distraction – to behavioral responses is not always delineable from experimental results (e.g., Grade and Sieving 2016; Mason et al. 2016; Senzaki et al. 2016). However, chronic exposure to our treatment playbacks throughout the breeding season (and the water-generated noise naturally present in the unmanipulated, ambient soundscape) may have reduced the mechanistic effect of

treatment-related distraction as our focal birds likely became habituated to its presence (Rankin et al. 2009). Alternately, given the irregular and eruptive presence of cicadas on the riparian landscape, attentional deficits from acute exposure to high-frequency, high-amplitude chorus noise may explain behavioral shifts in numerous species, including those sharing little or no acoustic overlap with cicada calls. Additional research aimed at separating the role of distraction from masking effects is necessary to identify the extent to which distraction may influence conspecific communication, especially when spectral energy of background sounds do not overlap conspecific signals.

1.4.1 Lazuli buntings: evidence for divergent behavioral responses to different natural noise

Buntings exhibited an increase in overall flights and movement within 5 m of the speaker during cicada chorus trials, with a positive relationship between flight response and chorus intensity. Although many playback studies (e.g., Wingfield and Hahn 1994; Akçay et al. 2010; Akçay et al. 2014) and previous bunting research (Baker 1991; Greene et al. 2014) consider increased number of flights indicative of aggression, the responses observed here also suggest that increased movement may serve as a strategy to attain spatial release from masking (Bee 2008). The pervasiveness of cicada chorus noise throughout the landscape may make an increase in flights necessary to improve signal-to-noise ratios and, ultimately, better assess the threat level posed by the simulated intruder. Based on their diminished approach and increased flight response along an increasing noise gradient – the prior regardless of frequency, and the latter in high-frequency noise alone – we can infer that buntings were able to discriminate, but not successfully localize

intruders when cicadas were chorusing. These results also complement previous studies focused on signaler behavior during insect choruses. Hart et al. (2015) and Stanley et al. (2015) found that Neotropical birds with vocalizations that overlap in frequency with the emerald cicada (*Zammara smaragdina*) avoid singing during naturally occurring and simulated cicada chorus bouts. The impaired listening conditions we quantify here in cicada chorus noise can likely explain the changes in signaler behavior observed in these studies.

Conversely, buntings displayed a reduced flight response as sound level increased in the absence of cicada song. This implies that bunting song is masked more heavily by moving water than cicada chorus noise and that the lower-frequency components of their song may carry important information required for conspecific recognition. Together these results indicate that the communication process may be obstructed at different points along the transmission pathway depending on the dominant background frequencies. If a male is unable to appropriately discriminate and localize conspecific signals or cues, he may fail to detect a potential mate, perceive an intruder, or respond to begging calls from offspring which could lead to reduced pairing success (Habib et al. 2007), increased extra-pair mating opportunities (Halfwerk et al. 2011), or inadequate nestling provisioning (Lucass et al. 2016) as has been suggested in anthropogenic noise.

1.4.2 Spotted towhees: evidence for geographic variation in responses to natural noise

Towhees in both locations displayed delayed and reduced approach behavior with increasing levels of low-frequency water-generated noise. However, California and Idaho towhees exhibited dissimilar behavioral responses in flight and song. In California,

responses differed by acoustic condition (i.e., trial type), whereas Idaho towhees showed no discernible difference in flight and song behavior across treatment-on, treatment-off, and control trials. This may indicate that sound levels across acoustic conditions in Idaho were above the threshold necessary to impair these behaviors, leading to an apparent uniformity in response (Dooling and Popper 2007; Shannon et al. 2016). Nevertheless, the Idaho population collectively sang more than California birds. The increase in vocal activity may reflect heightened sexual selection intensity in Idaho relative to California. Latitudinal gradients have repeatedly been linked to sexual selection intensity as more condensed breeding seasons associated with higher latitudes (and elevations in the case of our study; Idaho sites ranged ~1,700-2,000 m and California sites ranged ~15-155 m above sea level) should demand heightened male-male competition and rapid mate selection (Botero et al. 2009; Weir and Wheatcroft 2001), which could explain the increased song rate identified here. Consequently, the seasonally pronounced increase in species richness and density associated with Idaho's shorter breeding season could heighten biotic masking and/or distraction from heterospecific signals or competition for acoustic (i.e., desirable song perches) and territorial space, ultimately interfering with an individual's ability to appropriately parse between multiple impeding stimuli (Luther and Wiley 2009; Chan et al. 2010).

In California, towhees decreased their flight response during treatment noise exposure compared to controls. Interestingly, there was also a decreased response when treatment noise was off compared to controls. The difference in response may be a latent effect of chronic exposure to treatment noise. However, California birds likely did not experience high enough sound pressure levels for long enough durations to cause

temporary threshold shifts (TTS) in hearing ability (Dooling and Popper 2007).

Nonetheless, our knowledge on avian TTS comes from a study that exposed birds to sound levels of 76 to 106 dB SPL for 72 h (Saunders and Dooling 1974); whether TTS can occur at lower exposure levels, over longer durations is unknown.

In contrast, California spotted towhees had a weaker vocal response with treatment noise turned off relative to controls and treatment noise exposure. The subdued vocal response during treatment-off trials may be related to possible TTS or other carryover effects from chronic noise exposure. It could also indicate a shift in sensory modality preference, such that birds may choose to visually localize intruders first prior to responding vocally. These results oppose previous conspecific playback findings by Kleist et al. (2016) in which towhees exhibited a discernable difference in song behavior as gas compressor sound levels increased. However, the towhee population studied by Kleist et al. (2016) in the arid woodlands of New Mexico, USA, has a song dialect that includes a relatively low-frequency introductory phrase, which is absent from the populations in this study. The difference in habitat and song dialect may make the New Mexico population more susceptible to masking from increases in low-frequency noise, whereas the lack of introductory phrase in California and Idaho song could reflect selection against low-frequency song elements due to low-frequency noise from moving water and wind, which are less common sources of noise in New Mexico woodlands. Whether other widespread species demonstrate differences in song that are consistent with selection against low-frequency components due to natural sounds remains an open question that begs for comparative analysis.

1.5 Conclusion

The influence of natural background noise on animal communication remains largely unexplored in behavioral ecology compared to the numerous studies that have observed impacts on communication and territorial defense behaviors in relation to anthropogenic noise (e.g., Mockford and Marshall 2009; Luther and Magnotti 2014; McMullen et al. 2014; Kleist et al. 2016; Templeton et al. 2016). Recent work on signalers indicates that birds alter vocal behavior in low-frequency natural noise much like they do in response to human-generated noise (Brumm and Slater 2006; Davidson et al. 2017). This suggests that responses to anthropogenic noise may reflect broader plastic responses that evolved for coping with natural shifts in soundscapes due to daily and seasonal cycles when exposed to a variety of acoustic conditions within and across different habitats, or longer-term soundscape shifts due to environmental and climatic change. This possibility, plus the ubiquity of natural sounds, indicates that full diagnosis of altered behaviors in response to anthropogenic noise is not possible without first understanding how both signalers and receivers behave in natural soundscapes.

CHAPTER 2

EXPERIMENTALLY BROADCAST OCEAN SURF AND RIVER NOISE ALTERS SONG STRUCTURE IN SONGBIRDS

2.1 Introduction

Background noise is ubiquitous in all environments. Noise can impair acoustic communication and affect signal structure, effectively acting as a selective force on acoustic signals (Gentry and Luther 2019). Despite the ubiquity of noise, we currently understand far more about the effects of anthropogenic noise on acoustic communication (reviewed in Ortega 2012; Francis and Barber 2013; Shannon et al. 2016) than we do about the natural acoustic environment's influence on communication behavior (Ortega 2012; Derryberry et al. 2016; Davidson et al. 2017). Yet, many sources of natural noise, such as rain, rivers, and ocean surf, have acoustic power spectra similar to anthropogenic noise sources shown to influence signaling behavior in wildlife, particularly in birds (Dooling and Popper 2007; Derryberry et al. 2016; Davidson et al. 2017; Gomes et al. 2021). It therefore stands to reason that natural soundscapes play a role in shaping avian acoustic signals.

Song is critical to reproduction in songbirds through its role in mate attraction and territoriality (Wood and Yezerinac 2006; Lenske and La 2014; Redondo et al. 2013; Derryberry et al. 2016; Sierro et al. 2017; Phillips et al. 2020). Specifically, the structural components of song can encode information about signaler quality and individual identity (Blickley and Patricelli 2012). For example, trill rate and frequency bandwidth are used by female swamp sparrows (*Melospiza georgiana*) to evaluate mate quality (Ballentine et

al. 2004; reviewed in Blickley and Patricelli 2012) and male white-crowned sparrows (*Zonotrichia leucophrys*) use these same trill parameters to assess conspecific competitors (Phillips and Derryberry 2017; reviewed in Gentry and Luther 2019). However, background noise can pose communication challenges if signals are masked and the active space (i.e., communication distance) of a signal is sufficiently reduced (Wood and Yezerinac 2006; Derryberry et al. 2016; Gentry and Luther 2017; Phillips et al. 2020). To deal with noisy conditions, birds can alter vocalizations through changes in frequency (Davidson et al. 2017), temporal elements (Francis et al. 2011a; Redondo et al. 2013), amplitude (Derryberry et al. 2017), the diurnal timing of song (Stanley et al. 2015), and through changes in song type redundancy (Brumm and Slater 2006). However, the type and magnitude of signal modification varies broadly within and among species (Gentry and Luther 2019), and knowledge of how species respond to natural sources of noise (Gomes et al. 2021), which they have experienced over evolutionary timescales, may help shed light on intra- and interspecific variation in responses to anthropogenic noise with particular signal modifications.

Here, we investigated how the spectral and temporal characteristics of the songs of six songbird species vary with amplitude and frequency of water-generated noise. To achieve this, we used landscape-level playbacks of ocean surf noise in coastal California and river noise in riparian areas of Idaho. We analyzed songs of individuals defending territories on 19 California sites and 18 Idaho sites, with each site representing one of four acoustic environments (i.e., treatments): naturally quiet ‘control’ sites, naturally noisy ‘positive control’ sites adjacent to the ocean or a whitewater river, ‘phantom’ playback sites with continuous broadcast of low-frequency water noise, and ‘shifted’

playback sites with continuous broadcast of high-frequency water noise. We included shifted playback to further tease apart which noise frequencies influence vocal communication and the mechanisms by which they occur. These four different acoustic conditions enabled us to test whether different songbird species vary in their ability to adjust vocalizations in the face of background noise, and to explore how common any such adjustments might be by testing across ecologically disparate locations.

We hypothesized that songbirds alter song structure in response to ocean surf and river noise, and predicted that all birds exposed to positive control, phantom, or shifted noise would adjust song structure, but the type of modification would depend on the spectral profile of the background noise and the magnitude of signal modification would be larger in noisier locations. Specifically, we predicted that (i) song minimum frequency would be higher during phantom noise playback and on positive control sites; (ii) song frequencies would be lower during shifted noise playback; and (iii) frequency bandwidth would decrease in noisier locations, to improve signal transmission and avoid energetic masking. We also expected responses to vary at the species level due to species-specific differences in behavior and song attributes. We did not make *a priori* assumptions regarding temporal adjustments in noise due to conflicting evidence showing species-dependent increases and decreases in song/syllable length and rate in response to noise (e.g., Halfwerk and Slabbekoorn 2009; Francis et al. 2011a; McMullen et al. 2013; Lenske and La 2014; Luther et al. 2016; Sierro et al. 2017).

2.2 Methods

2.2.1 Study areas and study species

We recorded white-crowned sparrows (*Zonotrichia leucophrys*) and wrentits (*Chamaea fasciata*) spread across 19 sites on Vandenberg Air Force Base (VAFB), California (between 34°39'N and 34°46'N latitude and 120°36'W and 120°30'W longitude), between 5 April – 8 June 2017 and 26 March – 12 June 2018. Our control ($n = 5$), phantom ocean surf ($n = 5$), and shifted ocean surf ($n = 5$) sites occurred at varying distances from the coastline and our positive controls ($n = 4$) were located adjacent to the Pacific Ocean (Appendix A Figure S1.2b). All VAFB sites were spaced ≥ 0.89 km apart in coastal sage scrub habitat with similar species richness.

In Idaho, we recorded lazuli buntings (*Passerina amoena*), song sparrows (*Melospiza melodia*), warbling vireos (*Vireo gilvus*), and yellow warblers (*Setophaga petechia*) on 18 sites across Lava Lake Ranch in the Pioneer Mountains (between 43°33'N and 43°26'N latitude and 113°44'W and 113°38'W longitude), from 13 June – 12 July 2018. Our control ($n = 6$), phantom river ($n = 5$), and shifted river ($n = 5$) sites were located along riparian drainages with seasonal creeks running through them and positive control sites ($n = 2$) were located along whitewater rivers (all sites spaced ≥ 1.08 km apart; Appendix A Figure S1.2a). All sites shared similar species richness and vegetation structure.

The six species we investigated are common within their respective study areas and vocalize at frequencies susceptible to masking by low-frequency water noise and water noise shifted up in frequency. Both white-crowned sparrows and wrentits produce a single song type with little variation within and among individuals. The dominant white-

crowned sparrow dialect in our population is made of four sections: a pure tone whistle, buzz, short trill, and a low-frequency garble or buzz (2-8 kHz; Gentry et al. 2017; see Appendix C Table S2.1 for species-typical means \pm SD of analyzed song features).

Wrentit song consists of a series of short, overslurred notes that accelerate into a trill with little song frequency modulation (2-4 kHz; Grinnell 1913; Geupel and Ballard 2020).

Song sparrows possess a crystalized repertoire of 5-13 songs, typically containing pure tones, buzzes, trills, and harsh notes spanning 1.1-9.3 kHz (Wood and Yezerinac 2006).

Warbling vireo song consists of continuous, undulating warbles, with variation in warble complexes among songs (2.3-7 kHz; Howes-Jones 1985; Gardali and Ballard 2000).

Lazuli buntings and yellow warblers sing tonal songs consisting of a series of repeated syllables (Lowther et al. 1999; Greene et al. 2014). Lazuli buntings possess one individually unique song, ranging from 1.6-11.0 kHz (Thompson 1968; Greene et al. 2014), whereas yellow warblers sing one unique song type during the day (Type 1) and a separate repertoire of songs (Type II) predominantly during the dawn chorus (Spector 1991). Both Type I and Type II songs share a 3 to 10 kHz frequency range (Proppe et al. 2013). Yellow warbler minimum song frequency falls above the peak frequency of shifted river noise (Figure 2.1); thus, with shifted noise exposure, we speculated that individuals may increase instead of decrease frequencies as predicted for other species.

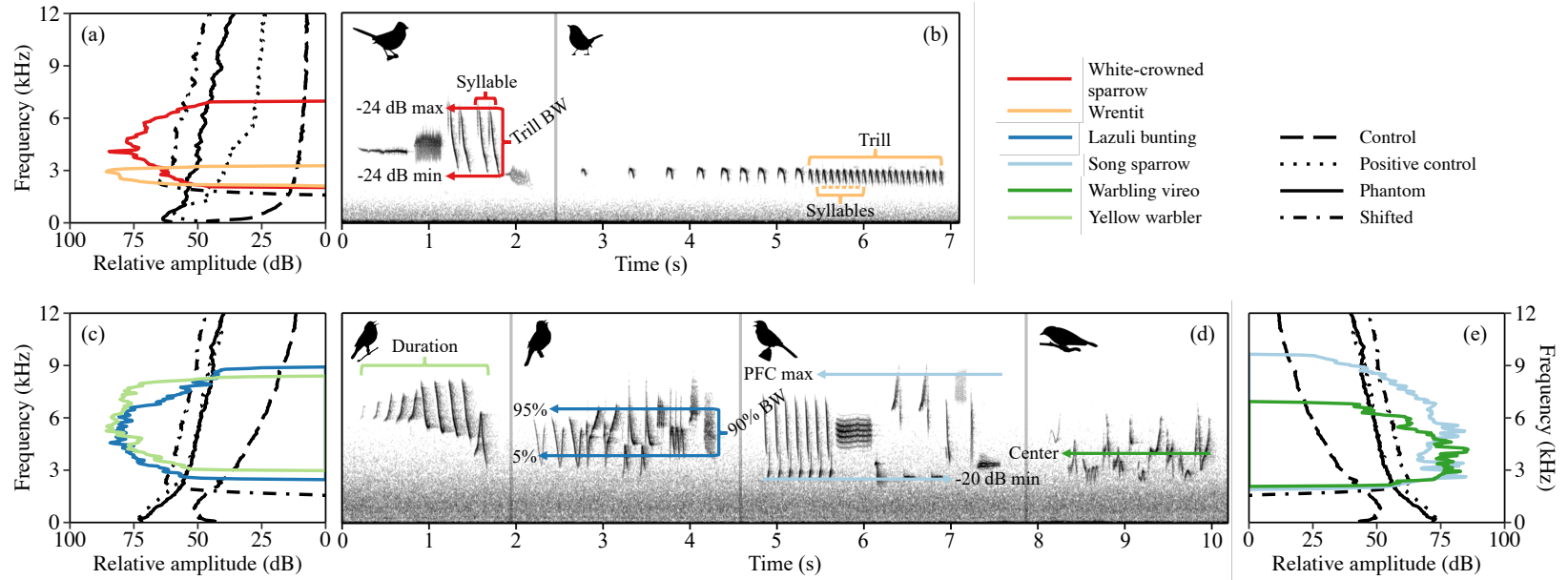


Figure 2.1 Power spectra of the four acoustic conditions are overlaid with song power spectra for California (a) and Idaho (c and e) songbirds. Spectra of acoustic conditions are approximated to reflect average sound level from by treatment type and songs are amplified to a relative peak amplitude of 85 dB (re 1 dimensionless sample units), reflective of typical song at 1 m from the source (amplification performed in Raven Pro v1.5, Bioacoustics Research Program 2017). Species-typical song spectrograms for California (b) and Idaho species (d) from individuals recorded under control conditions. Acoustic variables used in the analysis are marked on spectrograms; dB min/dB max = minimum/maximum frequency threshold for trill/song subset, PFC max = maximum peak frequency contour for song subset, BW = frequency bandwidth, and 5%, center, and 95% = 5%, center, and 95% frequencies, respectively (see text for detailed explanation of variables).

2.2.2 Experimental noise broadcasts

We created playbacks from uncompressed waveform files recorded on or near our positive control sites along the coastline in California and whitewater rapids in Idaho. We used a Roland R-05 recorder and custom windscreen to record ocean surf and a Zoom H4N Pro recorder and Rode NT-1A microphone to record river noise. All files were recorded with a 48 kHz sampling rate. After removing all non-water sounds and amplifying recordings to -2 dB of the maximum amplitude in Audacity 2.1.3 (Audacity Team 2017), we constructed separate 4.5 h ocean surf and river playbacks with a 7 s fade in/out and 5 s crossfade to avoid clipping. To create shifted playbacks, we additionally applied a 2 kHz high pass filter and split the recordings into two bands: 2-14 kHz and 14-24 kHz using the Frequency Band Splitter in Adobe Audition 10 CC 2017. The bands were amplified by 4 dB and 5 dB, respectively, and then recombined.

We broadcast ocean surf and river playbacks continuously from two loudspeakers (Octasound SP820A 360° × 180° Central Speaker, 35 Hz-20 kHz; Appendix A Figure S1.1) per phantom site. Because high-frequency noise attenuates faster than low-frequency noise, we broadcast shifted ocean surf and shifted river noise from three loudspeakers (Octasound SP810A 360° × 180° Central speaker, 40 Hz-20 kHz) per shifted site to achieve similar exposure areas. All loudspeakers were solar-powered and connected to an amplifier (Lepai LP-2020TI Mini Amp or PRV Audio AD1200.1-2 Amplifier) and audio player (Roland R-05 or R-09). We calibrated loudspeakers at 2 m to an average sound level (LA_{eq} , 3 min [continuous level A-weighted decibel equivalent re 20 μ Pa]) of ~95 dBA in Idaho and ~91 dBA in California with a Larson Davis 824 Sound Level Meter (SLM). In California, we placed phantom and shifted surf

loudspeakers ~85 m and ~55 m apart on their respective sites. In Idaho, we placed phantom and shifted river loudspeakers ~100 m and ~50 m apart, respectively, adjacent to the creek running through each site. To control for infrastructure presence, we set-up mock loudspeakers (that did not broadcast sound) and mock solar panels, mirroring phantom/shifted site layout on control and positive control sites.

2.2.3 Song recordings

We recorded song bouts as close to focal birds as possible (3-35 m) using one of several recording unit + microphone pairings (study area and year of pairing specified in parentheses): a Marantz PMD 660 digital recorder with an Audio-Technica AT815 directional shotgun microphone (California 2017), the TwistedWave Recorder iPhone/iPad application with a MicW iShotgun microphone (California 2017, Idaho 2018), a Zoom H4N Pro with an Audio-Technica AT815 microphone (California and Idaho 2018) or a Sennheiser ME66 microphone (Idaho 2018). We measured background sound level (LA_{eq} , 2 min) immediately following song recording as close to the bird's singing position as possible using a SLM or a MicWi436 microphone with the SPLnFFT Sound Meter v6.2 iPhone/iPad application (SPLnFFT). All song files were recorded in uncompressed waveform at either a 16-bit, 44.1 kHz sampling rate or 24-bit, 48 kHz sampling rate. We only collected song recordings and noise measures when wind speed was < 3 on the Beaufort Wind Scale.

We extracted additional white-crowned sparrow and wrentit song bouts from Wildlife Acoustics Song Meter SM3BAT recorders in 2018 to bolster sample sizes (see Appendix C Table S2.2 for sample sizes). Recorders were paired with SMM-A1 acoustic

microphones set to automatically record the dawn chorus at specific site locations. In two separate instances, we clearly identified two wrentits countersinging at the same SM3BAT recorder location and included songs from each individual for analysis. In all other instances, we only extracted one high-quality song bout per site location. We measured background sound level (LA_{eq} , 2 min; SLM or SPLnFFT) at the SM3BAT recorder on three separate mornings on or near the date of the song bout and averaged the measurements together to approximate the background sound level for extracted song bouts.

We recorded each individual once between 0515 and 1230 hours, with the exception of one warbling vireo and two yellow warblers recorded between 1750 and 1830, and eleven individuals that were opportunistically recorded twice under different acoustic conditions (see below). Targeted birds sang at distances ranging 6 to 403 m from the nearest mock or phantom/surf loudspeaker. When multiple birds of the same species were recorded at a site, we ensured individuals were greater than ~50 m apart and compared spectrograms against each other to reduce potential double counts. On phantom/shifted sites, we opportunistically recorded individuals with loudspeakers either turned on or off. All recorded birds sang spontaneously in California; however, conspecific playback was used to initiate song for 31 of 157 individuals recorded in Idaho (eleven lazuli buntings, six song sparrows, six warbling vireos, eight yellow warblers).

2.2.4 Song analysis

We resampled all recordings at 44.1 kHz and 16-bit format using Audacity 2.1.3 (Audacity Team 2017) and the R package *warbleR* (Araya-Salas and Smith-Vidaurre

2017; R Core Team 2018) and performed all acoustic measurements in Raven Pro v1.5 (Bioacoustics Research Program 2017; Hann window, window size = 1024 samples, overlap = 90%, hop size = 102 samples, DFT = 1024, grid spacing = 43.1 Hz). We sampled one to five songs per individual depending on the number of high-quality songs recorded, with an average of 4.27 ± 1.14 SD songs analyzed per individual. We recorded eleven individuals with phantom/shifted loudspeakers on and off (three lazuli buntings, one song sparrow, one warbling vireo, three white-crowned sparrows, three wrentits). In those instances, we selected songs from both acoustic conditions (i.e., phantom/shifted loudspeakers on and off) for analysis. We then applied a bandpass filter to all recordings, removing irrelevant noise below 1 kHz and 1-2 kHz above the established maximum song frequency for each species, and standardized peak amplitude across all song samples. For song sparrows, warbling vireos, and yellow warblers (singing Type II song), we randomly selected songs independent of song type/variation and made no attempt to compare within subject song characteristics (e.g., Wood and Yezerinac 2006).

To assess frequency characteristics for all songs, including those with low signal-to-noise ratios, we examined four robust frequency measures, automatically calculated from manually placed song selection boxes in Raven Pro v1.5 (Bioacoustics Research Program 2017): 5% frequency, center frequency, 95% frequency (i.e., the frequencies containing 5, 50, and 95% of total song energy), and 90% frequency bandwidth (95% frequency minus 5% frequency). We selected these frequency measures for their robustness against small changes to the selection border (Charif et al. 2010) that may arise from acoustic masking (e.g., Billings 2018). We also measured song duration (s) for all songs, trill rate (number of trill syllables divided by trill duration; see below) for all

California songs, and syllable rate (number of song syllables divided by song duration) for all Idaho songs.

Natural and experimental water noise precluded identification of minimum and/or maximum frequency from power spectra due to complete masking for $20.83\% \pm 4.62\%$ (mean \pm SD) of sampled songs across species (Appendix C Table S2.2). Because we could not accurately measure frequency bounds for all songs, we restricted analysis of minimum frequency, maximum frequency, and bandwidth to the subset of songs with large enough signal-to-noise ratios, enabling more precise examination of frequency responses to noise. We estimated minimum frequency (and maximum frequency for California species; see below) by subtracting a fixed amplitude threshold from the peak amplitude of power spectra (Podos 1997; Zollinger et al. 2012; Ríos-Chelén et al. 2017). This method ensures variation in frequency estimates are not due to song amplitude variation (Zollinger et al. 2012).

Previous research on white-crowned sparrows and other passerines indicate that trill rate and bandwidth are influenced by ambient noise conditions (e.g., Redondo et al. 2013; Davidson et al. 2017). For white-crowned sparrows and wrentits (the two species whose songs always include a trill) we therefore measured three trill-specific frequency characteristics: minimum and maximum frequency at -24 dB relative to the peak amplitude of the trill, and trill bandwidth (maximum frequency minus minimum frequency). For both species, trill measurements double as estimates of song minimum/maximum frequency and bandwidth (excluding the low-frequency, terminal buzz of white-crowned sparrow song, typically masked in noise).

For Idaho species, we measured song minimum frequency at -20 dB to the peak amplitude. However, a fixed amplitude threshold failed to adequately capture maximum frequency for Idaho songs. We instead used the peak frequency contour (PFC) of the maximum frequency (i.e., peak frequency of the highest note; e.g., Gentry et al. 2017), automatically calculated in Raven Pro v1.5 (Bioacoustics Research Program 2017), and measured bandwidth as the difference between maximum PFC and minimum frequency at -20 dB. The acoustic energy present in low-frequencies across our sites proved too great to utilize the PFC of the minimum frequency. Thus, the trill (California) and song (Idaho) subsets possess the most accurate minimum/maximum frequency and bandwidth estimates, yet by default exclude songs with the lowest signal-to-noise ratios (i.e., noisiest background conditions). All frequency variables were measured in kilohertz.

2.2.5 Statistical analysis

Preliminary analysis for each study area individually showed no difference between phantom-off, shifted-off, and control site song features. We therefore combined them into one factor level for analysis (hereafter control), and excluded samples if fewer than four individuals were recorded for a given treatment type. To determine the species-specific effects of noise on song features, we built linear mixed effect models (*lme4* package, Bates et al. 2015) with acoustic parameters for sound level (i.e., 2 min LA_{eq} from the bird's singing location; hereafter dBA) and treatment (categorical: phantom, shifted, control, or positive control). Models also included parameters for Julian date, year (2017 or 2018; California only), and conspecific playback (no or yes; Idaho only), with random intercepts for individual I.D. nested within site, and a combined factor

indicating the recordist and recording unit used. If random effects led to model singularity or accounted for zero variance, we systematically dropped them, following recommendations of Bates et al. (2015). However, all models contained the random intercept for individual I.D. For the categorical treatment variable, we rotated reference states as needed and reran each model to identify all pairwise relationships. To ensure model assumptions were met, we inspected variance inflation factors for multicollinearity and examined quantile-quantile plots of model residuals for deviations from normality (*car* package, Fox and Weisberg 2019). We examined residual outliers of global models using the “qqp” function (*car* package, Fox and Weisberg 2019); if removal of outliers did not alter parameter effects, we left them in the dataset. For wrentits we removed one extreme outlier from all models. To assess sound level across treatment types, we examined dBA averaged by individual (those recorded with phantom/shifted loudspeakers on and off had dBA averaged separately) in response to the treatment covariate with individual I.D. nested within site as random effects.

Following an information-theoretic approach, we ranked and evaluated models using AIC_c (Hurvich and Tsai 1989), and considered models with $\Delta AIC_c \leq 2.00$ from the highest-ranked model equivalent (Burnham and Anderson 2002; *MuMin* package, Barton 2019). We deemed predictors with apparent trends (i.e., 85% confidence intervals [CIs] that did not overlap zero) to warrant consideration for inference and trends with 95% CIs to reflect more precise estimates of effects (e.g., Ferraro et al. 2020). In the results, parameter effect sizes and CIs reflect estimates from the highest-ranked model with $\Delta AIC_c \leq 2.00$ in which the parameter had an apparent effect. We also focus our reporting on parameters relevant to our hypotheses about noise, but report influences of other fixed

effects in the appendix (Appendix C Tables S2.3-S2.8). All statistical analyses were performed in R (R Core Team 2018).

2.3 Results

We analyzed 1122 songs from 261 songbirds in California and Idaho (Appendix C Table S2.2) in background noise amplitudes ranging 27.5-62.0 and 34.8-73.1 dBA, respectively. Sound level (measured from the singing location of each bird) differed among all treatment types in California except phantom and shifted treatments, which did not differ (see Appendix C Table S2.9 for effect sizes $[\beta] \pm SE$; mean \pm SD dBA: control = 37.69 ± 4.84 , positive control = 41.71 ± 3.45 , phantom = 48.79 ± 5.95 , shifted = 50.03 ± 7.92). In Idaho, sound level at the singing location of each bird differed across all treatment types except positive controls and phantom treatments (mean \pm SD dBA: control = 46.37 ± 6.28 , positive control = 57.70 ± 8.89 , phantom = 54.89 ± 7.51 , shifted = 49.51 ± 6.48). Individuals of all six species responded to sound level (Table 2.1) and treatment type (Table 2.2) with spectral and/or temporal adjustments.

Table 2.1 Species-specific influence of sound level on song features for the highest-ranked model containing an effect.

Idaho	Song subset				All analyzed songs				
	Minimum frequency	Maximum frequency	Frequency bandwidth	Center frequency	5% frequency	95% frequency	90% bandwidth	Duration	Syllable rate
Lazuli bunting		<i>dB</i> A↓*	dBA ↓*			<div></div>			dBA ↓*
Song sparrow		dBA ↓*	dBA ↓*		<i>dB</i> A↑				<i>dB</i> A↓*
Warbling vireo	dBA ↑	<i>dB</i> A↑							
Yellow warbler					<i>dB</i> A↓*	<i>dB</i> A↑	dBA ↑		
California	Trill subset				All analyzed songs				
	Minimum frequency	Maximum frequency	Frequency bandwidth	Center frequency	5% frequency	95% frequency	90% bandwidth	Duration	Trill rate
White-crowned sparrow	dBA ↑*		dBA ↓*						
Wrentit	dBA ↓*		dBA ↑		dBA ↓*		dBA ↑*		

We considered noise to have an effect on song structure if a model with $\Delta AIC_c \leq 2.00$ included sound level (dBA) or treatment (Table 2.2) parameters and had 85% CIs excluding zero. Parameters with 85% CIs are italicized with hatched arrows (↑↓) and 95% CIs are bold with solid arrows (↑↓). Responses to increased sound level are indicated as positive (i.e., ↑/↑ = increased frequency/time), negative (i.e., ↓/↓ = decreased frequency/time), or no response (blank). An asterisk (*) denotes an effect of sound level in the top model ($\Delta AIC_c = 0.00$). Grey cells denote competitive model sets that include the null and an effect of sound level. The 95% frequency measure for lazuli buntings was excluded due to poor model performance (slashed cell).

Table 2.2 Species-specific influence of treatment type on song features for the highest-ranked model containing an effect.

Idaho	Song subset				All analyzed songs				
	Minimum frequency	Maximum frequency	Frequency bandwidth	Center frequency	5% frequency	95% frequency	90% bandwidth	Duration	Syllable rate
Lazuli bunting				<u>C>P, S>P</u>	<u>C>P*</u>		<u>C<S</u>		<u>C>S, P>S*</u>
Song sparrow	<u>C<P, S<P*</u>		<u>C>P, S>P*</u>	<u>C<S, P<S*</u>	<u>C<P</u>	<u>C>P</u>	<u>C>P, S>P*</u>	<u>C<P</u>	
Warbling vireo	<u>C>S, P>S*</u>			<u>C<PC, P<PC, S<PC</u>	<u>C>P>S, PC>S*</u>			<u>C>P, S>P, PC>P</u>	<u>C>S, P>S</u>
Yellow warbler	<u>P<S</u>					<u>C>P>PC, S>P>PC</u>	<u>C>P</u>	<u>C<P, S<P, PC<P*</u>	
California	Trill subset				All analyzed songs				
	Minimum frequency	Maximum frequency	Frequency bandwidth	Center frequency	5% frequency	95% frequency	90% bandwidth	Duration	Trill rate
White-crowned sparrow	<u>C>PC>S</u>	<u>C>PC>S, P>PC>S*</u>	<u>C<P, PC<P, S<P</u>			<u>C<S, P<S, PC<S</u>		<u>C>PC>S, P>S*</u>	
Wrentit	<u>C>P</u>		<u>C<P*</u>			<u>C<S, P<S*</u>			<u>C>P, S>P</u>

We considered noise to have an effect on song structure if a model with $\Delta AIC_c \leq 2.00$ included treatment or sound level (Table 2.1) parameters and had 85% CIs excluding zero. Treatment contrasts (C = control, PC = positive control, P = phantom, S = shifted) with 85% CIs are italicized and 95% CIs are in bold. Reference conditions are underlined and those yielding different effects depending on the level comparison are in bold, italic font. Greater than/less than signs (</>) denote direction of behavioral response relative to the underlined reference condition. Blank cells indicate no response to treatment type. An asterisk (*) denotes an effect of treatment type in the top model ($\Delta AIC_c = 0.00$). Grey cells indicate competitive model sets that include the null and an effect of treatment type. The 95% frequency measure for lazuli buntings was excluded due to poor model performance (slashed cell).

2.3.1 California songbirds

Sound level and treatment type predicted several white-crowned sparrow and wrentit frequency features. For white-crowned sparrows, trill minimum frequency and trill bandwidth were best explained by models including sound level, whereas trill maximum frequency was best explained by treatment type. Specifically, trill minimum frequency increased (Figure 2.2a; $\beta = 0.004 \pm 0.002$, 95% CI [0.001, 0.01]) and trill bandwidth decreased (Figure 2.2b; $\beta = -0.01 \pm 0.005$, 95% CI [-0.02, -0.003]) with increasing background amplitude. Trill maximum frequency was lower on positive control and shifted surf sites relative to phantom surf (Figure 2.3a; $\beta_{\text{PosControl}} = -0.27 \pm 0.12$, 95% CI [-0.51, -0.03]; $\beta_{\text{Shifted}} = -0.30 \pm 0.11$, 95% CI [-0.50, -0.09]) and controls ($\beta_{\text{PosControl}} = -0.25 \pm 0.11$, 95% CI [-0.48, -0.03], $\beta_{\text{Shifted}} = -0.28 \pm 0.09$, 95% CI [-0.45, -0.10]). Treatment type also influenced white-crowned sparrow song duration, eliciting a strong negative effect (i.e., shorter songs) on positive controls and shifted treatments in relationship to controls (Figure 2.3b; $\beta_{\text{PosControl}} = -0.14 \pm 0.06$, 95% CI [-0.25, -0.02]; $\beta_{\text{Shifted}} = -0.19 \pm 0.06$, 95% CI [-0.30, -0.07]), and a negative effect on shifted relative to phantom ($\beta = -0.13 \pm 0.07$, 85% CI [-0.24, -0.03]).

Contrary to our predictions, wrentits decreased 5% song frequency (Figure 2.2c; $\beta = -0.01 \pm 0.002$, 95% CI [-0.01, -0.004]), and increased 90% song bandwidth (Figure 2.2d; $\beta = 0.01 \pm 0.002$, 95% CI [0.002, 0.01]) as sound level increased across sites. Trill minimum frequency also decreased with increasing sound level ($\beta = -0.01 \pm 0.003$, 95% CI [-0.01, -0.0004]), although the null was considered equivalent to the top model (Appendix C Table S2.4). Treatment strongly influenced trill bandwidth and 95% song frequency; trill bandwidth increased on phantom sites (Figure 2.3c; $\beta = 0.14 \pm 0.06$, 95%

CI [0.03, 0.25]) and 95% song frequency increased on shifted compared to phantom surf noise (Figure 2.3d; $\beta = 0.10 \pm 0.03$, 95% CI [0.03, 0.17]) and controls ($\beta = 0.08 \pm 0.02$, 95% CI [0.03, 0.13]). Noise did not influence temporal aspects of wrentit song.

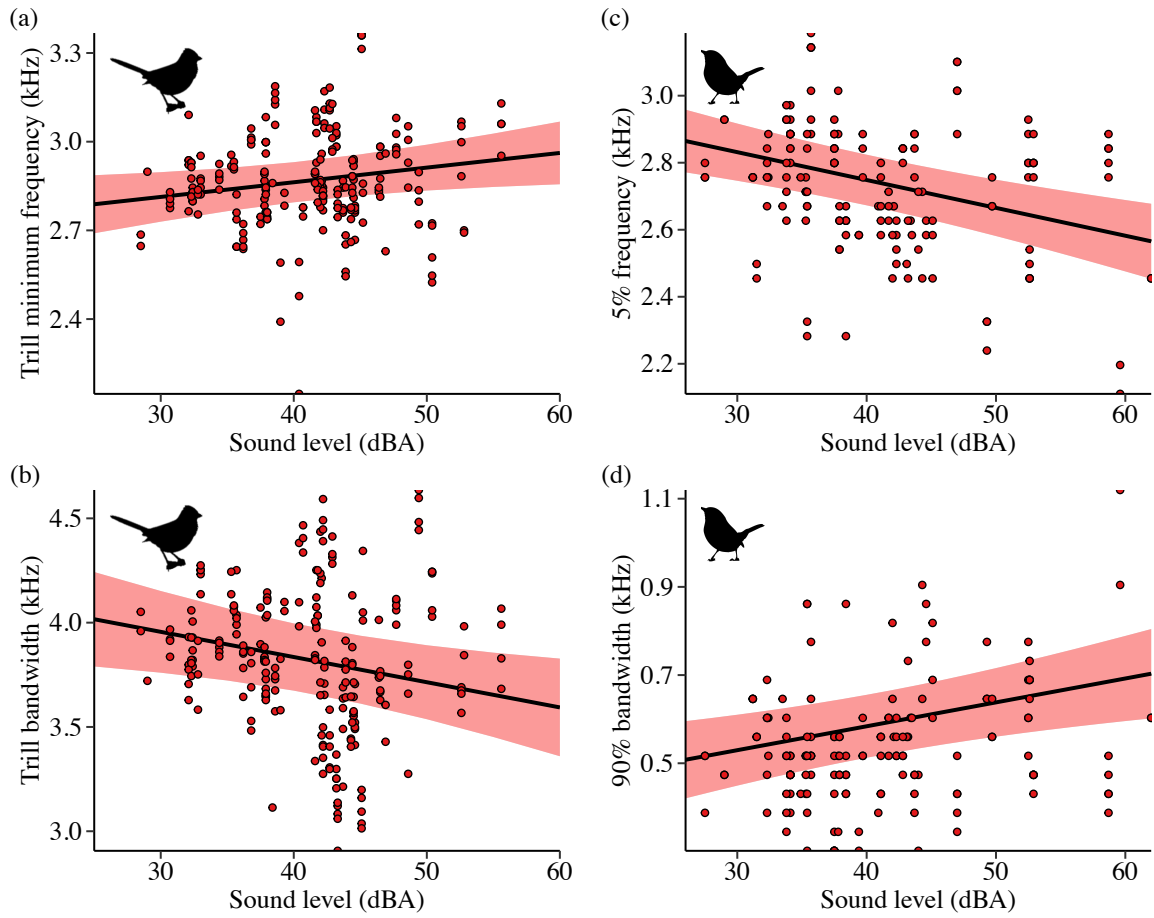


Figure 2.2 Influence of background sound level on song features for California white-crowned sparrows (a-b) and wrentits (c-d). Points denote individual songs. Only song features with a strong effect of sound level in the top model ($\Delta AIC_c = 0.00$) are shown.

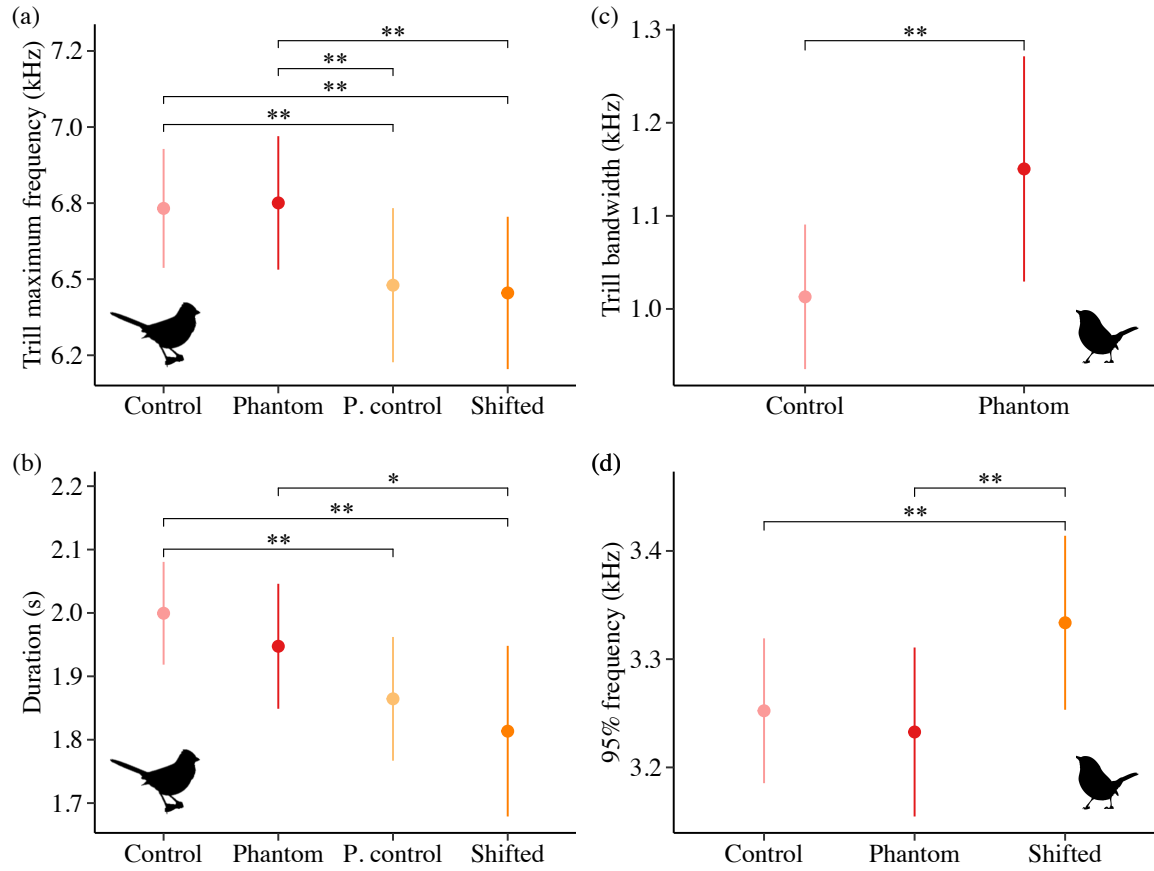


Figure 2.3 Influence of treatment type on California white-crowned sparrow (a-b) and wrentit (c-d) song features. Double asterisks indicate significant contrasts corresponding to 95% CIs and single asterisks correspond to 85% CIs. Only song features with a strong effect of treatment in the top model ($\Delta AIC_c = 0.00$) are shown.

2.3.2 Idaho songbirds

Noise influenced frequency and/or temporal features for all 4 species in Idaho.

For the song subset (songs with higher signal-to-noise ratios and most accurate frequency estimates), song sparrows decreased maximum frequency in response to increasing noise across sites (Figure 2.4a; $\beta = -0.03 \pm 0.01$, 95% CI [-0.05, -0.01]). Song sparrows sang at higher minimum frequencies on phantom river treatments relative to controls ($\beta = 0.14 \pm 0.07$, 95% CI [0.02, 0.27]) and shifted conditions ($\beta = 0.16 \pm 0.08$, 85% CI [0.04, 0.28]) supporting our prediction for low frequency noise exposure. However, the null was

considered equivalent to the top model for minimum frequency of the song subset (Appendix C Table S2.6). These changes led to a decrease in song bandwidth for individuals exposed to phantom river noise, with a strong negative effect relative to controls (Figure 2.5a; $\beta = -0.66 \pm 0.21$, 95% CI [-1.07, -0.26]) and a negative effect relative to shifted river conditions ($\beta = -0.49 \pm 0.27$, 85% CI [-0.87, -0.10]). Amplitude also had a strong negative effect on song bandwidth (Figure 2.4b; $\beta = -0.04 \pm 0.01$, 95% CI [-0.07, -0.02]), with 50% combined model weight in the candidate model set. For the full song set, song sparrow 90% bandwidth was narrower in the presence of phantom river noise compared to control (Figure 2.5b; $\beta = -0.77 \pm 0.30$, 95% CI [-1.37, -0.18]) and shifted river conditions ($\beta = -0.70 \pm 0.44$, 85% CI [-1.33, -0.07]), whereas song center frequency increased on shifted rivers relative to phantom (Figure 2.5c; $\beta = 0.49 \pm 0.20$, 95% CI [0.10, 0.89]) and control conditions ($\beta = 0.45 \pm 0.18$, 95% CI [0.10, 0.81]). For the warbling vireo subset, shifted river noise exerted a strong negative effect on minimum frequency relative to control (Figure 2.5d; $\beta = -0.27 \pm 0.06$, 95% CI [-0.39, -0.16]) and phantom river conditions ($\beta = -0.21 \pm 0.07$, 95% CI [-0.34, -0.07]). Noise did not influence temporal aspects of song sparrow or warbling vireo song.

Although lazuli buntings and yellow warblers tend to produce songs with greater acoustic energy at higher frequencies compared to the other species investigated, neither species clearly shifted their song frequency features in response to shifted river noise. However, buntings sang with a slower syllable rate on shifted river treatments relative to controls (Figure 2.5e; $\beta = -0.58 \pm 0.17$, 95% CI [-0.94, -0.23]) and phantom treatments ($\beta = -0.54 \pm 0.18$, 95% CI [-0.88, -0.20]). Lazuli buntings also reduced frequency bandwidth (Figure 2.4c; $\beta = -0.02 \pm 0.01$, 95% CI [-0.04, -0.001]) and song duration (Figure 2.4d; β

$= -0.01 \pm 0.01$, 95% CI $[-0.03, -0.002]$) as background noise increased. Although the null was included in the top model set, sound level had a negative effect on maximum frequency ($\beta = -0.02 \pm 0.01$, 85% CI $[-0.03, -0.002]$), which may explain the reduced bandwidth. The only feature of yellow warbler song influenced by noise was song duration. Individuals exposed to phantom river noise sang longer songs relative to other treatment types, resulting in a strong positive effect of phantom treatment relative to shifted noise (Figure 2.5f; $\beta = 0.21 \pm 0.08$, 95% CI $[0.06, 0.36]$) and controls ($\beta = 0.14 \pm 0.06$, 95% CI $[0.02, 0.26]$), and a positive effect in relation to positive controls ($\beta = 0.17 \pm 0.09$, 85% CI $[0.04, 0.31]$).

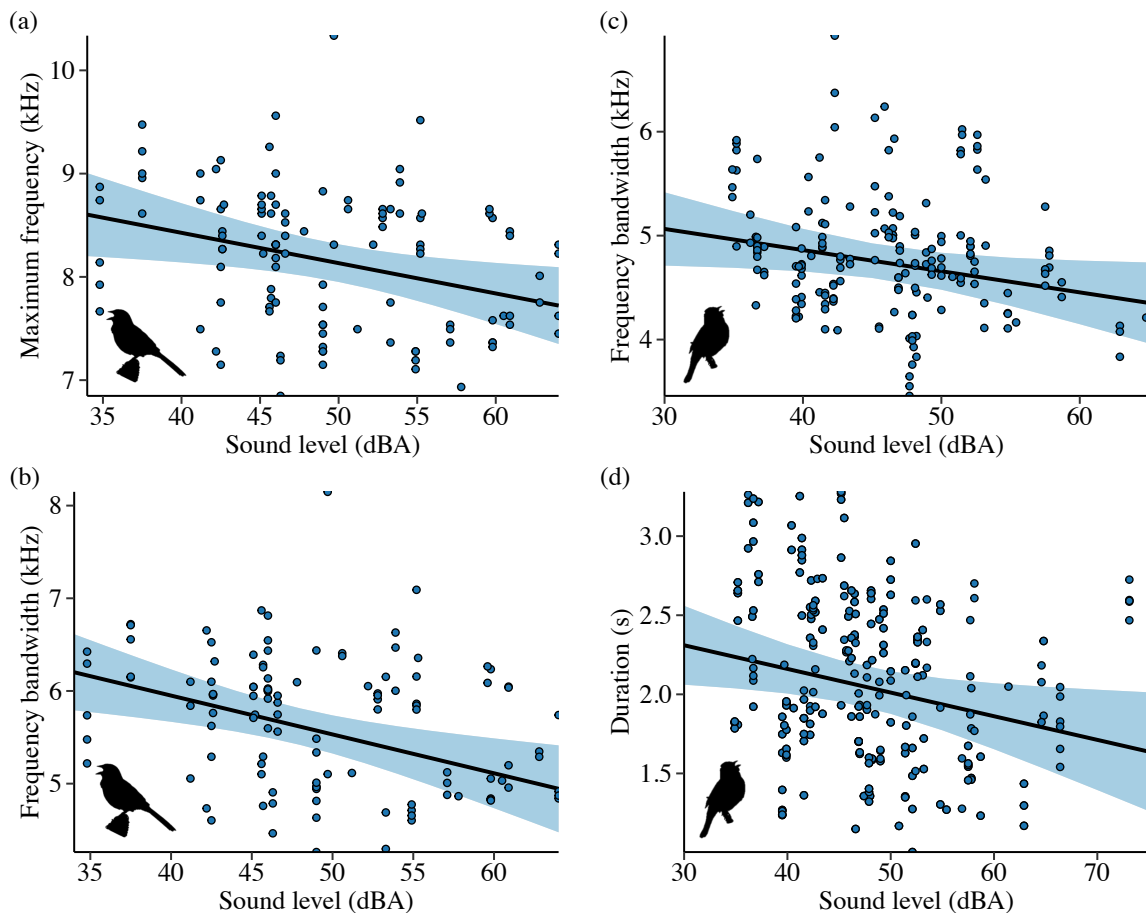


Figure 2.4 Influence of background sound level on song features for Idaho song sparrows

(a-b) and lazuli buntings (c-d). Points denote individual songs. Only song features with a strong effect of sound level in the top model ($\Delta AIC_c = 0.00$) are shown.

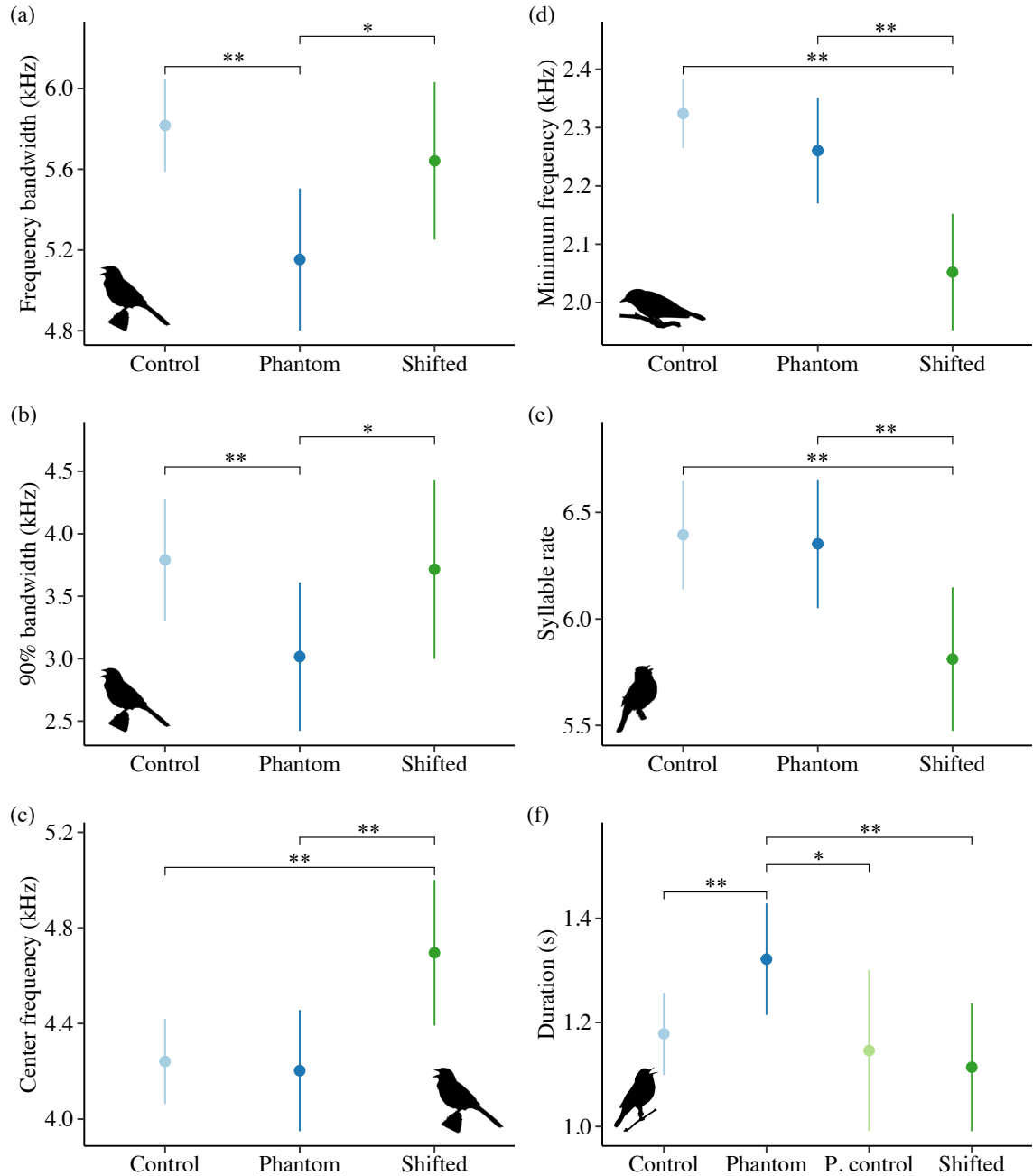


Figure 2.5 Influence of treatment type on song features for song sparrows (a-c), warbling vireos (d), lazuli buntings (e), and yellow warblers (f) in Idaho. Double asterisks indicate significant contrasts corresponding to 95% CIs and single asterisks correspond to 85% CIs. Only song features with a strong effect of treatment in the top model ($\Delta AIC_c = 0.00$) are shown.

2.4 Discussion

We examined differences in song characteristics for six songbird species exposed to ambient and experimental broadcasts of low- and high-frequency natural noise. Song structure of all six species varied with background noise, providing strong evidence that natural soundscapes influence vocal behavior. However, no two species altered songs in precisely the same way. It is not surprising that the songbirds investigated here displayed unique vocal behaviors in noise, as species rely on different acoustic elements for conspecific signal detection and discrimination. Though in practice our analyses are mainly correlational, given the strong evidence for short-term behavioral flexibility in response to anthropogenic noise across a variety of songbird species (e.g., Halfwerk and Slabbekoorn 2009; Derryberry et al. 2017; LaZerte et al. 2017), it is likely that the responses we documented also reflect short-term adjustments. If true, short-term vocal adjustments to mitigate masking would represent widespread coping strategies for dealing with the longstanding challenges of naturally noisy acoustic environments.

2.4.1 Variation in frequency bandwidth correlates with sound level

Individuals of three species decreased song bandwidth as noise amplitude increased via shifts in song maximum frequency (lazuli buntings and song sparrows) and trill minimum frequency (white-crowned sparrows). As frequency bandwidth narrows, signal tonality increases, which may improve signal transmission distance (Gentry et al. 2017), especially if the bandwidth is more concentrated within the region of peak hearing sensitivity for a species (Gentry et al. 2017; Gentry and Luther 2019).

By contrast, wrentits sang with broader bandwidths in noisy locations through differences in trill minimum frequency and song 5% frequency. Wrentit song is simple, narrow bandwidth, and highly tonal. Consequently, a small increase in frequency bandwidth (by ~200 Hz) may not impair communication (Nemeth and Brumm 2010), particularly if the active space of wrentit song typically extends far beyond intended receivers. The seemingly counterintuitive frequency decrease among wrentits may reflect noise-dependent changes in motivational state (e.g., Nemeth and Brumm 2009) or a by-product of changes to song features not measured here. For example, singing at greater amplitude in noise (i.e., Lombard effect) appears to be an immediate response shared across extant birds and can covary with spectral or temporal changes (reviewed in Brumm and Zollinger 2013). Increased amplitude is far more effective in reducing masking than the magnitude of typical frequency shifts exhibited in noise (~200-500 kHz; Nemeth and Brumm 2010). Even so, some species may be physiologically incapable of increasing vocal amplitude and may therefore have to rely upon signal changes that are less effective, but by no means inconsequential.

The direction of bandwidth and frequency adjustment by individuals of each species in response to noise may be further explained by how habitat structure and perch height influence sound propagation. High frequencies attenuate faster than low frequencies, particularly in closed habitats, and low frequencies transmit farther in closed relative to open habitats (Morton 1975; Marten and Marler 1977; Phillips et al. 2020). Attenuation is also differentially affected by height: all frequencies tend to dissipate faster from heights below versus above 1 m due to sound absorption by the ground, but

frequencies between ~1-3 kHz tend to transmit farther than other frequencies below 1 m (Morton 1975; Marten and Marler 1977).

In our generally closed riparian study area in Idaho, lazuli buntings and song sparrows frequently sing from perches 3-7 m above the ground. It is therefore possible that the two species reduced maximum frequency to limit excess attenuation and improve transmission in noisy acoustic environments. In California, the largely open vegetation structure of coastal sage scrub rarely exceeds 2 m, with the majority of scrub standing at or below 1 m. White-crowned sparrows frequently sing from visible perches atop vegetation (≥ 1 m), whereas wrentits often sing hidden within the scrub (≤ 1 m). Thus, height and singing location within the sage scrub habitat may explain the increase in minimum trill frequency for white-crowned sparrows and decrease in song minimum frequency for wrentits in noisy locations. Specifically, diverting energy to higher frequencies that transmit well in open habitats could alleviate some masking for white-crowned sparrows, and reduced minimum frequencies may boost transmission in noise for wrentits singing near the ground by tapping into the ~1-3 kHz transmission window.

In addition to reduced maximum frequency and bandwidth, lazuli buntings, and to a lesser extent song sparrows, sang shorter songs as noise amplitude increased. While songs were shorter, syllable rate did not change, suggesting birds eliminated superfluous song elements in noise, keeping only those critical for recognition. Although we did not measure song rate, singing shorter, narrower bandwidth songs may trade-off with faster song rate to increase song output, potentially improving signal detection and discrimination in noise.

Our white-crowned sparrow results bolster previous research on two additional white-crowned sparrow populations in noisy urban and coastal California environments dominated by low-frequency noise (Luther et al. 2016; Davidson et al. 2017), in which individuals exhibited the same vocal adjustment strategy identified here. Because white-crowned sparrows responded to increased sound level across all treatment types, including shifted surf, our findings show the amplitude-dependent response is not unique to low-frequency noise conditions, instead occurring with frequency overlap between noise and signal.

2.4.2 Noise-dependent responses to low-frequency phantom noise

We predicted birds would sing with higher minimum frequencies in areas with low-frequency phantom and positive control noise. Song sparrows, wrentits, and yellow warblers responded to phantom noise, though only song sparrows showed support for our prediction. Of the three species, only yellow warblers had enough positive control samples for analysis, and positive control responses did not differ from controls (i.e., quieter areas). In the presence of phantom noise, song sparrows reduced bandwidth and increased minimum frequency, whereas wrentits again displayed the opposite response. Our song sparrow results corroborate previous research by Wood and Yezerinac (2006), yet conflict with those of Dowling et al. (2011). In the prior study, song sparrows in noisy urban areas of Portland, Oregon, sang with higher minimum song frequencies, whereas the latter study found no effect of low-frequency sound level on song sparrow song in metropolitan Washington, D.C. A clear explanation for the differences between these studies is not clear, but could reflect historical differences between eastern and western

soundscapes. Washington, D.C. is significantly more populous than Portland, and eastern birds may have responded to increased urbanization over time through attrition of masked minimum frequencies, resulting in song repertoires better suited for urban environments (Dowling et al. 2011; Derryberry et al. 2017). Whether song sparrows actively increase minimum frequency of all repertoire songs or whether they favor higher frequency song types in response to low-frequency noise as evidenced in great tits (*Parus major*, Halfwerk and Slabbekoorn 2009) remains unclear.

We expected yellow warblers to be less affected by low-frequency river noise because they possess the highest minimum song frequency of the species investigated. The only strong noise-dependent response exhibited by yellow warblers occurred during phantom river noise exposure, under which birds produced songs that were approximately 0.14 s longer. Because high frequencies face greater excess attenuation and reverberations than low frequencies (Phillips et al. 2020), singing songs any higher than they already are may be both ineffective and costly for yellow warbler communication. Instead, longer songs can improve signal detection and localization (Brumm et al. 2004), particularly for frequencies less masked by noise. Temporal adjustments to vocalizations in noise have been documented for several songbirds (Bermúdez-Cuamatzin et al. 2011; Francis et al. 2011a; Lenkse and La 2014; Sierro et al. 2017), yet how effective these adjustments are, and why some species increase versus decrease temporal components remains unclear.

2.4.3 Noise-dependent responses to high-frequency shifted noise

All species save for yellow warblers sang songs with different features under high-frequency shifted noise conditions. Warbling vireos produced songs with lower minimum frequencies, wrentits sang songs with higher 95% frequencies, and white-crowned sparrows sang with lower trill maximum frequencies. The species-typical minimum frequency for warbling vireos and wrentits overlap with the peak frequencies of shifted river and shifted surf noise, respectively, hovering at ~ 2.3 kHz. With lower song minimum frequencies, warbling vireos likely experience a large release from masking, as there is far less spectral energy in frequencies below the shifted river peak frequency. Wrentit song should experience a similar release from masking at lower frequencies because its maximum song frequency lies within the frequencies containing the most shifted surf spectral energy. Interestingly, wrentits did not sing at lower frequencies in shifted surf noise conditions. No explanations emerge as most likely, but it is possible that physiological limitations play a role or that wrentits may be unable to sing at sufficiently low frequencies for meaningful masking release from shifted surf noise.

White-crowned sparrows also produced shorter songs with lower trill maximum frequencies on positive control and shifted sites relative to phantom and control sites. Shorter, narrower bandwidth songs may limit reverberations and transmit more tonal songs in noise. It is interesting that white-crowned sparrows sang songs with these features on positive controls, but not phantom sites. A plausible reason is that positive control sites may contain greater high-frequency energy than on phantom surf broadcasts due to limitations of the loudspeakers. Coastal white-crowned sparrows exhibited a similar response to white noise (Gentry et al. 2017) and surf noise (Davidson et al. 2017),

suggesting these responses are plastic and the conditions triggering them diverge across soundscapes.

Both lazuli buntings and song sparrows did not respond as predicted. Lazuli buntings decreased syllable rate and song sparrows increased center frequency when exposed to shifted river noise. By decreasing syllable rate, lazuli buntings may reduce signal distortion from reverberations of previous notes, ultimately enhancing detectability (Slabbekoorn et al. 2007; Phillips et al. 2020). By increasing center frequency, song sparrows may improve signal transmission, as most acoustic energy lies within the center frequencies of their songs.

Although eleven individuals were recorded with phantom/shifted loudspeakers on and off, which could shed light on whether birds make short-term vocal adjustments to cope with different signaling conditions, we obtained too few repeated measures for robust comparisons. Nevertheless, given the design of our study, it is likely that many of the behaviors exhibited in response to noise amplitude and frequency reflect short-term behavioral flexibility in natural noise settings rather than cultural evolution of song to local soundscapes. Still, the two mechanisms may not be mutually exclusive. For example, Lazerte et al. (2016) found that urban and rural black-capped chickadees sang higher-frequency songs as local sound level increased and displayed immediate signaling flexibility in pitch when exposed to traffic noise broadcast. However, in response to traffic broadcast, birds on noisy territories shifted the frequency of their song up and those on quiet territories shifted frequency down, suggesting a combination of behavioral plasticity, learning through prior experience, and cultural evolution occur collectively to facilitate evolutionary change (Lazerte et al. 2016). Species such as wrentits, that

responded opposite our predictions, may require prior experience in noise to learn to best adjust plastic components of song and appropriately avoid masking. Likewise, we cannot discount the possibility that individuals settled across our study sites non-randomly, such that those occupying noisier territories tended to sing at higher minimum frequencies. Non-random use of breeding habitat according to vocal frequency occurs across species (Francis et al. 2011b; Francis 2015). Whether this occurs within species is an important question for future research.

2.5 Conclusion

As anthropogenic noise continues to encroach upon natural areas, the window of opportunity to investigate how species respond to the dynamics of natural acoustic conditions diminishes, along with our ability to gauge how past selection may influence ongoing responses to global change. There are strong parallels between our results and those from avian studies focused on vocal change in response to anthropogenic noise, suggesting that vocal variation in response to ambient acoustic conditions is ancient and has been co-opted for coping with human-made noise. Future research should seek to disentangle whether signal attributes in areas dominated by human-generated noise reflect the use of strategies that evolved in response to the long-standing challenges of natural variation in acoustics or *de novo* selection from the din of humanity.

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APPENDIX A

STUDY AREAS AND EXPERIMENTAL BROADCAST SET-UP



Figure S1.1 Treatment river and ocean surf (pictured) playback set-up with solar panel and raised, omnidirectional loudspeaker system (30 Hz - 20 kHz +/-kHz). Battery and control panel located in control box under solar panel.

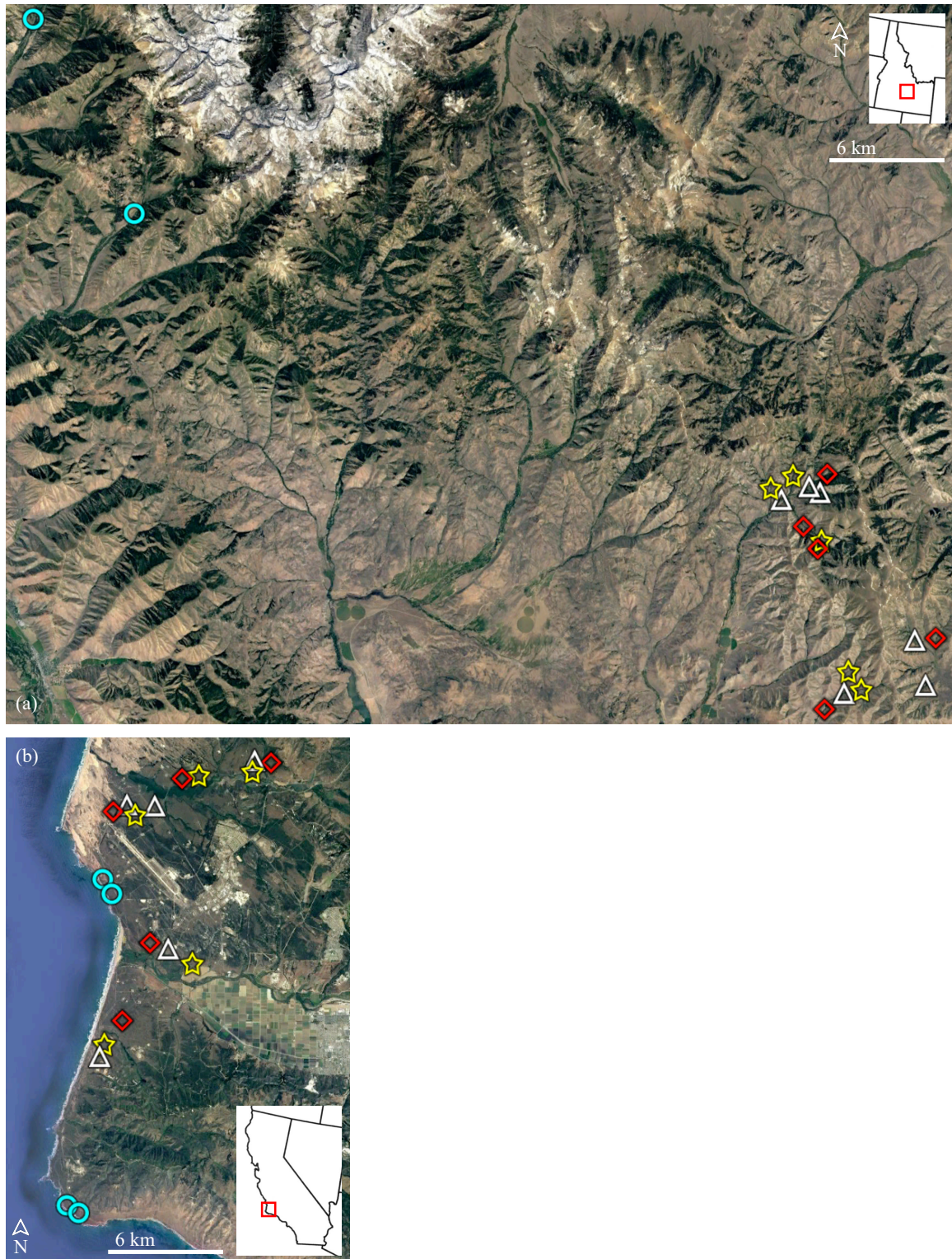


Figure S1.2 Overview of the Idaho study area (a) in the Pioneer Mountains and California study area (b) on Vandenberg Air Force Base. Map insets show the location of each study area within their respective state. White triangles = controls, turquoise circles = positive controls, red diamonds = phantom sites, and yellow stars = shifted sites.

APPENDIX B

CHAPTER 1 SUPPLEMENTARY TABLES

Table S1.1 Sound file information for Xeno-canto lazuli bunting recordings accessed and edited to create conspecific playback stimuli.

Recording	Recordist	Date	Location	CC License
XC192329	Paul Marvin	2011-06-06	Cherry Springs Natural Area, Caribou National Forest, Idaho	CC BY-NC-SA 4.0
XC375861	Jeremy Welch	2017-06-17	Bingham County, Idaho	CC BY-NC-SA 4.0
XC13883	Andrew Spencer	2007-06-23	California Park, Routt County, Colorado	CC BY-NC-ND 2.5
XC74088	Ryan P. O'Donnell	2010-07-08	City Creek Canyon, Salt Lake City, Utah	CC BY-NC-ND 2.5
XC82737	Ryan P. O'Donnell	2011-07-02	Goshen, Bingham County, Idaho	CC BY-NC-ND 2.5

Creative Commons (CC) licenses specify terms of use for each recording. CC BY-NC-SA 4.0 = Attribution-NonCommercial-ShareAlike 4.0, CC BY-NC-ND 2.5 = Attribution-NonCommercial-NoDerivs 2.5 Generic. For recording URLs, input the recording number (not including “XC”) after the last forward slash in <http://www.xeno-canto.org/>.

Table S1.2 The influence of fixed effects from the top-ranking models explaining lazuli bunting flight, song, and speaker approach behavior.

Lazuli bunting parameter (level)	Effect size \pm SE	Lower CI	Upper CI
PC1_{fly}			
<i>Intercept (No cicadas)</i>	0.83 \pm 0.04	0.74	0.91
Cicadas (Yes)	0.22 \pm 0.09	0.04	0.40
dBA	-0.14 \pm 0.05	-0.23	-0.05
Cicadas (Yes)*dBA	0.20 \pm 0.07	0.06	0.35
PC2_{song}			
<i>Intercept</i>	0.48 \pm 0.33	-0.17	1.14
Distance	-0.02 \pm 0.01	-0.04	0.004
PC3_{approach}			
<i>Intercept</i>	0.78 \pm 0.11	0.56	0.99
dBA	0.08 \pm 0.02	0.03	0.12
Distance	0.01 \pm 0.002	0.001	0.01

Flight, song, and approach components denoted PC1_{fly}, PC2_{song}, and PC3_{approach}. Parameter level of cicadas (No, Yes) indicated in parentheses. Intercept and categorical level of reference condition (parentheses) in italics. Bold denotes strong effects with 95% CIs that do not overlap zero.

Table S1.3 The influence of fixed effects from the top-ranking models explaining spotted towhee approach, flight, and song behavior.

Spotted towhee parameter (level)	Effect size \pm SE	Lower CI	Upper CI
PC1_{approach}			
<i>Intercept</i>	0.22 \pm 0.16	-0.10	0.54
dBA	0.01 \pm 0.003	0.01	0.02
Distance	0.01 \pm 0.003	0.001	0.01
PC2_{fly}			
<i>Intercept (California, Control)</i>	1.36 \pm 0.27	0.82	1.89
Location (Idaho)	-1.85 \pm 0.35	-2.53	-1.16
Trial type (Off)	-1.31 \pm 0.35	-1.99	-0.63
Trial type (On)	-1.79 \pm 0.35	-2.48	-1.11
Location (Idaho)*Trial type (Off)	1.82 \pm 0.47	0.90	2.74
Location (Idaho)*Trial type (On)	2.07 \pm 0.47	1.15	2.99
<i>Intercept (California, Treatment-off)</i>	0.05 \pm 0.22	-0.39	0.48
Location (Idaho)	-0.03 \pm 0.33	-0.67	0.62
Trial type (On)	-0.48 \pm 0.26	-0.99	0.03
Location (Idaho)*Trial type (On)	0.25 \pm 0.39	-0.51	1.00
<i>Intercept (California, Treatment-on)</i>	-0.44 \pm 0.23	-0.89	0.02
Location (Idaho)	0.22 \pm 0.33	-0.43	0.88
<i>Intercept (Idaho, Control)</i>	-0.49 \pm 0.22	-0.92	-0.06
Trial type (Off)	0.51 \pm 0.32	-0.12	1.13
Trial type (On)	0.28 \pm 0.32	-0.35	0.90
<i>Intercept (Idaho, Treatment-off)</i>	0.02 \pm 0.24	-0.46	0.50
Trial type (On)	-0.23 \pm 0.28	-0.79	0.32

Spotted towhee parameter (level)	Effect size \pm SE	Lower CI	Upper CI
PC3_{song}			
<i>Intercept (California, Control)</i>	0.56 \pm 0.55	-0.52	1.65
Distance	-0.02 \pm 0.01	-0.05	-0.003
Location (Idaho)	0.02 \pm 0.49	-0.94	0.98
Trial type (On)	0.71 \pm 0.50	-0.28	1.70
Location (Idaho)*Trial type (On)	-0.51 \pm 0.70	-1.88	0.86
<i>Intercept (California, Treatment-off)</i>	2.05 \pm 0.50	1.07	3.03
Location (Idaho)	-1.77 \pm 0.50	-2.75	-0.79
Trial type (Control)	-1.49 \pm 0.49	-2.46	-0.52
Trial type (On)	-0.78 \pm 0.29	-1.35	-0.21
Location (Idaho)*Trial type (Control)	1.79 \pm 0.69	0.43	3.15
Location (Idaho)*Trial type (On)	1.28 \pm 0.42	0.45	2.11
<i>Intercept (California, Treatment-on)</i>	1.27 \pm 0.46	0.38	2.17
Location (Idaho)	-0.49 \pm 0.50	-1.46	0.49
<i>Intercept (Idaho, Control)</i>	0.59 \pm 0.47	-0.33	1.50
Trial type (Off)	-0.30 \pm 0.49	-1.26	0.66
Trial type (On)	0.20 \pm 0.49	-0.76	1.16
<i>Intercept (Idaho, Treatment-off)</i>	0.28 \pm 0.49	-0.68	1.25
Trial type (On)	0.50 \pm 0.30	-0.09	1.09

Approach, flight, and song components denoted PC1_{approach}, PC2_{fly}, and PC3_{song}.

Parameter level of location (California, Idaho) and trial type (Control, Off = treatment-off, On = treatment-on) indicated in parentheses. See Appendix B Table S1.2 description for additional table detail.

APPENDIX C

CHAPTER 2 SUPPLEMENTARY TABLES

Table S2.1 Species-typical song feature characteristics within our study areas.

	Song subset				All analyzed songs				
	Minimum frequency	Maximum frequency	Frequency bandwidth	Center frequency	5% frequency	95% frequency	90% bandwidth	Duration	Syllable rate
Idaho	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Lazuli bunting	2.94 ± 0.24	7.75 ± 0.56	4.81 ± 0.58	4.92 ± 0.32	3.61 ± 0.27	6.61 ± 0.42	3.00 ± 0.41	2.11 ± 0.52	6.21 ± 0.80
Song sparrow	2.51 ± 0.26	8.18 ± 0.67	5.67 ± 0.70	4.32 ± 0.59	2.99 ± 0.44	6.50 ± 0.87	3.50 ± 1.00	2.58 ± 0.39	5.82 ± 1.64
Warbling vireo	2.26 ± 0.20	6.05 ± 0.43	3.78 ± 0.46	3.75 ± 0.25	2.74 ± 0.17	4.96 ± 0.40	2.22 ± 0.42	1.98 ± 0.55	5.75 ± 0.91
Yellow warbler	3.61 ± 0.36	8.36 ± 0.77	4.74 ± 0.73	5.44 ± 0.41	4.22 ± 0.33	6.98 ± 0.45	2.76 ± 0.41	1.28 ± 0.21	6.83 ± 0.97
	Trill subset				All analyzed songs				
	Minimum frequency	Maximum frequency	Frequency bandwidth	Center frequency	5% frequency	95% frequency	90% bandwidth	Duration	Trill rate
California	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
White-crowned sparrow	2.87 ± 0.17	6.69 ± 0.32	3.82 ± 0.34	4.49 ± 0.27	3.62 ± 0.27	5.50 ± 0.33	1.88 ± 0.42	1.91 ± 0.21	3.49 ± 0.28
Wrentit	2.37 ± 0.17	3.40 ± 0.16	1.03 ± 0.19	3.09 ± 0.16	2.73 ± 0.19	3.27 ± 0.15	0.54 ± 0.14	2.69 ± 0.57	11.08 ± 3.84

Mean ± SD for frequency measures are in kilohertz, duration is in seconds, and rate is in syllables or trills per second.

Table S2.2 Number of individuals per species recorded during each treatment type.

	Treatment type											
	Control		Phantom-off		Shifted-off		Positive control		Phantom		Shifted	
Idaho	SS	All	SS	All	SS	All	SS	All	SS	All	SS	All
Lazuli bunting (<i>n</i> = 232/52)		11 ₁	6 ₃ ¹	7 ₃ ²	7	9 ¹	0	1	10 ²	14 ₂ ²	10 ₃	14 ₅ ¹
Song sparrow (<i>n</i> = 130/30)		9 ₃		4 ¹		4		1	7 ₁ ¹	8 ₁ ¹		6 ₂
Warbling vireo (<i>n</i> = 164/34)		10 ₂		2 ¹		2	3 ₁	4 ₁	6 ₁	9 ₁ ¹	6 ₁	8 ₂
Yellow warbler (<i>n</i> = 160/39)	8 ₂	9 ₂		4 ₁		6	2	4 ₁	7 ₁	9 ₂		7 ₂
California	TS	All	TS	All	TS	All	TS	All	TS	All	TS	All
White-crowned sparrow (<i>n</i> = 281/62)	13	14		12 ²		5 ¹	16	17	8 ²	11 ²	4 ¹	6 ¹
Wrentit (<i>n</i> = 155/44)	9	12	11 ¹	15 ²	5 ¹	7 ¹	2	3	7 ¹	9 ¹	2	5 ¹

Phantom-off, shifted-off, and control site samples were combined into one factor level (light grey columns, differentiated for clarity). Samples of <4 individuals (dark grey cells) at positive control and shifted sites were excluded for analysis. SS (song subset) and TS (trill subset) denote the respective Idaho and California subsets with additional frequency measures collected. Centered numbers indicate no difference between the SS/TS subset and total (All) individuals. Subscripts denote number of Idaho individuals prompted to sing with conspecific playback. Superscripts indicate number of individuals recorded with treatment speakers both on and off. Number of songs per number of recorded individuals included for analysis is notated under species name.

Table S2.3 Model selection results for white-crowned sparrow song features.

White-crowned sparrow	K	$\log(\mathcal{L})$	AIC_c	Δ	w_i
Minimum frequency (Trill subset)					
dBA (+)	5	204.93	-399.57	0.00	0.45
dBA (+), Julian date (+)	6	205.74	-399.08	0.49	0.35
dBA (+), <i>Treatment</i> ($C > PC$, $C > S$)	8	207.32	-397.97	1.60	0.20
Null _{Site/ID}	4	202.48	-396.77	2.80	-
Maximum frequency (Trill subset)					
<i>Treatment</i> ($C > PC$, $C > S$, $P > PC$, $P > S$)	8	85.74	-154.79	0.00	0.48
dBA (-), <i>Treatment</i> ($C > PC$, $C > S$, $P > PC$, $P > S$)	9	86.45	-154.04	0.75	0.33
Julian date (+), <i>Treatment</i> ($C > PC$, $C > S$, $P > PC$, $P > S$)	9	85.84	-152.83	1.97	0.18
Null _{All}	5	79.22	-148.15	6.64	-
Frequency bandwidth (Trill subset)					
dBA (-)	6	47.83	-83.27	0.00	0.52
dBA (-), <i>Treatment</i> ($C < P$, $P > PC$, $P > S$)	9	50.31	-81.75	1.52	0.24
dBA (-), Year (-)	7	48.10	-81.67	1.60	0.23
Null _{All}	5	44.99	-79.70	3.57	-
Center frequency					
Null _{All}	5	89.66	-169.10	0.00	0.73
dBA (+)	6	89.70	-167.10	2.00	0.27
5% frequency					
Null _{ID+Rec}	4	67.87	-127.59	0.00	1.00
95% frequency					
Null _{All}	5	41.48	-72.73	0.00	0.28
<i>Treatment</i> ($C < S$, $P < S$, $PC < S$)	8	44.47	-72.40	0.33	0.23
dBA (+)	6	42.05	-71.78	0.95	0.17
Year (-)	6	41.58	-70.86	1.88	0.11
Julian date (-)	6	41.55	-70.79	1.94	0.10
dBA (+), <i>Treatment</i> ($C < S$, $P < S$)	9	44.70	-70.74	1.99	0.10

White-crowned sparrow	K	$\log(\mathcal{L})$	AIC_c	Δ	w_i
90% frequency bandwidth					
Null _{ID}	3	-65.45	136.98	0.00	0.31
Year (-)	4	-64.62	137.38	0.40	0.26
Julian date (-)	4	-65.15	138.44	1.46	0.15
dBA (+)	4	-65.18	138.50	1.52	0.15
Julian date (-), Year (-)	5	-64.24	138.70	1.72	0.13
Duration					
<i>Treatment</i> (C>PC, C>S, P>S), Year (+)	8	195.96	-375.39	0.00	0.36
Treatment (C>PC, C>S, P>S)	7	194.87	-375.32	0.07	0.35
Julian date (-), <i>Treatment</i> (C>PC, C>S, P>S), Year (+)	9	196.09	-373.52	1.86	0.14
Julian date (-), Treatment (C>PC, C>S, P>S)	8	195.00	-373.47	1.91	0.14
Null _{Site/ID}	4	188.42	-368.70	6.69	-
Trill rate					
Null _{Site/ID}	4	238.60	-469.05	0.00	0.23
dBA (+)	5	239.50	-468.79	0.26	0.20
Julian date (-)	5	239.34	-468.47	0.58	0.17
Year (-)	5	238.91	-467.60	1.44	0.11
dBA (+), Julian date (-)	6	239.87	-467.43	1.62	0.10
Julian date (-), Year (-)	6	239.70	-467.09	1.95	0.09
dBA (+), Year (-)	6	239.70	-467.08	1.96	0.09

Models with $\Delta AIC_c \leq 2.00$ and the null (intercept-only) are reported. K is the number of model parameters, $\log(\mathcal{L})$ is the maximized log-likelihood, AIC_c is the Akaike Information Criterion corrected for small sample size, Δ is the change in AIC_c from the top model (0.00), w_i is the Akaike weight for all strong supporting models. Parameters with 85% CIs that do not include zero are italicized and 95% CIs are in bold.

Positive/negative symbols (+/-) indicate direction of influence for variables. Greater/less than symbols (</>) indicate direction of influence between acoustic condition (labeled Treatment) levels (C = control, PC = positive control, P = phantom, S = shifted) with an effect. Treatment is in bold, italic font if different level comparisons yield different effects (85 and 95% CIs) in the same model. Null (intercept-only) subscripts indicate the random effects structure for all models of a given song feature (ID = individual bird I.D., Site = site name, Rec = recordist and recording unit type, All = all three random intercepts, “/” indicates nesting, “+” indicates random intercepts without nesting).

Table S2.4 Model selection results for wrentit song features.

Wrentit	<i>K</i>	$\log(\mathcal{L})$	AIC_c	Δ	w_i
Minimum frequency (Trill subset)					
dBA (-), Julian date (-)	6	77.74	-142.69	0.00	0.20
dBA (-), Julian date (-), Year (+)	7	78.87	-142.67	0.02	0.19
dBA (-)	5	76.47	-142.37	0.31	0.17
<i>Treatment (C>P)</i>	5	75.99	-141.40	1.28	0.10
Null _{Site/ID}	4	74.88	-141.38	1.30	0.10
Julian date (-), <i>Treatment (C>P)</i>	6	76.92	-141.03	1.65	0.09
Julian date (-)	5	75.72	-140.88	1.81	0.08
<i>dBA (-), Year (+)</i>	6	76.80	-140.80	1.88	0.08
Maximum frequency (Trill subset)					
Null _{All}	5	143.48	-276.40	0.00	0.64
Year (+)	6	144.02	-275.24	1.16	0.36
Frequency bandwidth (Trill subset)					
Julian date (+), Treatment (C<P)	6	71.37	-129.94	0.00	0.67
dBA (+), Julian date (+)	6	70.65	-128.50	1.44	0.33
Null _{Site/ID}	4	65.95	-123.53	6.41	-
Center frequency					
Null _{All}	5	190.26	-370.13	0.00	0.31
Julian date (-)	6	191.17	-369.77	0.35	0.26
<i>Julian date (-), Year (+)</i>	7	192.13	-369.50	0.63	0.23
Year (+)	6	190.88	-369.19	0.93	0.20
5% frequency					
dBA (-), Julian date (-), Year (+)	7	113.69	-212.62	0.00	1.00
Null _{Site/ID}	4	99.17	-190.08	22.54	-
95% frequency					
Treatment (C<S, P<S)	6	212.62	-412.67	0.00	0.38
Treatment (C<S, P<S), Year (+)	7	213.60	-412.43	0.24	0.33
Julian date (+), Treatment (C<S, P<S)	7	212.77	-410.79	1.89	0.15
dBA (+), Treatment (C<S, P<S)	7	212.74	-410.71	1.96	0.14
Null _{Site/ID}	4	207.30	-406.33	6.34	-

Wrentit	K	$\log(\mathcal{L})$	AIC_c	Δ	w_i
90% frequency bandwidth					
dBA (+), Julian date (+)	7	127.04	-239.32	0.00	0.60
dBA (+), Julian date (+), Year (-)	8	127.75	-238.51	0.82	0.40
Null _{All}	5	119.76	-229.12	10.20	-
Duration					
Null _{Site/ID}	4	-118.52	245.30	0.00	0.54
Year (+)	5	-118.20	246.81	1.51	0.25
Julian date (+)	5	-118.42	247.24	1.94	0.20
Trill rate					
Julian date (+)	4	-143.42	295.12	0.00	0.57
Julian date (+), Treatment ($C>P$, $P<S$)	6	-141.58	295.72	0.60	0.43
Null _{ID}	3	-148.07	302.30	7.18	-

See Appendix C Table S2.3 description for additional table details.

Table S2.5 Model selection results for lazuli bunting song features.

Lazuli bunting model	K	$\log(\mathcal{L})$	AIC_c	Δ	w_i
Minimum frequency (Song subset)					
<i>Playback</i> (-)	6	90.73	-168.96	0.00	0.26
Null _{All}	5	89.63	-168.91	0.05	0.26
dBA (+)	6	90.28	-168.07	0.90	0.17
Julian date (-), <i>Playback</i> (-)	7	91.30	-167.95	1.01	0.16
dBA (+), <i>Playback</i> (-)	7	91.27	-167.88	1.09	0.15
Maximum peak frequency contour (Song subset)					
<i>dBA</i> (-)	5	-75.79	161.92	0.00	0.35
Null _{ID+Rec}	4	-77.10	162.44	0.52	0.27
<i>dBA</i> (-), <i>Playback</i> (+)	6	-75.20	162.88	0.96	0.21
<i>Playback</i> (+)	5	-76.50	163.34	1.42	0.17
Frequency bandwidth (Song subset)					
dBA (-), <i>Playback</i> (+)	5	-85.21	180.78	0.00	0.49
dBA (-)	4	-86.67	181.57	0.79	0.33
<i>dBA</i> (-), Julian date (+), <i>Playback</i> (+)	6	-85.13	182.75	1.97	0.18
Null _{ID}	3	-89.01	184.16	3.39	-
Center frequency					
Null _{All}	5	24.52	-38.78	0.00	0.36
Julian date (-)	6	24.91	-37.44	1.33	0.18
<i>Treatment</i> ($C>P$, $P<S$)	7	25.95	-37.40	1.37	0.18
dBA (+)	6	24.62	-36.87	1.90	0.14
dBA (+), Treatment ($C>P$, $P<S$)	8	26.74	-36.84	1.94	0.14
5% frequency					
Treatment ($C>P$)	5	78.36	-146.46	0.00	0.30
Null _{ID}	3	76.26	-146.41	0.05	0.29
dBA (-)	4	76.69	-145.21	1.25	0.16
Julian date (+), Treatment ($C>P$, $P<S$)	6	78.60	-144.82	1.64	0.13
<i>Playback</i> (-), Treatment ($C>P$, $P<S$)	6	78.44	-144.51	1.94	0.11
95% frequency					
Excluded due to poor model performance	-	-	-	-	-

Lazuli bunting model	K	$\log(\mathcal{L})$	AIC_c	Δ	w_i
90% frequency bandwidth					
Null _{ID+Rec}	4	-34.42	77.01	0.00	0.47
dBA (+)	5	-33.93	78.12	1.11	0.27
<i>Treatment (C<S)</i>	6	-32.88	78.13	1.12	0.27
Duration					
dBA (-), Playback (+)	5	-95.69	201.65	0.00	0.67
dBA (-), Julian date (+), Playback (+)	6	-95.36	203.10	1.45	0.33
Null _{ID}	3	-99.41	204.93	3.28	-
Syllable rate					
Julian date (-), Treatment (C>S, P>S)	6	-46.82	106.01	0.00	0.69
dBA (+), <i>Julian date</i> (-), Treatment (C>S, P>S)	7	-46.57	107.65	1.64	0.31
Null _{ID}	3	-63.32	132.74	26.73	-

See Appendix C Table S2.3 description for additional table details.

Table S2.6 Model selection results for song sparrow song features.

Song sparrow model	K	$\log(\mathcal{L})$	AIC_c	Δ	w_i
Minimum frequency (Song subset)					
<i>Treatment</i> (C<P, P>S)	6	-5.17	23.13	0.00	0.27
<i>Julian date</i> (+), <i>Treatment</i> (C<P, P>S)	7	-4.20	23.45	0.32	0.23
Null _{Site/ID}	4	-7.58	23.52	0.39	0.22
Julian date (+)	5	-6.89	24.34	1.21	0.15
dBA (-), <i>Treatment</i> (C<P, P>S)	7	-4.81	24.67	1.54	0.13
Maximum peak frequency contour (Song subset)					
dBA (-)	4	-96.93	202.23	0.00	0.47
dBA (-), Playback (+)	5	-96.14	202.84	0.61	0.35
dBA (-), Julian date (-)	5	-96.81	204.18	1.95	0.18
Null _{ID}	3	-100.00	206.21	3.99	-
Frequency bandwidth (Song subset)					
<i>Treatment</i> (C>P, P<S)	5	-103.34	217.23	0.00	0.34
dBA (-), Playback (+)	5	-103.52	217.60	0.36	0.29
dBA (-)	4	-104.91	218.18	0.94	0.21
dBA (-), <i>Treatment</i> (C>P)	6	-102.96	218.70	1.47	0.16
Null _{ID}	3	-107.98	222.18	4.95	-
Center frequency					
<i>Treatment</i> (C<S, P<S)	5	-102.32	215.12	0.00	0.45
dBA (+), <i>Treatment</i> (C<S, P<S)	6	-101.56	215.80	0.68	0.32
Julian date (-), <i>Treatment</i> (C<S, P<S)	6	-101.88	216.44	1.32	0.23
Null _{ID}	3	-105.63	217.44	2.32	-
5% frequency					
Null _{All}	5	-46.18	102.84	0.00	0.27
Playback (-)	6	-45.54	103.76	0.92	0.17
<i>Treatment</i> (C<P)	7	-44.50	103.93	1.09	0.16
dBA (+), Playback (-)	7	-44.55	104.02	1.18	0.15
dBA (+)	6	-45.80	104.27	1.43	0.13
Playback (-), <i>Treatment</i> (C<P)	8	-43.72	104.63	1.79	0.11

Song sparrow model	K	$\log(\mathcal{L})$	AIC_c	Δ	w_i
95% frequency					
Null _{ID+Rec}	4	-116.06	240.45	0.00	0.42
<i>Treatment (C>P)</i>	6	-114.52	241.73	1.28	0.22
Playback (+)	5	-115.75	241.99	1.54	0.19
dBA (-)	5	-115.87	242.21	1.77	0.17
90% frequency bandwidth					
<i>Treatment (C>P, P<S)</i>	6	-134.97	282.63	0.00	0.47
Playback (+), Treatment (C>P)	7	-134.41	283.74	1.12	0.27
dBA (+), Treatment (C>P, P<S)	7	-134.46	283.84	1.21	0.26
Null _{ID+Rec}	4	-138.28	284.88	2.26	-
Duration					
dBA (-)	4	-28.11	64.54	0.00	0.27
Playback (-)	4	-28.25	64.83	0.29	0.23
Null _{ID}	3	-29.45	65.09	0.55	0.21
dBA (-), <i>Treatment (C<P)</i>	6	-26.54	65.76	1.22	0.15
dBA (-), Playback (-)	5	-27.65	65.79	1.25	0.14
Syllable rate					
Null _{ID}	3	-235.27	476.74	0.00	0.29
Playback (+)	4	-234.29	476.90	0.16	0.27
Julian date (+), <i>Playback (+)</i>	5	-233.53	477.55	0.81	0.20
Julian date (+)	4	-235.07	478.47	1.73	0.12
dBA (+)	4	-235.17	478.65	1.92	0.11

See Appendix C Table S2.3 description for additional table details.

Table S2.7 Model selection results for warbling vireo song features.

Warbling vireo	K	$\log(\mathcal{L})$	AIC_c	Δ	w_i
Minimum frequency (Song subset)					
Julian date (-), Treatment (C>S, P>S)	7	50.28	-85.47	0.00	0.32
dBA (+), <i>Julian date</i> (-), Treatment (C>S, P>S)	8	51.14	-84.88	0.60	0.23
dBA (+), Treatment (C>S, P>S)	7	49.89	-84.69	0.78	0.21
<i>Julian date</i> (-), Playback (+), Treatment (C>S, P>S)	8	50.47	-83.52	1.95	0.12
Treatment (C>S, P>S)	6	48.15	-83.49	1.98	0.12
Null _{Site/ID}	4	41.56	-74.75	10.72	-
Maximum peak frequency contour (Song subset)					
<i>Julian date</i> (-)	5	-50.10	110.77	0.00	0.21
Null _{ID+Rec}	4	-51.39	111.15	0.38	0.18
<i>Playback</i> (+)	5	-50.34	111.24	0.47	0.17
dBA (+)	5	-50.39	111.35	0.58	0.16
dBA (+), <i>Julian date</i> (-)	6	-49.75	112.30	1.53	0.10
<i>Julian date</i> (-), Playback (+)	6	-49.77	112.36	1.59	0.10
dBA (+), Playback (+)	6	-49.93	112.67	1.90	0.08
Frequency bandwidth (Song subset)					
Null _{ID+Rec}	4	-60.18	128.74	0.00	0.44
dBA (+)	5	-59.90	130.38	1.64	0.19
<i>Julian date</i> (-)	5	-59.92	130.42	1.68	0.19
Playback (+)	5	-59.95	130.46	1.73	0.18
Center frequency					
Julian date (-)	6	6.17	0.20	0.00	0.39
Julian date (-), Treatment (C<PC, P<PC, PC>S)	9	9.19	0.80	0.60	0.29
dBA (-), Julian date (-)	7	6.44	1.84	1.64	0.17
Julian date (-), Playback (-)	7	6.30	2.12	1.92	0.15
Null _{All}	5	2.83	4.73	4.53	-
5% frequency					
<i>Playback</i> (+), Treatment (C>P, C>S, PC>S)	8	85.56	-154.19	0.00	0.28
Treatment (C>P, C>S, P<PC, PC>S)	7	84.40	-154.08	0.11	0.27
<i>Playback</i> (+)	5	81.92	-153.46	0.73	0.20
Null _{Site/ID}	4	80.52	-152.79	1.40	0.14
<i>Julian date</i> (-), Treatment (C>P, C>S, P<PC, PC>S)	8	84.66	-152.38	1.81	0.11

Warbling vireo	<i>K</i>	$\log(\mathcal{L})$	AIC_c	Δ	w_i
95% frequency					
Julian date (-)	5	-55.33	121.03	0.00	0.71
dBA (+), Julian date (-)	6	-55.12	122.78	1.75	0.29
Null _{ID+Rec}	4	-58.11	124.48	3.45	-
90% frequency bandwidth					
<i>Julian date (-)</i>	5	-56.31	123.01	0.00	0.43
Null _{ID+Rec}	4	-57.97	124.20	1.19	0.24
dBA (+), <i>Julian date (-)</i>	6	-56.11	124.75	1.74	0.18
<i>Julian date (-)</i> , Playback (-)	6	-56.21	124.96	1.95	0.16
Duration					
Null _{ID}	3	-85.38	176.91	0.00	0.17
<i>Julian date (+)</i> , <i>Treatment</i> (C>P, P<PC, P<S)	7	-81.19	177.09	0.18	0.16
<i>Julian date (+)</i>	4	-84.50	177.25	0.35	0.15
<i>Julian date (+)</i> , Playback (+)	5	-83.57	177.52	0.62	0.13
<i>Treatment</i> (C>P, P<PC, P<S)	6	-82.53	177.59	0.68	0.12
<i>Julian date (+)</i>, Playback (+), <i>Treatment</i> (C>P, P<PC, P<S)	8	-80.37	177.67	0.76	0.12
Playback (+)	4	-85.19	178.64	1.73	0.07
<i>Julian date (+)</i> , dBA (+), <i>Treatment</i> (C>P, P<PC, P<S)	8	-80.87	178.67	1.77	0.07
Syllable rate					
<i>Julian date (-)</i>	4	-128.07	264.39	0.00	0.29
Null _{ID}	3	-129.18	264.50	0.11	0.28
<i>Treatment</i> (C>S, P>S)	6	-126.58	265.69	1.30	0.15
<i>Julian date (-)</i> , <i>Treatment</i> (C>S, P>S)	7	-125.54	265.80	1.41	0.15
<i>Julian date (-)</i>, Playback (-)	5	-127.84	266.07	1.68	0.13

See Appendix C Table S2.3 description for additional table details.

Table S2.8 Model selection results for yellow warbler song features.

Yellow warbler	K	$\log(\mathcal{L})$	AIC_c	Δ	w_i
Minimum frequency (Song subset)					
<i>Julian date</i> (-)	6	-16.20	45.14	0.00	0.40
Null _{All}	5	-17.87	46.27	1.13	0.23
Julian date (-), <i>Treatment</i> ($P < S$)	8	-14.57	46.45	1.31	0.21
Julian date (-), Playback (-)	7	-15.96	46.94	1.80	0.16
Maximum peak frequency contour (Song subset)					
Null _{Site/ID}	4	-97.36	203.08	0.00	0.53
<i>Julian date</i> (-)	5	-97.00	204.53	1.46	0.26
Playback (+)	5	-97.16	204.86	1.78	0.22
Frequency bandwidth (Song subset)					
Null _{ID+Rec}	4	-95.65	199.66	0.00	0.45
Playback (+)	5	-95.38	201.29	1.63	0.20
<i>Treatment</i> (-) ^a	6	-94.36	201.46	1.81	0.18
<i>Julian date</i> (-)	5	-95.51	201.55	1.89	0.17
Center frequency					
Julian date (-), Playback (-)	5	-35.15	80.69	0.00	0.71
Julian date (-)	4	-37.12	82.50	1.80	0.29
Null _{ID}	3	-45.17	96.49	15.79	-
5% frequency					
<i>dba</i> (-), Julian date (-)	5	-12.10	34.60	0.00	0.33
Julian date (-)	4	-13.30	34.86	0.26	0.29
Julian date (-), Playback (-)	5	-12.68	35.76	1.16	0.19
Julian date (-), <i>dba</i> (-), Playback (-)	6	-11.61	35.77	1.18	0.19
Null _{ID}	3	-18.75	43.65	9.05	-
95% frequency					
Julian date (-), <i>Playback</i> (-)	5	-51.17	112.72	0.00	0.48
Julian date (-)	4	-52.56	113.38	0.66	0.34
<i>dba</i> (+), Julian date (-), Playback (-), <i>Treatment</i> ($C > P$, $C > PC$, $P < S$, $PC < S$)	9	-47.71	114.62	1.90	0.18
Null _{ID}	3	-56.57	119.30	6.58	-

Yellow warbler	<i>K</i>	$\log(\mathcal{L})$	AIC_c	Δ	w_i
90% frequency bandwidth					
Null _{ID}	3	-64.64	135.44	0.00	0.30
dBA (+)	4	-63.90	136.06	0.61	0.22
Julian date (-)	4	-64.43	137.12	1.68	0.13
Playback (-)	4	-64.49	137.24	1.80	0.12
dBA (+), Treatment (C>P)	7	-61.27	137.29	1.84	0.12
dBA (+), Playback (-)	5	-63.52	137.44	2.00	0.11
Duration					
Julian date (+), Playback (+), Treatment (C<P, P>PC, P>S)	10	93.02	-164.57	0.00	0.44
Julian date (+), Playback (+)	7	89.48	-164.23	0.34	0.37
Playback (+)	6	87.74	-162.93	1.65	0.19
Null _{All}	5	84.51	-158.62	5.95	-
Syllable rate					
Julian date (-)	5	-139.52	289.44	0.00	0.55
Julian date (-), Playback (-)	6	-139.25	291.06	1.62	0.24
dBA (+), Julian date (-)	6	-139.43	291.40	1.96	0.21
Null _{Site/ID}	4	-143.60	295.46	6.02	-

See Appendix C Table S2.3 description for additional table details.

^aTreatment (acoustic condition) had a negative influence relative to control reference condition; no level comparisons yielded an effect.

Table S2.9 Pairwise differences in ambient and experimental sound level from bird singing locations across treatment types, differentiated by study area.

Acoustic condition		Control	Positive control	Phantom	Shifted
Control	$\beta \pm \text{SE}$		11.14 ± 2.72	9.33 ± 1.28	3.52 ± 1.49
	95% CI		5.80 – 16.48	6.82 – 11.84	0.60 – 6.45
Positive control	$\beta \pm \text{SE}$	3.96 ± 1.41		-1.81 ± 2.84	-7.62 ± 2.90
	95% CI	1.21 – 6.72		-7.34 – 3.75	-13.31 – -1.93
Phantom	$\beta \pm \text{SE}$	11.11 ± 1.31	7.14 ± 1.70		-5.81 ± 1.73
	95% CI	8.54 – 13.67	3.81 – 10.48		-9.20 – -2.42
Shifted	$\beta \pm \text{SE}$	12.41 ± 1.67	8.45 ± 1.99	1.31 ± 1.93	
	95% CI	9.14 – 15.69	4.54 – 12.36	-2.48 – 5.09	

Effect sizes (β) \pm SE and 95% CIs are shaded red for California comparisons and blue for Idaho comparisons. Reference conditions are listed in the top row of corresponding columns for California and the left column of corresponding rows for Idaho. Sound level (dBA) differed strongly between all treatment types at each location except positive control and phantom samples in Idaho, and phantom and shifted samples in California (black bordered cells).