

NATURAL NOISE CAN INFLUENCE BIRD FORAGING AND VIGILANCE
BEHAVIOR

by

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ABSTRACT

Natural sounds are an often overlooked, yet important component of an animal's habitat. The acoustic environment may be especially significant during foraging, because a noisy world can limit auditory surveillance. Here, we investigated how natural noise structures the foraging vigilance trade-off to understand how intense acoustic environments may have shaped antipredator behavior across the evolutionary past, and better inform conservation efforts in the present.

First, in Chapter 1, I directly compared the foraging and vigilance behaviors of captive song sparrows (*Melospiza melodia*) in anthropogenic and natural noise. We recorded foraging trials in 4 playback conditions (roadway traffic, whitewater rivers, whitewater rivers shifted upwards in spectrum, and amplitude-modulated rivers), along with an ambient control to assess which acoustic characteristics make a foraging habitat risky. We found that sparrows increased vigilance or decreased foraging in 4 of 6 behaviors when foraging in higher sound levels, regardless of playback type, indicating a broad role for noise in antipredator behavior.

Next, in Chapter 2, I sought to understand the ecological relevance of these findings by examining wild bird behavior. To do so, we broadcast the same whitewater river noise as used in our lab experiment across a riparian landscape. To understand if the spectra of the acoustic environment affected bird behavior, we also presented spectrally-shifted whitewater noise to produce a gradient of frequencies. Using 18 bird feeders placed across this landscape, we recorded and analyzed behavior of the three most

common bird species. Black-headed grosbeaks (*Pheucticus melanocephalus*) and lazuli buntings (*Passerina amoena*) demonstrated an increase in at least one vigilance behavior in high sound levels, while American goldfinches (*Spinus tristis*) and grosbeaks altered some behaviors according to background frequency. Clearly, adjusting antipredator behavior in noise is conserved across diverse bird species.

Taken together, our findings imply that natural soundscapes have likely shaped behavior long before anthropogenic noise, and that high sound levels negatively affect the foraging vigilance trade-off in both anthropogenic and naturally intense acoustic environments. These results are concerning in light of ever-increasing anthropogenic noise pollution.

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LIST OF ABBREVIATIONS

SPL	Sound pressure level
L50	Sound pressure level that is exceeded 50 percent of the hour
LEQ	Equivalent continuous sound pressure level
dBA	A-weighted decibels
US EPA	United States Environmental Protection Agency
CI	Credible interval
PD	Probability of direction
kHz	Kilohertz
VIF	Variance inflation factor
RMSE	Root mean square error
SD	Standard deviation
SE	Standard error

INTRODUCTION

Understanding how animals perceive the world can better inform their conservation and management (Dominoni et al. 2020; Greggor et al. 2020), especially as sensory pollution becomes increasingly rampant. Light and noise pollution levels have increased in unprecedented ways in the last century (Gaston et al. 2013; Buxton et al. 2017), leaving animals to cope with a sensory world in which they did not evolve.

Specifically, noise pollution can adversely affect fitness (Halfwerk et al. 2011; Ware et al. 2015) or survival (Simpson et al. 2016), and can shape distributions (McClure et al. 2013). Although it is important to understand how animals survive within a rapidly changing acoustic environment (see Shannon et al. 2016 for review), research has largely neglected how listening animals have evolved to cope with natural noises such as wind, rushing water, and biotic choruses (see Gomes et al. 2021 for review). Understanding how animals respond to natural noise may allow us to better predict anthropogenic noise impacts, and provide insight regarding how noise has likely shaped antipredator behavior for millennia.

One way in which noise influences behavior is through the foraging vigilance trade-off. Foraging can be a risky endeavor, and even more so in noisy environments. Noise may obscure auditory informative cues for survival, like alarm calls or the sounds of predator locomotion (Barber et al. 2010). In an attempt to cope with this reduced auditory awareness, animals will often increase visual surveillance, which may reduce foraging opportunities (Lima and Dill 1990). Noise in particular has been shown to

increase vigilance or decrease foraging in many taxa including invertebrates, mammals, and birds (Krebs et al. 1997; Quinn et al. 2006; Wale et al. 2013). This trade-off is important to understand, since it could result in downstream fitness consequences or may render even a naturally-noisy area as unsuitable habitat.

Here, I address knowledge gaps regarding the possible impact of natural noise on the foraging-vigilance trade off. To do so, I collected behavioral data in both a field and lab setting under experimental acoustic environments to achieve a more complete understanding of natural noise and animal risk perception as it exists in isolation and *in situ*.

First, I conducted behavioral lab experiments with 27 individuals of a common bird species, the song sparrow (*Melospiza melodia*). This study expanded on previous research, where white-crowned sparrows (*Zonotrichia leucophrys*) were shown to increase vigilance and decrease foraging in traffic noise playbacks (Ware et al. 2015). In my captive bird experiments I directly compared the effects of natural and anthropogenic noise and deciphered what acoustic characteristics of these noises (frequency, modulation, and amplitude) might shape perceived risk. My lab study offered an opportunity to look more closely at what makes a sound stimulus riskier, while controlling for several external variables like cover or predator presence, that might impact behavior in a wild setting.

Then, I assessed whether the same behavioral trade-off can be seen in wild birds by using long-term and large-scale river noise playbacks in multiple drainages of the Pioneer mountains of Idaho. I began this study by opportunistically filming birds foraging in the wild under these experimental soundscapes. This data collection effort

yielded low sample sizes and challenges in quantification, so in addition, we deployed 18 bird feeders across the landscape. We paired bird feeders with game cameras and continuous sound recording equipment. Game cameras were able to capture standardized observations of foraging and vigilance behavior without observer confounds (Buxton et al. 2018), and sound recording devices provided detailed data on frequency and sound pressure levels. Additionally, our behavioral field research was situated within a larger study, which allowed us to interpret our behavioral results within the context of bird abundance data from the same system.

My study design thus allowed me to explore how different characteristics of noise influence foraging and vigilance behavior, and how this trade off plays out in a truly wild setting across multiple species of birds. Examining behavior across a variety of contexts and scales provided me an opportunity to test the biological relevance of antipredator behavior in natural noise.

CHAPTER ONE: NATURAL AND ANTHROPOGENIC NOISE INCREASE
VIGILANCE AND DECREASE FORAGING IN SONG SPARROWS (*Melospiza
melodia*)

To be submitted to Behavioral Ecology

Introduction

Animals alter their behavior in response to predation risk (Lima and Dill 1990, for review also see Caro 2005). Perceived risk alone, without an actual increase of danger, can alter behavior so strongly that it may even lead to reproductive costs (Zanette et al. 2011). Animals glean information about risk from their surrounding habitat, such as vegetation structure or lunar phase (Laundré and Hernández 2003; Orrock 2004). An underappreciated ecological axis that likely informs perceived habitat quality and risk is the acoustic environment (Gomes et al. 2021). Natural noise, from rushing water and biotic choruses for example, can provide animals with valuable information (Simpson et al. 2004; Zhao et al. 2017). In addition to natural noise, many organisms now vie with the much larger acoustic footprint of anthropogenic noise. Anthropogenic noise has become so pervasive that it has doubled the natural sound levels in almost two thirds of protected natural areas in the U.S. (Buxton et al. 2017). Noise deserves our attention because it shapes the communication, reproduction, and distributions of diverse animal taxa (Barber et al. 2010; Halfwerk et al. 2011; Shannon et al. 2016; Gomes et al. 2020, Gomes et al. *in press*).

Noise may also limit foraging opportunities. Vital environmental sounds may be masked by noise, such as the movement sounds of prey and predators, contact calls, and alarm calls (Goerlitz et al. 2008; Haff and Magrath 2010; Magrath et al. 2015; Templeton et al. 2016; Lilly et al. 2019). Reduced auditory awareness for acoustic cues important to survival can lead to increased reliance and time spent on visual vigilance, and thus less time foraging (Quinn et al. 2006). Environmental noise may also serve as a cognitive distraction (Chan et al. 2010; Purser and Radford 2011; Voellmy et al. 2014) or informational masker (Bee 2015), and in turn decrease foraging efficiency. Experiments with anthropogenic noise and white noise (noise with equal energy across the spectrum) suggest that foraging and vigilance behaviors in noise match those seen in areas with increased predator presence or riskier aspects of cover (Lima 1987; Skinner and Hunter 1998; Caro 2005). Crabs are more likely to stop feeding when exposed to ship noise (Wale et al. 2013), while prairie dogs (*Cynomys ludovicianus*) increase vigilance and decrease foraging in traffic noise (Shannon et al. 2014). The same trade-off can be seen in chaffinches (*Fringilla coelebs*) and zebra finches (*Taeniopygia guttata*) when foraging in white noise (Quinn et al. 2006; Evans et al. 2018). These documented increases in vigilance behaviors suggest that animals perceive foraging in high sound levels as risky.

The foraging-vigilance trade-off is a common response to noise exposure. However, compared to anthropogenic and white noise, little is known about how animals react to noise common in natural environments. In the literature that exists, both noise sources have been shown to have similar effects. For example, bird abundances decrease in both gas compressor, and white water noise (Cinto Mejia et al. 2019, Gomes et al. *in press*). White-crowned sparrows (*Zonotrichia leucophrys*) in surf noise and chipping

sparrows (*Spizella passerina*) in anthropogenic noise suffer similar reduced song performances (Davidson et al. 2017). Cicada noise and river noise shape ground squirrel foraging and vigilance in similar ways to wind turbine noise (Rabin et al. 2006; Le et al. 2019). These studies, however, are not direct comparisons across the same species, or even in the same system. In a previous study on wild animals (KA Sweet and colleagues, unpublished data), birds increased vigilance in response to whitewater noise playbacks, but with relatively high variability. It is not clear how these behavioral changes compare to those that might be observed in anthropogenic noise, or if the effect sizes described in the that field study are conservative due to the confounds of other sources of risk in a wild habitat.

Understanding how animals respond to specific and quantifiable characteristics of noise (amplitude, frequency, and temporal structure) might help us better predict their response to novel anthropogenic noise. To assess potential differences across foraging and vigilance behaviors in anthropogenic and natural noise, we conducted foraging trials in a lab setting with a widespread passerine, the song sparrow (*Melospiza melodia*). We compared behavior under two common environmental noise sources, automobile traffic and whitewater river noise, which have similar spectral properties (Gomes et al. 2021). Additionally, we broadcast river noise that was shifted upwards in frequency to determine if lower frequencies are more important for maintaining auditory awareness, since these low frequencies may contain important information (e.g., predators approaching from a distance) and allow a greater area of auditory surveillance (Barber et al. 2010; Haff and Magrath 2010). Lastly, we altered river noise to have the same temporal profile as traffic noise in order to separate how amplitude modulation of noise

affects vigilance behavior. Using this suite of treatments, plus a quiet control, we explore what makes an acoustic environment a riskier foraging habitat.

Methods

Song Sparrows

During October and November of 2018 and 2019, we captured cohorts of 4 to 6 song sparrows (for a total sample size of 27 sparrows used in trials) at CJ Strike Wildlife Management Area, Idaho (42°54'05.8"N 115°51'52.3"W and 43°00'22.2"N 116°06'07.3"W). Song sparrows have hearing ranges typical of an average songbird, with the sensitive hearing from approximately 1-8 kHz, and the highest sensitivity at 2 kHz (Okanoya and Dooling 1988). We kept sparrows in separate, adjacent cages at Boise State University under a light cycle mimicking fall conditions (13:11 light: dark cycle with half hour twilight periods). When birds were not foraging in trials, we provided them with water and a ground forager's seed mix (Country Blends Dove and Quail) *ad libitum*, along with supplemental sunflower seeds to help them maintain healthy weights. We held birds in the lab for 6 to 8 days and released them at their capture site when trials were completed. All work was conducted under Idaho State Permit 120422, USFWS Permit MB72226C, and a special use permit for CJ Strike Wildlife Management Area. Experiments were approved by Boise State's Institutional Animal Care and Use Committee under protocol 140625.

Noise treatments

We conducted experiments in a 38 m² room lined with anechoic foam. We used an Octasound speaker (35 Hz to 20 kHz ± 10 dB; KDM Electronics Incorporated), an

amplifier (AD1200.1, PRV audio), and a Roland RO5 audio player to broadcast all noise treatments.

In order to understand the effects of sound level, frequency and temporal structure, we broadcast river, shifted river, roadway traffic, and amplitude-modulated river (Figure 1.1), alongside a control where no track was played (ambient acoustic conditions; ~32 dBA). River noise was used to determine how birds forage in naturally intense acoustic environments. River sounds occupy a wide bandwidth of frequencies, with the most energy at low frequencies (river treatment median frequency of 1.6 kHz). We used shifted river noise (median frequency 4.9 kHz) to determine if birds were less vigilant when lower frequencies were unmasked (see Figure 1.1 for spectrograms). Both shifted river and river treatments were previously used in landscape level manipulation experiments, and were designed so that the broadcast energy across the two treatments weighted by the average birds' hearing threshold was equal (see Gomes et al. *in press*). Full meta data for river and shifted river sound treatments can be found in Gomes and colleagues in press.

To broadcast roadway traffic, we used traffic recordings from Ware and colleagues (2015). Many anthropogenic noises, including roadway traffic are characterized by amplitude modulation (temporal variation in the intensity of acoustic energy in noise). Compared to river noise, roadway traffic has less energy in high frequencies (Gomes et al. 2021). In order to parse out if any differences observed between river and traffic noise were due to temporal pattern, or because of spectral differences between the two, we created an amplitude-modulated river playback file. To make this treatment, we imposed the amplitude envelope of our traffic noise on the

whitewater river file using the Adobe Audition 3 envelope follower tool. All files were 16-bit WAV, with a 5 second fade in and out period to prevent broadband onset and offset clicks. Our traffic file was produced at a 44.1kHz sampling rate, while our river files were sampled at a 48kHz sampling rate to capture the slightly higher bandwidth. A low pass filter was applied to the traffic file at 16 kHz (well above the hearing range of passerines) to remove extraneous noise.

For foraging trials, we created a 2m X 2m arena of sand in the anechoic foamed room. We originally set sound pressure levels at 55, 61, and 68 dBA at the center of the foraging arena. While measuring sound levels, we observed that they varied consistently across the foraging area ($\pm \sim 5$ dBA). In order to obtain a more detailed understanding of the acoustic environments experienced by sparrows, we measured sound levels across the foraging arena. To do this, we divided the foraging arena into a 3 by 3 grid. At the center of each grid square, for each treatment and sound level combination, we took a 3-minute LEQ (the sound pressure level containing equal energy of all fluctuating sound levels across a given period of time). We used an A-weighting for sound level measurements because it is most appropriate for the hearing range of birds (Dooling and Popper 2007) and a Larson Davis decibel meter (model 824; Depew, NY, USA), set to dBA fast, to take all sound pressure measurements.

Behavior trials

We used a similar experimental paradigm to Ware and colleagues (2015) for behavioral trials. Foraging trials consisted of individual birds foraging in the arena of sand, saturated with white proso millet (such that search time for seed was not a confound), for 8-minute sound treatment playbacks.

Before beginning trials, we acclimated birds to our experimental room as a group. To do so, we released the cohort of sparrows together into the flight room, and allowed them to begin foraging and using provided water dishes. Once multiple birds had been observed foraging, we began allowing them access to the foraging arena for only 8-minute periods (the length of our trial treatments), before covering the foraging arena with a tarp between each ‘practice’ trial. This acclimated birds to both an observer entering the flight room, and to using the foraging arena within only this 8-minute time period.

After an initial day of training, we randomized the order of individual birds to complete trials alone in the foraging arena. Each bird typically performed 2-4 trials sequentially to minimize handling stress. We released each bird into the anechoically-foamed flight room and allowed 60 minutes of acclimation time before the first foraging trial. During each trial we played a randomized sound treatment while we recorded video (using a Canon XA10 placed on a tripod approximately 1m high) remotely from an adjacent room. If a bird did not forage during the first play of the soundtrack, we would play the track one additional time, such that the sound was continuous. We then allowed birds a 40-minute period before the next trial to accumulate similar levels of hunger, during which we covered the arena with a tarp to prevent access to seeds.

Behavioral coding

We used Adobe Premiere CC 2018 to quantify behaviors. To reduce bias, we muted videos before scoring so that observers were blind to the noise treatment. We scored 6 behaviors: pecks to the ground, average time of head down, visual head scans, proportion of time spent with head up (vigilance), time of entering the foraging arena,

and sum of foraging durations. We recorded enter time (the first time a bird entered the arena with both feet) and the total summed foraging bout length from the duration of the full 8-minute trial.

To obtain all other behaviors, we used frame-by-frame analysis of the first continual 30 seconds of a foraging bout, with a bout defined as at least 5 consecutive pecks not separated by more than 10 seconds (Quinn et al. 2006; Ware et al. 2015). We assessed the proportion of time vigilant by recording the time the bird's head was above the line of the back (with the inverse being time foraging, where the head is below the line of the back; Ware et al. 2015). To calculate the average duration of head down, we took the total time of head down during the foraging bout, and divided it by the number of head down occurrences. We also counted the number of visual head scan movements, which we considered any head movement while the bird's head was above the line of its back (with each scan being from when the bird's head started moving to when it was stationary again; Fernández-Juricic et al. 2011). Lastly, we counted the number of pecks within this 30 second bout. We then matched the position of the bird within the arena during the foraging bout with the measured LEQ. If the bird spent time in multiple grids during the foraging bout, we log averaged those values (this occurred in only 4 trials).

Statistical analysis

We built Bayesian generalized linear mixed models with the package 'rstanarm' (Goodrich et al. 2020) in R (R version 4.0.2, R Core Team 2020) for each behavior. Initially, we fit models including both parameters of interest, treatment and sound pressure level. However, we found that these terms exhibited multicollinearity with one another for every behavior model (VIF: 5.46 – 8.65). A VIF of 3 can be

potentially concerning (Zuur et al. 2010), so we decided to analyze these parameters separately in an iterative fashion. This collinearity is likely a reflection of our study design, where our ambient control treatment had uniquely low sound pressure levels in comparison to the 4 noise treatments. Therefore, we first modeled whether sound pressure level impacted each behavior by excluding treatment type as a parameter. Then we built a second group of models comparing all noise treatments (all trials excluding ambient conditions), where we set the river treatment as the reference level. We also included sound level as a parameter in our treatment models, since we varied sound pressure level.

In both treatment and sound pressure level models we included hour of the day the trial took place, and sound pressure level as fixed effects. As noted earlier, if a bird did not forage during the first trial attempt, we reattempted the trial after the 40-minute between trial interval. Due to this, we included the number of trial attempts as a fixed effect, because hunger levels may have increased during longer gaps between foraging.

For both model types we created a varying (random) slope for trial number experienced, and a varying intercept for bird identity to account for baseline variation in behavior, possible habituation across time, and learning differences observed across individuals. We centered all parameters by their mean and divided by 2 standard deviations to allow comparisons between continuous and categorical predictors and to improve model convergence (Gelman 2008).

We modeled count behaviors (pecks and head scans) using negative binomial and Poisson distributions. We then ranked models using leave one out cross validation information criterion (LOOIC) and posterior predictive checks to assess the fit of the

models. A Poisson distribution fit both pecks and head scans the best. Time variables (enter time, average head down time, and sum foraging duration) were modeled with gamma distributions. Lastly, we modeled the proportion of a 30-second foraging bout that a bird had its head up (i.e., being vigilant) with a beta distribution. For all models, we used weakly informative priors standard in the ‘rstanarm’ package (Goodrich et al. 2020), and ran four chains for 2,000 iterations (1,000 of these iterations were a warm up). We checked that models had large effective sample sizes (N_{eff} or ESS), that Gelman-Rubin convergence diagnostics (Rhat) were below 1.1, and visually checked trace plots for evidence that sampling chains were well mixed (suggesting model convergence) (McElreath 2009).

To determine if inclusion of bird identity and experience improved model fit, we created each of the same models without the varying slope for trial experience and varying intercept for bird identity. We then ranked them against our full models which included varying slopes and intercepts using LOOIC.

When assessing results, we interpreted a parameter to be influential on behavior if its probability of direction 95% or greater (rounded to nearest whole percent). Probability of direction (PD) refers to the probability of an effect being either entirely positive or negative. We note if a parameter was trending towards an effect if it had a probability of direction 90% or greater. Additionally, we interpreted parameters as influential if their credible interval at 90% excluded 0, and note trending parameters if their credible intervals excluded 0 at 80% (rounded to 2 decimal places). Credible intervals are reported at 90% unless otherwise stated.

Results

We recorded 148 foraging trials across 27 individual song sparrows (average trial per bird = 5.5, SD = 0.98). The logarithmic mean dBA for each treatment calculated in the R package 'seewave' (Sueur et al. 2008) were as follows; control: 32.3 dBA, whitewater river: 63.9 dBA, shifted river: 61.7 dBA, roadway traffic: 64.3 dBA, and amplitude-modulated river: 62.8 dBA.

Sound pressure level models

We found evidence that song sparrows increased vigilance with higher sound pressure levels in 4 of the 6 behaviors we modeled (Table 1.1 and Figure 1.2). Visual scanning behavior and proportion of time spent with head up in the vigilant posture approached 100% probability of increasing in higher sound pressure levels [CI: 0.07 - 0.15, (n = 148), and CI: 0.14 - 0.44 (n = 148) respectively]. Foraging duration had a 99.8% probability of decreasing [CI: $\bar{0}$.38 - $\bar{0}$.10 (n = 146)]. Birds spent shorter time periods with their head down in high sound levels [PD: 99.9%, CI: $\bar{0}$.34 - $\bar{0}$.13]. The only behaviors unaffected by sound level were time of entering the foraging arena and number of pecks, although there was a qualitative trend of the lowest number of pecks being observed in high sound pressure levels (see Figure 1.2).

To assess effect size, we compared the percent change of a behavior between our control treatment (~ 32 dBA) and our highest sound level treatments (~ 68 dBA). Since dBA values are on a logarithmic scale, every 6 dBA increase translates to a doubling of sound energy. Thus, across the 36 dBA range of sound levels we presented (32 - 68 dBA) there is a 6-fold increase in energy. Visual head scanning movements increased by 19% (~ 8 scans), and proportion of time spent with head up increased 8% (Figure 1.2b and a,

respectively) from 32 to 68 dBA. The time a bird spent foraging decreased by 31% - approximately one minute less in our highest sound level treatments compared to our control.

Treatment models

Noise treatment had no effect at our defined credible intervals or probability of direction thresholds. However, we did find trending effects for some behaviors (Table 1.2). Scanning trended towards decreasing in both traffic and shifted treatments compared to river noise (both probability of direction (PD): 92%, CI 80%: -0.10 - -0.01 , $n=123$). We also found that the number of pecks increased (~ 2 pecks) in the shifted treatment compared to river noise treatment [PD: 94%, CI 80%: 0.02 - 0.19]. Traffic noise also trended towards producing longer head down durations compared to river noise [PD: 90%, CI 80%: 0.01 - 0.26].

Inclusion of bird identity and experience model improvement

All models with a varying slope for trial number experienced and a varying intercept for individual bird ranked higher than models without these parameters included in LOOIC, with no overlapping standard error. This result suggests that adding these effects improved model fit for all behaviors.

Discussion

Our data suggest that birds may perceive intense, noisy acoustic environments as risky, regardless of whether they are natural or anthropogenic in origin, and largely regardless of the variation in spectral or temporal structure we presented. These similar effects of high sound level acoustic environments imply that noise has likely influenced

anti-predator behavior long before the world became rife with anthropogenic noise (Gomes et al. 2021).

Our findings of increased antipredator behavior in noisy anthropogenic environments matches results from similar studies across several listening taxa, including birds, mammals, and invertebrates (Krebs et al. 1997; Quinn et al. 2006; Wale et al. 2013; Klett-Mingo et al. 2016; Evans et al. 2018). Likewise, comparable vigilance increases have been described in wild populations of black-headed grosbeaks (*Pheucticus melanocephalus*; KA Sweet and colleagues, unpublished data) and California ground squirrels (*Otospermophilus beecheyi*; Le et al. 2019) in response to broadcast of whitewater river noise. In our study, sparrows increased both number of visual scans, and the proportion of time vigilant, indicating that noise increased reliance on visual vigilance (see Figure 1.2). Birds may have perceived noisy environments as dangerous because they limit access to information useful for risk assessment, such as alarm calls, or predator movement sounds via distraction or masking (Dominoni et al. 2020). Birds in our study had shorter head down durations on average in more intense noise, indicating that longer durations foraging without visual information may increase perceived risk in noise. Further, the cognitive costs of simultaneously assessing risk and performing tasks like seed manipulation (Dukas 2004) may decrease foraging efficiency (Halfwerk and van Oers 2020), perhaps even more so in higher sound levels (Chan 2010). Distraction may have increased seed handling errors and led to reduced food intake in higher sound levels. While birds did not change peck rates in noise, they did reduce the amount of time spent foraging in high sound levels. Although we did not directly measure seed

consumption in this study, the same peck rate combined with reduced time foraging could point to reduced caloric intake in high sound levels.

Indeed, behavioral changes in areas of higher sound levels may have latent negative impacts on fitness. Although some of the effect sizes we describe in sparrows are modest, such as increased vigilance and decreased foraging (8% increase in time spent vigilant from ambient conditions (~32 dBA) to 68 dBA), these changes may lead to downstream consequences, like reduced body condition. For example, white-crowned sparrows also increased vigilance and decreased foraging by 8% in another laboratory experiment that broadcast traffic noise (over the range of 32 to 61 dBA; Ware et al. 2015). These behavioral changes may underlie the reduction in ability to gain weight documented in migrating white-crowned sparrows exposed to the same traffic noise treatment in a large-scale field experiment (Ware et al. 2015). In addition to possible reductions in food intake, animals could also bear unseen physiological costs of stress hormone dysregulation (Kleist et al. 2018). Further experiments that link measures of body condition and stress with foraging and vigilance behavior could reveal whether these behaviors lead to lower survival or reproduction.

It seems animals likely avoid noisy areas at least partially because of perceived predation risk and the associated costs of performing antipredator behaviors. Several experiments have demonstrated altered bird distributions due to noise (e.g., Bayne et al. 2008; Francis et al. 2009; McClure et al. 2013; Cinto Mejia et al. 2019), although the mechanisms driving these changes are not entirely clear. In related work to that which we present here, song sparrows decreased in abundance as sound level increased during experimental broadcast of whitewater river noise (over a range of 30.6 to 73.8 dBA;

Gomes et al. *in press*). Although it has been hypothesized that masked songs may be problematic for song sparrows (Wood and Yezerinac 2006), Gomes and colleagues showed that spectral overlap between noise and song did not affect song sparrow abundance, while increasing sound levels and increasing median frequency of the acoustic environment both decreased abundance. These results seem to indicate that general auditory surveillance of the environment (e.g., for sounds of predators and prey) is more likely to underpin distributional changes for this species.

Interestingly, we also found that lower frequency noise trended towards greater perceived risk in sparrows. Compared to lower frequency river noise, the higher frequency shifted river treatment produced trends of less vigilance (scans) and more foraging (pecks) behavior. Listening in low frequencies may allow increased spatial auditory surveillance, as these low frequencies propagate farther. Communication calls, or critical spectral components of these calls, may also be received in lower frequency listening channels. Similar results have been found in other species when comparing behaviors in noise broadcast at similar intensities (as in this study) with different spectra. Field studies indicate that ground squirrels increase vigilance in river noise compared to higher frequency cicada noise (Le et al. 2019) and black-headed grosbeaks increase vigilance in lower frequency river noise compared to river noise shifted upward in spectrum (KA Sweet and colleagues, unpublished data). Although, other work in superb fairy-wrens (*Malurus cyaneus*) found no differences in vigilance behavior in white noise of high and low spectra (Zhou et al. 2019), this may be because the low spectra treatments did not have any energy below 2kHz (i.e., where most energy is located in traffic and river noise). We also note that traffic noise produced trends of decreased

vigilance (scans) and increased foraging compared to river noise, while amplitude-modulated river noise had no such effect. This could again indicate that birds are listening in low-frequency channels as the inherent amplitude modulation of traffic noise created larger “spectral relief” compared to river noise with amplitude modulation. Clearly, more work that quantifies antipredator responses to the frequency and temporal modulation of the acoustic environment will be important to understanding and predicting behavior in noise.

Future work should also focus on individual differences in noise (Harding et al. 2019). We found that the inclusion of bird identity and number of trials experienced improved model fit for every behavior. Indeed, behaviors associated with vigilance in birds (Cresswell et al. 2003) and foraging in bats, primates, and birds (Quinn et al. 2006; Dammhahn and Almeling 2012; Gomes and Goerlitz 2020) have been found to vary strongly by individual or personality. When exposed to white noise, personality and sex affects parental behavior in birds (Naguib et al. 2013), while social rank in mongooses impacts vigilance in traffic noise playback (Eastcott et al. 2020). Thus, some individuals may be better able to behaviorally cope with noisier environments or be more likely to persist in a noisy territory. Differences in how individuals respond to noise could in turn spatially structure personality type and have consequences for evolution (Miranda et al. 2013).

Our work demonstrates that natural and anthropogenic noise can shape antipredator behavior in similar ways, suggesting that the acoustic environment is an indicator of habitat quality and likely an important niche axis. The foraging-vigilance trade off may contribute to underlying causes of altered bird distribution in natural noise

(Gomes et al. *in press*), by degrading the quality of foraging habitat. Although the effects on behavior we present here are similar across anthropogenic and natural noise, anthropogenic noise has become much more extensive and intense in comparison to natural ambient sound levels (Buxton et al. 2017). Due to this pervasiveness, anthropogenic noise is particularly concerning for wildlife as human expansion continues into once quieter natural soundscapes.

Figures

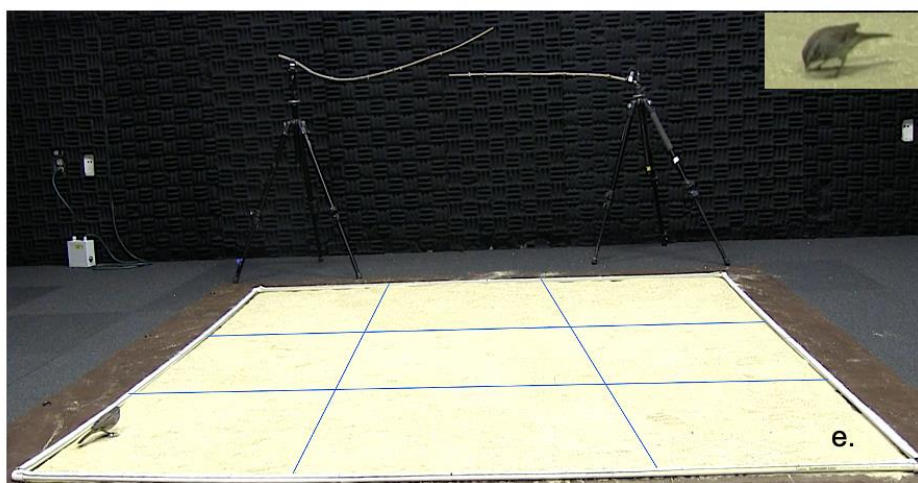
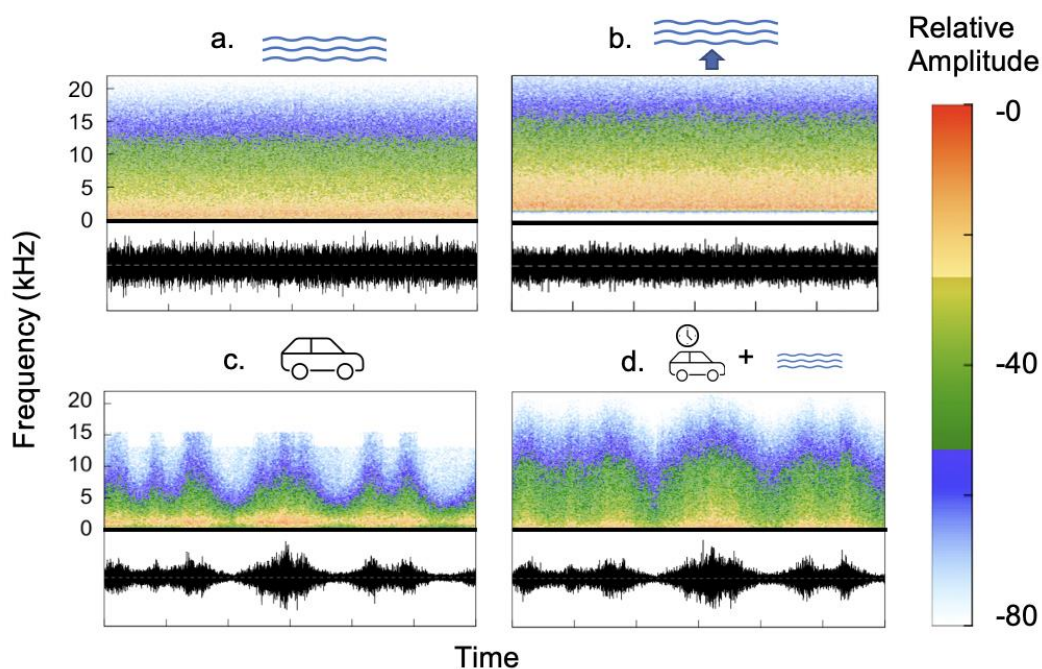


Figure 1.1 Spectrograms (frequency x time, top of each treatment panel) and oscillograms (amplitude x time, bottom of each panel) of a 1-minute section of our playback files. The legend indicates relative sound level in decibels. Treatments included: (a) whitewater river playback, (b) shifted whitewater river playback, (c) traffic playback, and (d) whitewater river spectra in traffic amplitude envelope. Note that traffic noise playbacks had a low pass filter applied at 16kHz to eliminate extraneous noises in the recording. (e) Song sparrow foraging inside the arena. We added lines to visualize the 3 by 3 grid used to measure sound pressure levels.

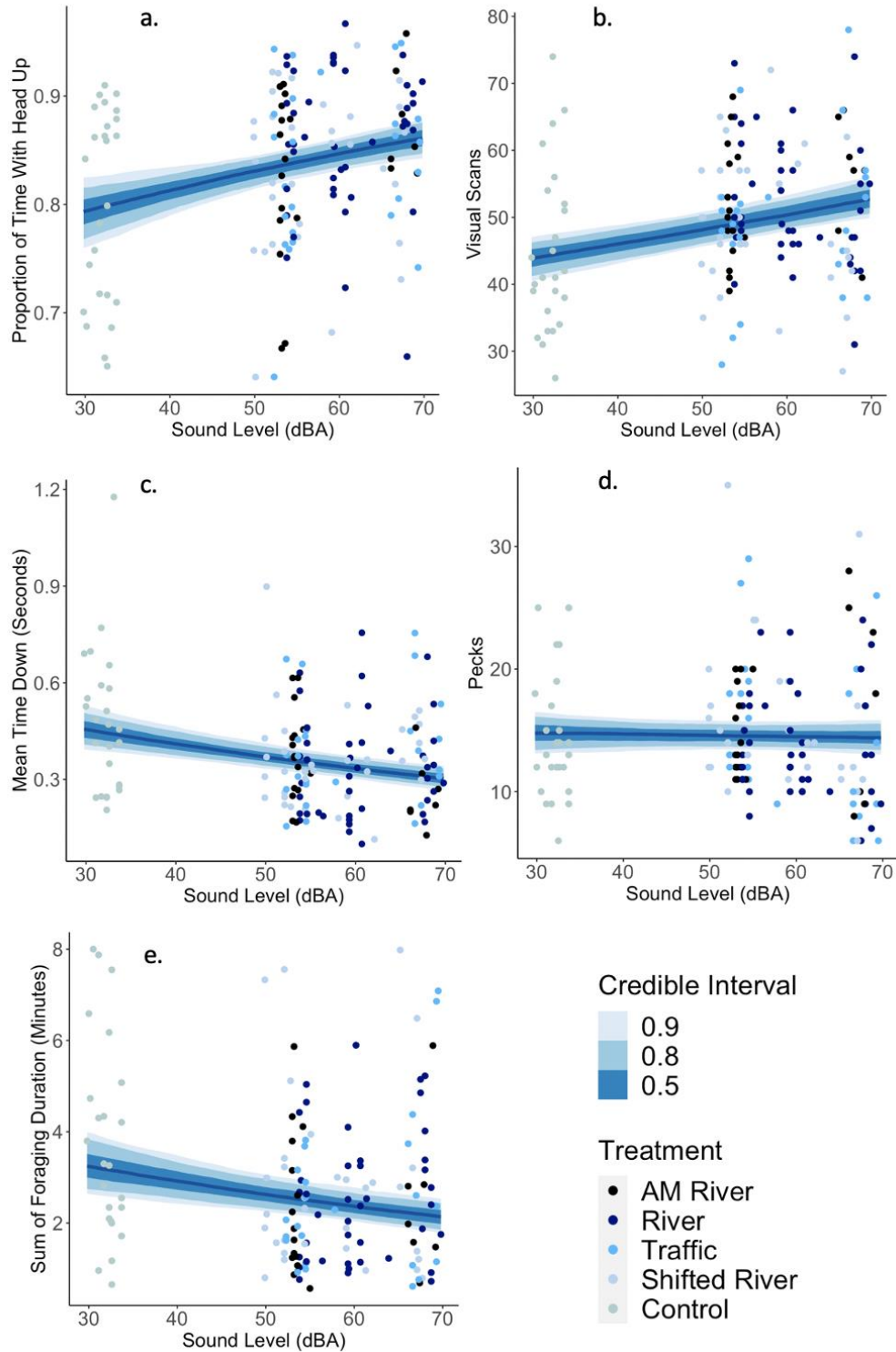


Figure 1.2 Sparrows increased vigilance (a & b) and decreased foraging (c & e) in every behavior we modeled when exposed to increasing sound pressure levels, except for time of entering the foraging arena (not pictured) and pecks (d).

Tables

Table 1.1 Model summaries for sound pressure level models by behavior. SE refers to standard error and CI refers to credible interval. Rows with bolded text indicate parameters with effects on behavior at 90% credible intervals excluding 0. Italic rows have trending parameter effects with 80% credible intervals excluding 0.

Behavior	Parameter	Mean	SE	CI 80%	CI 90%
Visual Scans	Sound pressure level	0.11	0.03	[0.08, 0.14]	[0.07, 0.15]
	<i>Hour of day</i>	<i>-0.04</i>	<i>0.03</i>	<i>[-0.08, -0.00]</i>	<i>[-0.08, 0.01]</i>
	Trials before eating	-0.02	0.03	[-0.05, 0.01]	[-0.06, 0.02]
Pecks	Sound pressure level	-0.01	0.05	[-0.07, 0.05]	[-0.09, 0.07]
	Hour of day	-0.01	0.05	[-0.08, 0.06]	[-0.10, 0.07]
	Trials before eating	0.00	0.05	[-0.07, 0.06]	[-0.08, 0.08]
Head Up Time	Sound pressure level	0.29	0.09	[0.17, 0.40]	[0.14, 0.44]
	Hour of day	0.01	0.10	[-0.12, 0.14]	[-0.15, 0.17]
	Trials before eating	-0.05	0.10	[-0.18, 0.07]	[-0.22, 0.11]
Foraging Duration	Sound pressure level	-0.24	0.09	[-0.35, -0.13]	[-0.38, -0.10]
	<i>Hour of day</i>	<i>0.13</i>	<i>0.10</i>	<i>[0.00, 0.26]</i>	<i>[-0.05, 0.29]</i>
	Trials before eating	-0.24	0.09	[-0.35, -0.12]	[-0.40, -0.10]
Enter Time	Sound pressure level	0.14	0.13	[-0.03, 0.30]	[-0.06, 0.36]
	<i>Hour of day</i>	<i>-0.19</i>	<i>0.15</i>	<i>[-0.39, -0.02]</i>	<i>[-0.43, 0.04]</i>
	Trials before eating	0.05	0.15	[-0.13, 0.23]	[-0.21, 0.27]
Mean Time Down	Sound pressure level	-0.24	0.06	[-0.32, -0.16]	[-0.34, -0.13]
	Hour of day	0.00	0.07	[-0.10, 0.08]	[-0.12, 0.11]
	<i>Trials before eating</i>	<i>0.11</i>	<i>0.07</i>	<i>[0.02, 0.19]</i>	<i>[-0.00, 0.21]</i>

Table 1.2 Model summaries for noise treatment models by behavior. SE refers to standard error and CI refers to credible interval. Rows with bolded text indicate parameters with effects on behavior at 90% credible intervals excluding 0. Italic rows have trending parameter effects with 80% credible intervals excluding 0.

Behavior	Parameter	Mean	SE	CI 80%	CI 90%
Scan	Sound pressure level	0.01	0.05	[-0.04, 0.07]	[-0.06, 0.09]
	Modulated river	0.03	0.04	[-0.02, 0.08]	[-0.04, 0.10]
	<i>Traffic</i>	<i>-0.05</i>	<i>0.04</i>	<i>[-0.10, -0.01]</i>	<i>[-0.11, 0.01]</i>
	<i>Shifted river</i>	<i>-0.05</i>	<i>0.04</i>	<i>[-0.10, -0.01]</i>	<i>[-0.11, 0.01]</i>
	<i>Hour of day</i>	<i>-0.04</i>	<i>0.03</i>	<i>[-0.08, 0.00]</i>	<i>[-0.09, 0.01]</i>
	Trials before eating	-0.02	0.03	[-0.05, 0.02]	[-0.07, 0.03]
Pecks	Sound pressure level	-0.05	0.08	[-0.15, 0.05]	[-0.18, 0.09]
	Modulated river	0.09	0.08	[-0.01, 0.18]	[-0.03, 0.22]
	Traffic	0.07	0.07	[-0.02, 0.16]	[-0.04, 0.20]
	<i>Shifted river</i>	<i>0.11</i>	<i>0.07</i>	<i>[0.02, 0.19]</i>	<i>[-0.00, 0.22]</i>
	Hour of day	-0.05	0.06	[-0.13, 0.02]	[-0.14, 0.06]
	Trials before eating	0.01	0.06	[-0.07, 0.08]	[-0.09, 0.10]
Head Up Time	Sound pressure level	0.16	0.13	[-0.02, 0.31]	[-0.06, 0.38]
	Modulated river	-0.09	0.16	[-0.28, 0.11]	[-0.34, 0.16]
	Traffic	-0.14	0.15	[-0.33, 0.04]	[-0.37, 0.13]
	Shifted river	-0.16	0.14	[-0.34, 0.02]	[-0.38, 0.08]
	Hour of day	-0.00	0.12	[-0.14, 0.15]	[-0.19, 0.19]
	Trials before eating	-0.03	0.11	[-0.18, 0.10]	[-0.21, 0.16]
Foraging Duration	Sound pressure level	0.05	0.15	[-0.14, 0.23]	[-0.19, 0.29]
	Modulated river	-0.14	0.15	[-0.33, 0.05]	[-0.38, 0.11]

	Traffic	-0.05	0.14	[-0.22, 0.14]	[-0.27, 0.19]
	Shifted river	0.11	0.14	[-0.06, 0.29]	[-0.12, 0.34]
	<i>Hour of day</i>	<i>0.18</i>	<i>0.12</i>	<i>[0.04, 0.33]</i>	<i>[-0.02, 0.36]</i>
	Trials before eating	-0.25	0.11	[-0.39, -0.11]	[-0.43, -0.08]
Enter Time	<i>Sound pressure level</i>	<i>0.26</i>	<i>0.18</i>	<i>[0.04, 0.49]</i>	<i>[-0.03, 0.54]</i>
	Modulated river	0.00	0.19	[-0.27, 0.22]	[-0.31, 0.33]
	Traffic	0.11	0.18	[-0.13, 0.33]	[-0.20, 0.40]
	Shifted river	0.07	0.18	[-0.14, 0.30]	[-0.20, 0.37]
	<i>Hour of day</i>	<i>-0.23</i>	<i>0.15</i>	<i>[-0.43, -0.04]</i>	<i>[-0.48, 0.02]</i>
	Trials before eating	0.06	0.16	[-0.15, 0.26]	[-0.21, 0.31]
Mean Time Down	Sound pressure level	-0.05	0.11	[-0.19, 0.09]	[-0.24, 0.12]
	Modulated river	0.02	0.11	[-0.12, 0.15]	[-0.15, 0.21]
	<i>Traffic</i>	<i>0.13</i>	<i>0.10</i>	<i>[0.01, 0.26]</i>	<i>[-0.03, 0.30]</i>
	Shifted river	0.08	0.10	[-0.05, 0.19]	[-0.07, 0.25]
	Hour of day	0.06	0.08	[-0.04, 0.17]	[-0.08, 0.19]
	Trials before eating	0.10	0.08	[0.01, 0.21]	[-0.02, 0.23]

CHAPTER TWO: LARGE-SCALE EXPERIMENTAL EVIDENCE DEMONSTRATES
NATURAL NOISE CAN INFLUENCE WILD BIRD ANTIPREDATOR BEHAVIOR

To be submitted to Functional Ecology

Introduction

Listening animals have faced constraints imposed by noisy acoustic backgrounds throughout their evolutionary history (Gomes et al. 2021). Natural intense acoustic environments are still prevalent components of modern landscapes. For example, the sounds of moving water fill contiguous areas of the over 5 million km of rivers and streams that snake across the United States (US EPA 2014). Indeed, natural noise has been demonstrated to be a shaping force of abundance and behavior across taxa (Jouventin et al. 1999; Lengagne and Slater 2002; Geipel et al. 2019; Gomes et al. 2020; for review see Gomes et al. *in press*). Birds and bats alter their abundance and activity, respectively, in response to whitewater river noise (Gomes et al. *in press*), while some fish use reef noises as a cue for settlement (Simpson et al. 2004).

The information contained in the acoustic environment may be especially important while animals forage. Foraging is essential for survival as it fulfills necessary energy demands, but it can put animals at greater risk from predation. Noise can mask critical adventitious cues from predators (Barber et al. 2010) and prey (Siemers and Schaub 2011; Gomes et al. 2016; Mason et al. 2016), information from hetero- or conspecific vocalizations (Morris-Drake et al. 2017; Zhou et al. 2019), or serve as a

cognitive distractor during foraging tasks (Purser and Radford 2011). In laboratory experiments, white-crowned sparrows (*Zonotrichia leucophrys*) increased vigilance behavior and decreased foraging in traffic noise (Ware et al. 2015), and chaffinches (*Fringilla coelebs*) exposed to white noise (a broadband stimulus with equal energy across all frequencies) showed similar changes in behavior (Quinn et al. 2006). The same behavioral tradeoff has been observed in great tits (*Parus major*) in response to airplane noise (Klett-Mingo et al. 2016). These behavioral changes might allow animals to persist in noisy environments by mitigating potential costs allowing exploitation of food resources. Conversely, these modifications may not be adequate to offset increased risk of predation (Watson et al. 2007), or become so calorically costly that they could result in reduced fitness.

In addition to changing foraging and antipredator behavior, anthropogenic noise has been shown to alter animal distributions (Bayne et al. 2008; McClure et al. 2013; Kleist et al. 2017; Cinto Mejia et al. 2019), body condition (Ware et al. 2015), survival (Simpson et al. 2016), and reproduction (Halfwerk et al. 2011; Senzaki et al. 2020). Increased vigilance behavior and concomitant decreases in foraging may contribute to these downstream consequences. Yet, there is limited work that investigates if natural noise causes similar changes in foraging and vigilance behavior. Understanding how animals respond to natural noise may reveal behavioral trade-offs animals have used for millennia to persist in noisy environments long before anthropogenic sources emerged. Likewise, much of the research generated on foraging and vigilance behavior has been done in lab settings. Examining this behavioral trade-off under natural conditions in the

wild will help us understand these behaviors in ecological context, where other factors influence antipredator behavior.

Here, we manipulated riparian drainages in the mountains of Idaho by broadcasting whitewater river recordings to understand if, and how, birds alter foraging and vigilance in natural noise. To determine how birds behave in natural intense noise, we broadcast whitewater river recordings (avg. median frequency 2.1 kHz, SD: 1.3 kHz) in riparian drainages that contained naturally quiet streams at 5 sites. To understand how birds respond to differing spectra, at 5 additional sites we broadcast ‘shifted’ river recordings of the same amplitude modulation as our preceding river recordings, but with heightened frequencies (avg. median frequency 4.8 kHz, SD:1.3 kHz). Our study also included 10 acoustically-unaltered ‘control’ riparian sites, ranging from trickling streams to raging rapids. Together this created acoustic environments that spanned a wide gradation of background frequencies and sound pressure levels.

We hypothesized that birds would perceive higher sound level acoustic environments as riskier. Thus, we predicted birds would forage less and increase vigilance behavior in those situations. In addition, we hypothesized that birds are more reliant on low frequencies for auditory surveillance because prey and predator cues are more often low frequency, especially at greater distances from the listener (Barber et al. 2010). Therefore, we predicted that birds would be more vigilant in lower spectra noise, since lower background frequencies may interfere with important information extraction.

Methods

Data Collection

Sound Treatments

We studied bird behavior in riparian drainages surrounded by sage-steppe in the Pioneer Mountains of central Idaho (see Figure 2.1a). To create our experimental acoustic environments, we suspended speakers approximately 3 meters off the ground on metal tripods and played treatment tracks at manipulated sites for 24 hours a day, powered by 12-volt batteries (DURDC12-100P; Duracell) and solar panels (Suniva OPT285-60-4-100; MidNite Solar Inc., WA, USA). We began broadcasting treatments mid-May before most bird territory establishment and continued broadcasting until mid-July. To create the same sound propagation across the two treatment types (given the reduced propagation of the higher frequencies contained in the shifted river playbacks), we hung 2 speakers (Octasound SP820A) at river sites, and 3 speakers (Octasound SP800A) at ‘shifted’ river sites. We recorded our playback files for these treatments at 48 kHz sampling rate, at 16 bits and at 5 meters from high sound level whitewater sites. Both shifted and river treatments had the same broadcast energy according to an average birds’ hearing threshold (Gomes et al. *in press*). Full metadata for sound stimulus recordings and playbacks can be found in Gomes et al. *In Press*.

Foraging Point Counts

We conducted foraging point counts to establish a baseline and understand whether birds were willing to forage in noisier areas. During foraging point counts in the summer of 2018, we surveyed 20 sites composed of 10 control, 5 shifted, and 5 river sites (Figure 2.1). We navigated to the center point of each site and looked for actively

foraging birds for 20 minutes. All point counts took place before 12:30 in the afternoon. During each point count, we wore earplugs and ear protection headphones so that differences in auditory detection across treatments did not influence results. At the end of each count we measured a 1-minute LEQ (similar to an average of sound pressure values) using the phone app SPLnFFT, and a type 2 sound level meter (MicW; i436). We took all sound measurements with an A weighting (dBA) because it is the most relevant to the hearing range of birds and most other vertebrates (Dooling and Popper 2007). Median frequency values were extracted from automated recording units (RO5s) placed at each site (see Acoustic Quantification section below for detail).

Opportunistic filming of birds

We then attempted to understand how noise might shape foraging and vigilance behavior in wild birds. At the same sites used for our foraging points counts, we opportunistically filmed foraging birds using a Sony Alpha 6000 or a Canon XA10 camera. We recorded the distance between the observer and the bird, and its perch height using a laser range finder (TruPulse 360 R, Laser Technology). After each recorded observation, we took a sound level measurement (1-minute LEQ) at the position of the bird with a MicW.

Bird Feeders

The following summer of 2019, we deployed 18 bird feeders across 6 of our sites from May through July. We studied 2 acoustically unaltered control sites, 2 river, and 2 shifted river sites. Each site contained 3 feeders, with feeders linearly arranged along the riparian corridor (Figure 2.1b). In the center of each site we placed one feeder near the speakers. To capture a range of sound levels, we placed the remaining 2 feeders at

unequal distances from the speakers, such that one feeder was closer ($113.3 \text{ m} \pm 26.2$), and one feeder was further away ($174.3 \text{ m} \pm 37.8$). Sites without speakers (i.e., controls) had this same feeder arrangement.

Each feeder unit had a tray style seed feeder, along with a wire mesh peanut feeder. We used both feeder types in order to maximize the number of videos and potential species visiting the feeders. We quantified only videos with birds foraging at the tray style feeders because these videos were more numerous and had a higher number of the same species visiting. Tray feeder videos were also easier to quantify consistently because of greater visibility of the bird's head. In the tray feeders we placed a mix of millet, peanut pieces, unshelled sunflower seed chips, and corn pieces. In order to prevent any germination at the study site, we baked seeds at $65 \text{ }^{\circ}\text{C}$ (Kate Thibault, NEON Science Lead, April 2019, personal communication). We attached the feeders using pegboard to allow for more placement flexibility at locations with appropriate sound level gradients and similar vegetation (Figure 2.1c). We affixed feeders at approximately the same height on trees ($145 \text{ cm} \pm 15.5$), and to the extent possible, placed them in similar levels of vegetative cover and proximity to streams ($7.12 \text{ m} \pm 7.89$). Once the feeders were attached, we placed a Bushnell HD game camera directly across ($1.77 \text{ m} \pm 0.51$), and set it to record a 60 second video when triggered.

Acoustic Quantification

We paired each camera with a sound recording device (Roland, RO5) covered by a wind screen protector within ~5 meters of the feeder. Recording units captured continuous sound data in MP3 compression (128 kbps). This approach allowed for quantification of the frequencies birds can hear (Mennitt and Fristrup 2012). We then

extracted hourly L50 levels (sound pressure level that is exceeded 50 percent of the hour), from these recordings using Acoustic Monitoring Toolbox and AUDIO2NV SPL software (Damon Joyce, National Parks Service) and matched these values to each observation by hour and date. To extract median frequency, we first used FFMPEG (FFmpeg Developers 2018) in a Windows command prompt to trim 3-minute clips from the beginning of each hour of recording (see Gomes 2021 for details). Once we had these clips, we read the files into R using package ‘tuneR’ (Ligges 2013), and then extracted the median frequency using ‘seewave’ (Sueur et al. 2008).

Feeder Video Quantification

We quantified the three most common bird feeder visitors: lazuli buntings (*Passerina amoena*), American goldfinches (*Spinus tristis*), and black-headed grosbeaks (*Pheucticus melanocephalus*). We quantified videos in which a bird was actively foraging for at least 30 seconds, there was only one bird on the feeder, the bird was clearly visible and in focus, the bird was perched on the edge of the tray feeder rather than inside the feeder, and the bird was not visibly engaged in other behaviors such as singing, begging, or otherwise interacting with a bird offscreen (such that the bird was not focused on one spot offscreen, suggesting induced rather than routine vigilance, Blanchard and Fritz 2007). Videos that did not meet these criteria were not analyzed. We selected the first video from each presumed individual per day, based on the previous criteria to avoid sampling the same individual under the same conditions. Once videos were selected, we visually assessed and recorded the sex of each bird. Black-headed grosbeak females and males that were not in adult plumage were aggregated into one category because they can have indistinguishable plumage patterns (Hill 1987). Specifically, all birds were placed in

the ‘immature and female’ category unless they had bright orange chest and black head plumage distinctive of adult males.

To behaviorally code videos we used freely available software (BORIS; Friard & Gamba 2016). Before coding, each video was muted to minimize bias. We quantified the first 30 seconds of each video starting at the first ‘head down’ movement (each time the bird’s head went below the line of its back). We counted the number of ‘head down’ movements as a proxy for pecks, since the feeder sometimes obscured the bird’s beak contacting a food item. We also calculated the average length of time that a bird spent with its head below the line of its back, since this is a standard metric of bird foraging vigilance (Cresswell et al. 2003; Quinn et al. 2006; Jones et al. 2007; Ware et al. 2015). To calculate this metric, we took the total time a bird spent with its head down and divided it by the number of head down events. Finally, we counted visual head scans (i.e., head movements in the head up position in any direction, each movement defined as when the head started moving to when it stopped, Fernández-Juricic et al. 2011)), because head scan movements may indicate level of perceived risk (Jones et al. 2007).

Opportunistic Foraging Video Quantification

Using BORIS software, we coded any video where the bird was visible, in focus, actively foraging, not singing, and the video was at least 10 seconds long. We quantified up to 30 seconds of foraging footage per video recording. We split videos into three foraging behavior categories – gleaning, perched, or ground foraging consumption. Gleaning referred to a bird moving through vegetation searching for food items, whereas perched consumption refers to a stationary perched bird consuming food. Ground foraging was coded as foraging behavior on the ground level. We extracted head scans

and proportion of time with head down (for perched consumption and ground foraging only). In addition, we measured movement rate (number of distinct movements from one position to another) and proportion of time spent moving (both measures for gleaning and ground foraging only).

Data Analysis

General Model Information

To create models, we chose variables based on the knowledge of our system and research question. We ran all models using weakly informative priors that are standard in the package ‘rstanarm’ (Goodrich et al. 2020) in R (version 4.0.2). Each model was run with 4 chains and for 2000 iterations (1000 iteration warmup). We centered all continuous variables at the mean and scaled by 2 standard deviations in order to compare them to binary factors (Gelman 2008). To increase sampling effectiveness and eliminate divergences we raised adapt delta to 0.999 (Goodrich et al. 2020).

We then assessed the sampling and fit of each model. We inspected all models to ensure that they had large effective sample sizes (ESS), that Gelman-Rubin convergence diagnostics (Rhat) were below 1.1, and that chains appeared mixed (McElreath 2009). These checks are collectively performed to indicate proper Markov Chain Monte Carlo sampling of the posterior. We checked fit by evaluating how well simulated data from the posteriors compared with our observed data, using posterior predictive checks (with function ‘pp_check’ in package ‘bayesplot’ (Gabry and Mahr 2017)). Finally, we calculated RMSE (using the package ‘performance’) to provide additional heuristic goodness of fit information for our whole model structure (note that Bayesian R² values are not available for the distributions we chose). Although the goals of our models were

directional hypothesis testing and not prediction, we still include these heuristics of predictive quality in the appendix.

Bird Feeder Analysis

Using a Bayesian mixed effects framework, we built separate models for each species and each behavioral response. For example, we made four models in total for lazuli buntings - one for the response variable head scans, one for head downs, one for proportion of time with head up, and one for average time with head down. We built separate models for each species because we assumed species would likely have different baseline foraging behaviors.

We utilized a mixed model structure to control for several location-specific effects important to foraging and vigilance. While we attempted to identify locations for feeders that had similar characteristics of vegetative cover, we also included feeder as a varying (random) intercept to statistically account for characteristics of the immediate environment. This incorporates a wide range of factors known to influence vigilance including cover, distance of feeder to cover, visual obstructions, and predator density. We include feeder as a varying effect and not a fixed effect both because of collinearity with sound level due to our experimental design, and to account for possible pseudoreplication caused by the same individual bird returning to the same feeder multiple times. For fixed effects, we included hour of the day, Julian date, median frequency, L50 (sound level), and the interaction between frequency and L50. Hour was included because birds have been found to increase vigilance as the day continues (Pravosudov and Grubb, 1998). We include Julian date to account for possible habituation and seasonal vegetation changes

across the study period. Julian date may also capture changes in energy demand due to breeding phenology (Martin 1987).

The models for lazuli bunting were structured differently from goldfinches and grosbeaks because of limitations imposed by their small sample size. Lazuli buntings fed at only four of our feeder locations, so we did not fit feeder as a varying intercept because it had fewer than five levels (Harrison et al. 2018). We also did not include feeder as a fixed effect in bunting models because of high multicollinearity.

In addition, we made models for grosbeaks to include a sex parameter for each behavior, since vigilance and foraging can vary according to sex in birds and mammals (Caro 2005). For grosbeaks, these models included sex as a fixed term, as an interaction with L50 (sex:L50), and an interaction with frequency (sex:frequency), in addition to the parameters mentioned in the preceding paragraph. For goldfinches, we excluded the sex:frequency interaction term because of high multicollinearity. We were unable to create sex interaction models for buntings because of high multicollinearity and low sample sizes.

For models both with and without sex terms, we compared negative binomial and Poisson distributions with log link functions for count behaviors (head scan and down movements), using leave-one-out cross validation information criterion (LOOIC), and the resulting expected log predictive densities (ELPDs), in conjunction with ‘pp_check’ (McElreath 2009). In our “proportion of time vigilant models”, we used a beta distribution with a logit link function because the modeled response variable was a continuous proportion of the 30 second foraging bout. The beta distribution models were run in ‘rstanarm’ using ‘family=mgcv::betar’, which allowed us to include varying

intercepts in ‘rstanarm’. Lastly, for average head down duration models we used a log normal distribution.

Foraging Point Count Analysis

To model bird foraging point counts we created models that included Julian date, hour, median frequency, sound level, the interaction of sound level and median frequency as fixed effects, and site as a varying intercept to account for site-level effects. We created models with Poisson and negative binomial distributions with log link functions. We checked the Poisson model for possible zero inflation and found no evidence of it. We then compared the Poisson and negative binomial model using LOOIC and found that the Poisson model fit best. Thus, we interpreted those results.

Opportunistic Foraging Video Analysis

To analyze our opportunistic foraging videos, we included group size, sound level, perch height and observer distance as fixed effects. We included a varying intercept for both site and species. For proportion of time spent moving and proportion of time with head down, we used a beta distribution with a logit link function. We used a negative binomial distribution with a log link function for movement and scan numbers, with an offset specified as the log of the length of video to account for varying video lengths.

Parameter Interpretation Criteria

To judge whether a parameter had a meaningful effect on behavior, we used both probability of direction and credible intervals. Probability of direction is the probability that an effect is either entirely negative or positive (Makowski et al. 2019). We calculated probability of direction (here after referred to as PD) by determining what percentage of

the posterior mass was greater or less than 0 using function ‘p_direction’ in package ‘bayestestR’(Makowski et al. 2019). Probability of direction values range from 50% to essentially 100%. We interpreted support for parameter effect if at least 95% of the posterior predictive mass excluded 0 (>95, or <5 rounded to the nearest whole percent). If the PD was 90% or greater for parameters of interest, we viewed these instances as possible trends in parameter effect. We considered a parameter to have an effect on a behavior if the credible interval excluded 0 at 90%. All credible intervals (here after referred to as CI) listed are at 90% unless otherwise noted. We also report possible trending effects if CI excluded 0 at 80%.

Results

A total of 12 bird species visited the feeders. The three most common species used for analysis were lazuli buntings (n=48), American goldfinches (n=117), and black-headed grosbeaks (n=395).

Although models had good fits as indicated by posterior predictive checks, they had large RMSE values (Table A.7). This implies that other unmeasured variables are likely important for assessing the foraging vigilance trade-off.

Black-headed Grosbeaks

Black-headed grosbeaks showed increases in vigilance behavior with increasing sound level. Behavioral responses appeared to be more driven by the female and immature bird grouping, in comparison to adult male birds. When both groups were included in our models there was no effect of sound level on scanning or head downs. There was a 96% probability that time with head up vigilant increased in high sound levels (CI: 0.01 - 0.29, n=395). The proportion of time individuals spent with their head

up (vigilant) increased by a small 5% from the lowest to highest sound levels in which we recorded grosbeaks foraging (37 -74 dBA L50). Additionally, individuals had shorter head down foraging periods as sound levels increased (PD: 98%, CI: $-0.32 - -0.03$, although note that PD decreased to 93% when an extreme outlier was not included in the analysis). Visual scanning increased as frequencies decreased (PD: 99%, CI: $-0.12 - -0.02$). Grosbeaks increased head scanning by 15% as frequencies decreased from highest to lowest across our study area (10,734 - 657 Hz).

Models with sex included as an interaction term showed that female and immature grosbeaks (Figure 2.2) react differently to noise. Adult male birds only changed mean time head down with noise. Female and immature birds showed slight trends in head down numbers, with a decrease in head down movements at low frequencies (PD: 92%, CI 80%: 0.01 - 0.19) and decreases in higher sound levels (PD: 90%, CI 80%: $-0.19 - 0.00$). Female and immature grosbeaks increased scanning in higher sound levels (PD: 98%, CI: 0.02 - 0.16, increase of 20 %), and in lower frequencies (PD: 99.9 %, CI: $-0.18 - -0.06$, increase of 27%). Female and immature birds also increased the proportion of time spent with their head up in higher sound levels (PD: 97 %, CI: 0.02 - 0.40, increase of 8%) and they spent less time on average with their head down in increasing sound levels (PD: 98%, CI: $-0.36 - -0.03$).

American Goldfinches

American goldfinches had shorter head down periods in higher frequencies (PD: 97%, CI: $-0.18 - -0.01$). We found a trend of increased head scanning movements in higher frequencies in sex included models (PD: 92%, CI 80%: 0.01 - 0.25). Interestingly in sex interaction term models, goldfinches had shorter times spent with their head down

in higher frequencies (PD: 95%, CI: $-0.16 - 0.00$), but longer mean down times in high sound pressure levels in female birds (PD: 99.7%, CI: $0.11 - 0.35$). This was in contrast to male birds which showed a trend of shorter mean head down times in increasing sound level (PD: 93%, CI 80%: $-0.17 - -0.01$). Goldfinches had different behavior rates depending on sex for head down number and proportion of time spent vigilant, but only had an interaction of sound level and sex for mean head down time. There was no effect of frequency or sound level on the time goldfinches spent with their head up.

Lazuli Buntings

Lazuli buntings increased visual scanning head movements as sound level increased (PD: 96%, CI: $0.02 - 0.46$, $n = 48$, see Figure 2.3). These scanning movements increased by 57% across the full range of sound levels that buntings were recorded in ($33 - 67$ dBA). Like grosbeaks, we found a slight trend of more scanning in lower frequencies (PD: 90%). Buntings also showed a trend of shorter average head down times in greater sound level (PD: 90%, CI 80%: $-0.32 - 0.00$) There was no evidence of noise impacting any other behavior.

Foraging Point Counts

During May to July of 2018, we completed a total of 107 foraging point counts with 6 observers across 20 sites. In total 97 foraging birds were detected (all except 4 of these individuals were within 50 meters of the observer). There was no evidence that foraging birds were observed less as sound pressure level increased.

Videos

We acquired 68 videos of birds foraging, across 19 different species. There was no relationship between visual scanning movements, duration of movements, or

proportion of time with head down and noise. However, we did find a trend of decreased number of movements in higher sound pressure level (PD: 94 %, CI 80%: $-0.65 - -0.06$, see Figure 2.4). Strangely, the number of movements increased when the filming observer was closer to the bird (PD: 96%, CI: $-0.83 - -0.03$), while a closer observer had a trend of increasing scans (PD: 90%).

Discussion

Our results indicate that intense, natural acoustic environments can influence vigilance behaviors in wild birds. We found that species varied in their specific responses to the spectrum of the environment, while higher sound levels increased vigilance in certain behaviors across multiple species. These findings are in congruence with increased vigilance documented in California ground squirrels (*Otospermophilus beecheyi*) foraging in river noise (Le et al. 2019), suggesting that vigilance in response to intense natural noise could be a general phenomenon across different taxa. Our results are further supported by findings in a controlled lab experiment, where we found that song sparrows (*Melospiza melodia*) increased vigilance and decreased foraging in the same river noise treatment (Sweet et al. *in progress*). Here, we note that behavioral changes in our wild bird study were highly variable and sometimes demographic specific, but were generally consistent with our predicted changes in noise (see Figure 2.2 & 2.3 and appendix Table A.1 and A.7). This suggests that while other variables are important for informing risk assessment, noise can be an influential environmental pressure. Importantly, increased vigilance in our study was not due to disturbance novelty (either through startle response or neophobia), since our river playback was continuous across a summer breeding season.

The behavioral changes we documented in river noise are similar to increases in antipredator behaviors seen in anthropogenic noise (Ware et al. 2015; Klett-Mingo et al. 2016), suggesting that vigilance as a reaction to intense noise is a conserved response. Although reactions to natural and anthropogenic noise appear somewhat similar, the rapid growth of anthropogenic noise in comparison to natural noise is unprecedented (Buxton et al. 2017), making this conserved foraging vigilance trade-off in high sound levels a potential concern.

The perceived riskiness of a noisy environment could clearly contribute to altered distributions. In our same study system, overall bird abundance decreased in higher sound levels of river noise (Gomes et al. 2021 *in press*). Although we lacked the sample size to model grosbeak abundance specifically, this species has been found to decrease in low-frequency gas compressor station noise (Francis et al. 2009). In contrast, some species distributions remained unaffected by noise in our study system, such as the lazuli bunting (Gomes et al. 2021 *in press*). The vigilance increase (visual scanning) measured here may help buntings cope with noise and occupy habitats with higher sound levels. However, there may be hidden costs. For example, birds nesting in closed vegetation (such as riparian areas) across the continental U.S. have decreased nest success in higher noise levels (Senzaki et al. 2020), while other birds can suffer hormone dysregulation in noise (Kleist et al. 2018).

In addition to increased vigilance or avoidance, some animals may exhibit more cryptic behavior when they perceive a situation as riskier. Our season-long effort at filming foraging birds indicated a trend towards decreased movement rates as sound levels increased (Figure 2.4). Limiting movement in risky situations may be an

antipredator defense, since moving prey may be more easily detected by predators (Lima and Dill 1990). Other taxa show similar movement reductions in risky environments. Rats decrease movement in illuminated pathways (Farnworth et al. 2019), while degus take longer locomotion pauses in riskier habitat (Vasquez 2002). Under river noise exposure, ground squirrels move shorter distances, and spend less time moving (Le et al. 2019). Notably, we also found that birds moved more often when the filming observer was closer, a trend opposite to what we expected based on the risk disturbance hypothesis (Frid and Dill 2002). Perhaps birds perceived themselves as already detected and were thus more ready to employ an escape strategy, or were possibly attempting to advertise that were aware of the human observer.

Cryptic behaviors and vigilance changes may differ by demographic groupings. Specifically, sex has been shown to affect vigilance patterns across a variety of mammal and bird species (Caro 2005). We found influential sex and sound parameter interactions in both grosbeaks and goldfinches. Additionally, goldfinches (see appendix, Table A.1) and buntings (see Figure 2.3) sometimes had different baseline vigilance rates between sexes. Previous work has demonstrated that female birds often behave more cryptically or are more vigilant while foraging in riskier areas than males. Female skylarks (*Alauda arvensis*) maintain consistent food intake in risky habitats by staying stationary, potentially as a camouflage mechanism, whereas males decrease their rate of intake and move more often (Powolny et al. 2014). Female Western sandpipers (*Calidris mauri*) forage in riskier habitats compared to males, but behaviorally compensate for this risk by increasing head scans at a higher rate (Fernández and Lank 2010). Female grosbeaks in our study might continue to forage longer in dangerous, yet productive areas (e.g., bird

feeders in noise), while male grosbeaks may leave the feeder more readily, rather than employ behavioral adjustments. This may also be because adult males have brighter plumage, and thus may be more easily detected by predators. As we grouped both female and immature grosbeaks in our analyses due to similar plumage, differences in experience could partially account for these patterns. In another study, migrating hatch-year birds avoided noise more strongly than adult birds, perhaps because a lack of experience foraging and detecting predator cues led to higher vigilance costs (McClure et al. 2017).

Increased perceived risk while foraging could be caused by the masking of biologically relevant frequencies in our system. Grosbeaks were impacted by both higher sound levels and low frequency environments, perhaps due to the masking of their low-frequency songs (peak frequency of ~3 kHz, Cardoso supplement 2010). Goldfinches showed an opposite trend of increased vigilance or less foraging in higher frequency acoustic environments, perhaps because of their high song peak frequency of over 9 kHz (Coutlee 1971). Buntings have an intermediate peak song frequency (5 kHz, Cardoso 2010 supplement), and showed no frequency associated behavior changes (although they trended towards scanning more in lower frequencies). A meta-analysis indicates that song frequency and anthropogenic noise sensitivity are linked (Francis 2015). In our system, spectral overlap of song frequency predicted bird abundance declines in lower sound levels but did not affect abundances at high sound levels. This suggests that in loud environments mechanisms other than conspecific song masking may be important to bird abundance, and the same may be true for foraging and vigilance behavior. For example, the masking of heterospecific information regarding safety could have increased

vigilance levels (Templeton et al. 2016; Lilly et al. 2019). Masking in low frequencies may also be particularly problematic. Low frequency noise, like river noise, may mask locomotion cues of prey or predators (Montgomerie and Weatherhead 1997; Goerlitz et al. 2008; Haff and Magrath 2010; Onrust et al. 2017). Furthermore, low frequencies travel farther than high frequencies, therefore animals may rely on low frequencies to maximize their listening area for auditory surveillance while foraging (Barber et al. 2010).

In addition to masking sounds relevant to auditory surveillance, perceived risk in noise could be driven by distraction (i.e., limited attentional resources). Noise has been shown to distract animals while foraging, making them potentially more vulnerable to predators (Chan et al. 2010), and less efficient foragers (Purser and Radford 2011; Allen et al. 2021). Although there were no distinct changes in American goldfinch vigilance behavior, foraging behavior may have been impacted by distraction in our experiment. Female goldfinches had longer head down times in high sound levels. This increase of head down times in high sound levels is the opposite of what we predicted according to the foraging vigilance trade-off and may reflect slowed seed search and handling due to limited attention in noise. Although our feeder study only recorded seed-eating behavior, predation behaviors may be more impacted by distraction in intense noise because capturing motile and/or cryptic prey can be especially cognitively demanding (Francis 2015; Halfwerk and van Oers 2020). Further, in our study system high sound levels decreased bird predation rates in a visual foraging task with clay caterpillars (Gomes et al. *in press*).

When interpreting our results, we note that there are additional unmeasured, yet important, factors which almost certainly shaped vigilance and foraging behaviors in this study. Group size has been shown to strongly affect vigilance behavior across diverse taxa (Caro 2005; Beauchamp 2008; Creel et al. 2014). However, we could not fully incorporate group size into our study design because we had no way to account for birds just out of camera view. Likewise, cover can affect foraging and vigilance (Caro 2005). Although we attempted to control for cover differences by choosing similar feeder locations, we could not control for small differences that could be meaningful to bird vigilance. Lastly, animals may exhibit differing degrees of behavioral coping mechanisms in noise because of variation at the individual level (Harding et al. 2019; Gomes and Goerlitz 2020). Individual birds in our study likely revisited the same feeder multiple times because of territoriality. However, the birds in our system were not marked, so we could not account for the influence of individual identity on behavior.

Natural noise is likely an underappreciated aspect of habitat quality. In a large-scale field experiment, we have shown that natural sounds can shape vigilance and foraging behavior in wild, free-ranging birds. Our results suggest that alterations in the foraging-vigilance trade-off in intense noise are not novel to anthropogenic noise, but have existed for millennia. Yet, this connection to evolved responses still leaves room for concern. In a world that is becoming increasingly noisy from the acoustic footprint of humankind, the evidence we present here strengthens the call for greater awareness and management of noise.

Figures

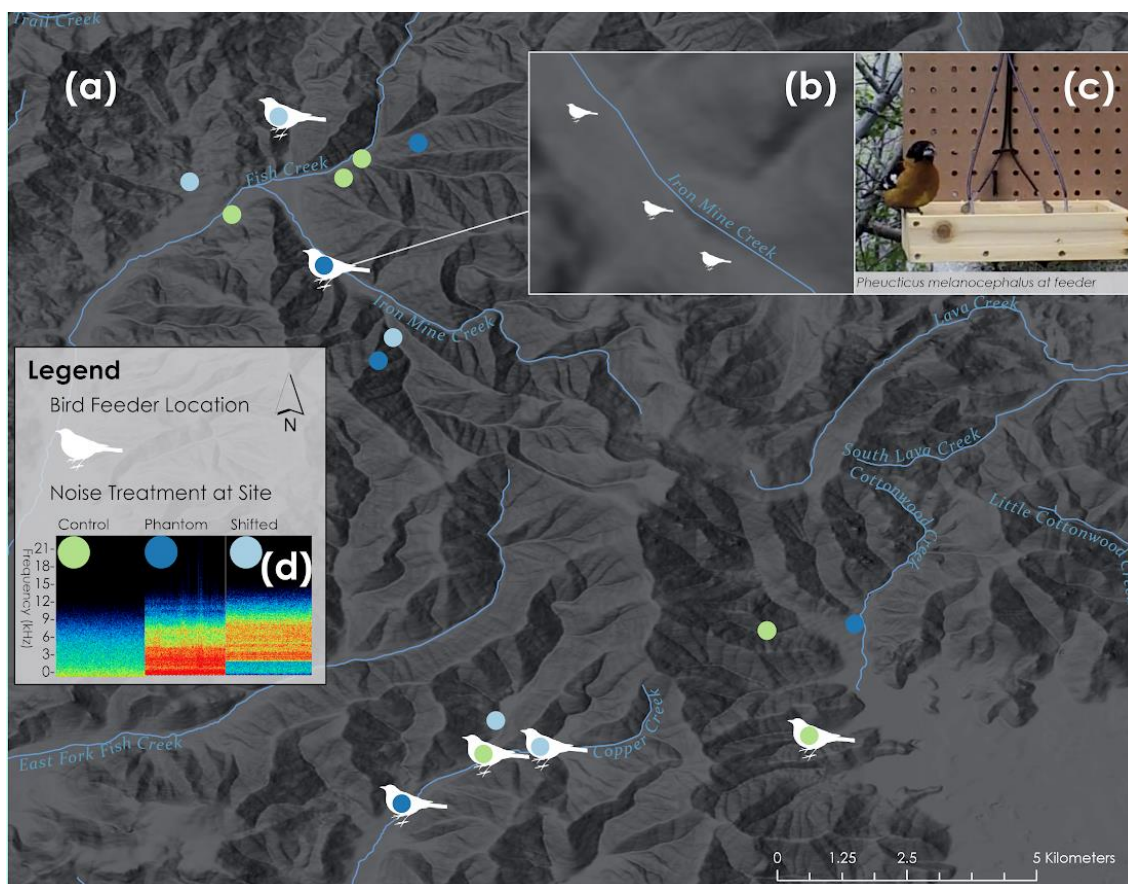


Figure 2.1 (a) Our study sites and feeder locations in the Pioneer Mountains, Idaho, USA. Circles indicate sites where point counts were performed, and the color of the circle indicates the treatment type. Bird symbols denote that we placed a suite of three bird feeders at this site. Not pictured are 4 sites that included forage point counting further north near Ketchum, Idaho. (b) The inset depicts the spacing of bird feeders typically found at a site. (c) The top right inset shows our tray style feeders, with an adult male grosbeak visiting. The left legend includes spectrograms of control, river, and shifted river treatments recorded at our sites.

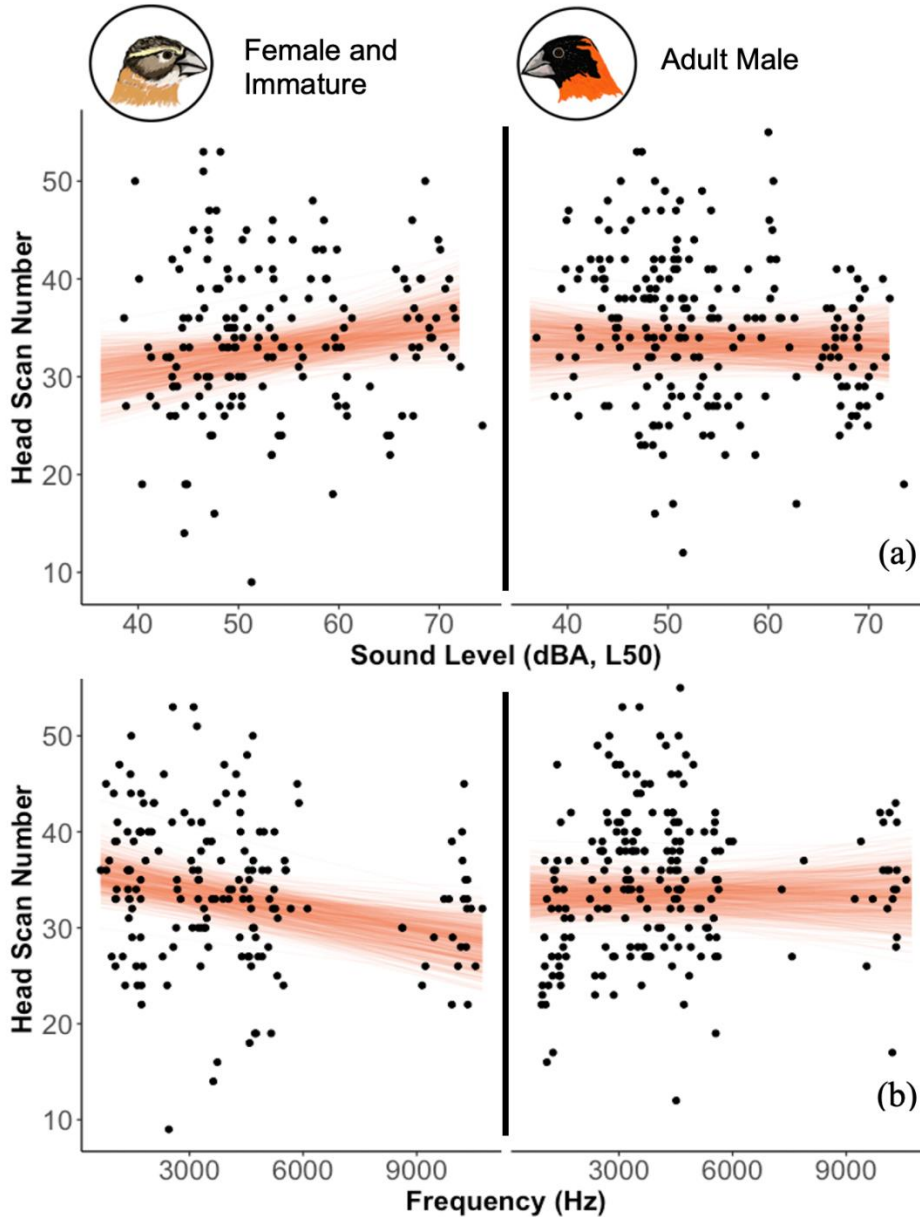


Figure 2.2 Behavior changes in grosbeaks were overall small and variable, and usually driven by immature and female birds. (a) Immature and female grosbeaks increase the number of head scans in higher sound levels. (b) They also increase scanning in lower frequencies. Adult males (right column) comparatively showed no behavioral change. To create these graphs 500 posterior draws are plotted in orange that show the relationship between the behavior and sound variable when all other variables (Julian date, hour, frequency or sound level) were held at their mean. Data points are plotted alongside the model in black ($n = 395$ foraging observations).

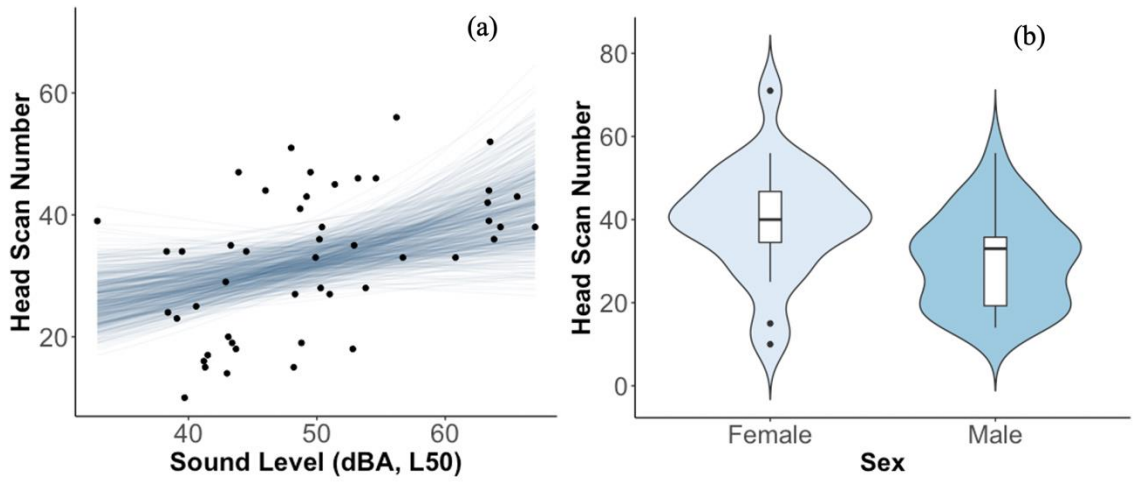


Figure 2.3 (a) Lazuli buntings showed increasing head scan numbers in higher sound levels (n = 48). (b) Males scanned less than females overall, indicating that they showed lower vigilance behavior (n = 52).

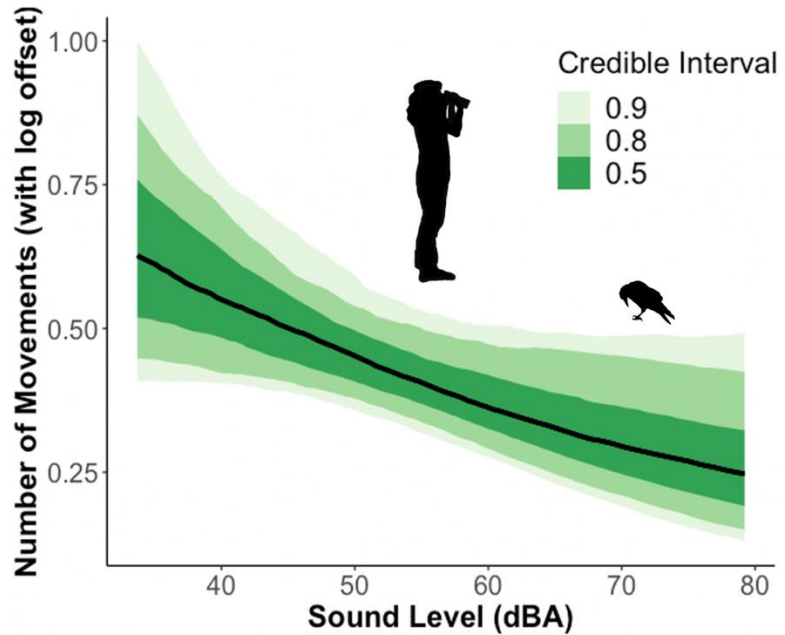


Figure 2.4 Movements decreased in opportunistic foraging videos as sound levels increased (n = 50).

CONCLUSION

In both our lab and field experiments, we find that natural noise can shape foraging and vigilance behavior. Specifically, high sound pressure levels increased antipredator behaviors in both studies. In wild birds, we found that the effects of frequency can be more species specific. While our wild bird data was inherently noisy, these results generally showed increases in vigilance in high sound levels. Given that bird abundances decreased in high sound levels within our same study system, the behavioral modifications we observed may not be sufficient for some bird species to cope and thus persist in noise.

Future Directions for Study

Our study provides valuable insight on the foraging vigilance trade-off in natural noise across multiple species. However, questions remain regarding how other variables interact with antipredator behavior in intense natural soundscapes, including seasonality, group size, and variation at the species, demographic, and personality level. Additionally, continued refinement and collection of larger *in situ* observational data sets are important because of their inherent ecological relevance. Finally, further research should address possible links between foraging in noise and fitness outcomes to understand the implications of the behavioral changes seen here.

Although our opportunistic foraging videos and foraging point count data sets suffered from small sample sizes, projects using this approach to research animal behavior are still important to pursue. Data sets which represent organisms interacting

with sensory stimuli in natural contexts are important for accurate inferences, since animals exist in a complex combination of sensory and environmental constraints at any given time (Dominoni et al. 2020). Although lab studies are indeed useful, their applicability can be inherently limited in this way. Despite the need for *in situ* studies, they can be incredibly laborious given the sample sizes likely needed for inference. Filming may be more productive in habitats with less obstructive vegetation in comparison to the riparian habitats studied here, or during winter seasons where food resources are less abundant and possibly more concentrated. Using a blind or ghillie suit may also have helped limit observer confounds and increase sample sizes.

Due to the variable and complex nature of wild animal behavior, controlling for additional biologically relevant factors will be beneficial to determining the relative importance of the foraging vigilance trade-off in noise. The models for our bird feeder data had somewhat poor fits as indicated by RMSE, which likely would have been improved by the inclusion of group size, better control of vegetation, and food density data. This could be accomplished by placing game cameras further from feeding stations, increasing field-of-view, and using a similar experimental design in areas with less dense vegetative cover compared to our riparian drainages. Food density could be controlled without compromising sample size by using a feeder style that continually dispensed seed as it was depleted, rather than our tray style feeders.

Additionally, individual animal personality, social status, and experience may play a role in shaping foraging and/or vigilance behavior (Harding et al. 2019; Eastcott et al. 2020; Gomes and Goerlitz 2020). Future lab studies could personality type birds prior to data collection in order to understand how personality interacts with risk perception

and mitigation in noise. Likewise, using individuals from populations with different levels of natural and anthropogenic noises experience (i.e., from an urban versus natural area) could clarify the role of experience in risk perception of noise. Completing a study similar to our birdfeeder research on a color-banded population of wild birds could account for resampling of the same individuals and provide data on the influence of personality or social status on vigilance behavior in noise. Birds equipped with tracking devices could determine how noise structures the spatial use of a habitat, and furthermore, how animal personalities may disperse across soundscapes.

In addition to individual level variation, research that continues to explore behavioral responses across different species and demographics is essential (Harding et al. 2019). Our research demonstrated that female and immature grosbeaks reacted differently to noise compared to adult males, and the sexes of buntings and goldfinches often had differing baseline vigilance behaviors in noise. Previous research on a variety of animals has demonstrated sex specific responses to risk (Winnie and Creel 2007; Naguib et al. 2013; Powolny et al. 2014). Likewise, each species may respond differently to noise given its unique vocalization range or foraging guild (Francis 2015; Petrelli et al. 2017). Additional lab experiments using an insectivorous species that must perform more difficult food localization and handling tasks in various noise treatments may show different results compared to our lab experiment, which used a ground forager consuming seed. A phylogenetically-controlled behavioral analysis across several species may be especially informative, perhaps using video collected by citizen scientists to make the necessary sample size for such an analysis feasible.

Even more broadly, we note that there are still outstanding questions concerning avian sensory systems that could affect the interpretation of our results. For example, audiograms (i.e., hearing thresholds across frequency) exist for relatively few bird species (Okanoya and Dooling 1987). In addition, some species have seasonally varying auditory processing abilities (Lucas et al. 2007), making this small number of audiograms possibly less reliable. Knowledge gaps also remain regarding how exactly birds utilize audition. For example, some studies suggest that birds other than owls may also use auditory cues to locate prey items (Floyd and Woodland 1981; Montgomerie and Weatherhead 1997; Onrust et al. 2017), although this concept is relatively unexplored. Both how birds perceive noise and what information they can glean from it are integral when considering how birds will respond to both anthropogenic and natural noise. In addition, the foraging vigilance tradeoff is built on the assumption that while an animal is foraging with its head down, it has reduced visual surveillance. However, some birds may be able to visually detect predators in the head down position (Fernández-Juricic et al. 2008). Again, relatively little is known regarding the field of view of different bird species, which may impact the foraging vigilance trade-off in noise.

Most importantly, further research that links foraging and vigilance behavior with potential downstream impacts is necessary. Pairing foraging and vigilance observations in noise with measures of reproduction, body condition, predation, and stress hormone levels could clarify the importance of behavioral changes. For example, do increases in vigilance adequately compensate for any increased likelihood of predation? In addressing these topics, further examining trophic cascades may be important. In one study western scrub jays (*Aphelocoma californica*), a nest predator, decreased in noise and thus reduced

nest predation in noisy locations (Francis et al. 2009). These trophic cascades further complicate the possible implications of vigilance and foraging changes in terms of fitness. Game cameras paired with nests across a marked animal population, paired with observations of foraging in noise, could be one way to connect behavior changes to larger scale effects in a wild system.

Concluding Remarks

Our research demonstrates that natural noise can influence foraging and vigilance behaviors. This implies that behavior changes seen in anthropogenic noises are not novel responses, but likely evolved long ago. Our results suggest that the natural soundscape can be an important habitat axis. For example, noisy natural areas may not be a suitable habitat for some bird species, because of perceived risk while foraging. Although further studies are needed to understand the possible implications of the behavior changes seen in this research, these results are potentially concerning. The footprint of anthropogenic noise continues to increase at unprecedented rates (Buxton et al. 2017), making quiet habitats increasingly rare. Bird populations are already at peril from a slew of other environmental degradations (Rosenberg et al. 2019), increasing sound pressure levels from noise may further exacerbate existing anthropogenic pressures.

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APPENDIX

Table A.1 Bird feeder model summaries by behavior and species with credible intervals shown at 90 and 80 percent. ESS refers to effective sample size of the parameter.

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
Black-headed grosbeak	Down	(Intercept)	2.45	0.03	[2.39, 2.50]	[2.41, 2.49]	2404
Black-headed grosbeak	Down	Median Frequency	0.02	0.06	[-0.07, 0.11]	[-0.05, 0.09]	3244
Black-headed grosbeak	Down	Sound Pressure Level	-0.07	0.06	[-0.16, 0.03]	[-0.14, 0.01]	2468
Black-headed grosbeak	Down	Hour	-0.07	0.04	[-0.14, 0.00]	[-0.12, -0.01]	5727
Black-headed grosbeak	Down	Date	0.04	0.06	[-0.05, 0.12]	[-0.03, 0.10]	4104
Black-headed grosbeak	Down	Frequency SPL Interaction	0.07	0.11	[-0.12, 0.25]	[-0.07, 0.21]	4907
Black-headed grosbeak	Down:Sex	(Intercept)	2.41	0.04	[2.34, 2.47]	[2.36, 2.46]	3706
Black-headed grosbeak	Down:Sex	Median Frequency	0.10	0.07	[-0.02, 0.22]	[0.01, 0.19]	2350

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
Black-headed grosbeak	Down:Sex	Sound Pressure Level	-0.09	0.08	[-0.22, 0.03]	[-0.19, 0.00]	2764
Black-headed grosbeak	Down:Sex	Sex	0.07	0.04	[0.00, 0.14]	[0.01, 0.12]	6665
Black-headed grosbeak	Down:Sex	Hour	-0.07	0.04	[-0.14, 0.01]	[-0.12, -0.01]	5502
Black-headed grosbeak	Down:Sex	Date	0.04	0.05	[-0.05, 0.13]	[-0.03, 0.11]	3772
Black-headed grosbeak	Down:Sex	Frequency SPL Interaction	0.07	0.11	[-0.12, 0.26]	[-0.07, 0.21]	4255
Black-headed grosbeak	Down:Sex	Frequency Sex Interaction	-0.18	0.09	[-0.32, -0.03]	[-0.29, -0.06]	3181
Black-headed grosbeak	Down:Sex	SPL Sex Interactions	0.06	0.09	[-0.08, 0.20]	[-0.05, 0.17]	3585
Black-headed grosbeak	Scans	(Intercept)	3.51	0.04	[3.45, 3.57]	[3.46, 3.55]	780
Black-headed grosbeak	Scans	Median Frequency	-0.07	0.03	[-0.12, -0.02]	[-0.11, -0.03]	2104
Black-headed grosbeak	Scans	Sound Pressure Level	0.05	0.04	[-0.02, 0.12]	[-0.01, 0.10]	1874

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
Black-headed grosbeak	Scans	Hour	-0.03	0.02	[-0.06, 0.00]	[-0.05, -0.01]	6321
Black-headed grosbeak	Scans	Date	0.05	0.03	[0.01, 0.09]	[0.02, 0.08]	2508
Black-headed grosbeak	Scans	Frequency SPL Interaction	0.05	0.06	[-0.05, 0.15]	[-0.02, 0.13]	2991
Black-headed grosbeak	Scans:Sex	(Intercept)	3.49	0.04	[3.43, 3.55]	[3.45, 3.54]	906
Black-headed grosbeak	Scans:Sex	Median Frequency	-0.12	0.04	[-0.18, -0.06]	[-0.17, -0.07]	2299
Black-headed grosbeak	Scans:Sex	Sound Pressure Level	0.09	0.04	[0.02, 0.16]	[0.03, 0.14]	1956
Black-headed grosbeak	Scans:Sex	Sex	0.02	0.02	[-0.01, 0.04]	[-0.01, 0.04]	6189
Black-headed grosbeak	Scans:Sex	Hour	-0.03	0.02	[-0.06, 0.00]	[-0.05, -0.01]	6172
Black-headed grosbeak	Scans:Sex	Date	0.04	0.03	[0.00, 0.08]	[0.01, 0.07]	3575
Black-headed grosbeak	Scans:Sex	Frequency SPL Interaction	0.02	0.06	[-0.08, 0.12]	[-0.06, 0.10]	2880

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
Black-headed grosbeak	Scans:Sex	Frequency Sex Interaction	0.12	0.04	[0.05, 0.18]	[0.07, 0.16]	3396
Black-headed grosbeak	Scans:Sex	SPL Sex Interactions	-0.10	0.04	[-0.16, -0.04]	[-0.14, -0.05]	3801
Black-headed grosbeak	Head Up	(Intercept)	1.50	0.05	[1.40, 1.58]	[1.43, 1.56]	1648
Black-headed grosbeak	Head Up	Median Frequency	0.05	0.09	[-0.11, 0.20]	[-0.06, 0.17]	1915
Black-headed grosbeak	Head Up	Sound Pressure Level	0.14	0.09	[0.01, 0.29]	[0.04, 0.25]	2236
Black-headed grosbeak	Head Up	Hour	0.04	0.06	[-0.06, 0.14]	[-0.04, 0.12]	5190
Black-headed grosbeak	Head Up	Date	-0.12	0.08	[-0.25, 0.02]	[-0.22, -0.01]	2417
Black-headed grosbeak	Head Up	Frequency SPL Interaction	0.22	0.16	[-0.05, 0.49]	[0.02, 0.43]	3651
Black-headed grosbeak	Head Up	(phi)	16.02	1.12	[14.23, 17.90]	[14.62, 17.46]	5043

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
Black-headed grosbeak	Head Up:Sex	(Intercept)	1.46	0.06	[1.36, 1.55]	[1.39, 1.53]	3230
Black-headed grosbeak	Head Up:Sex	Median Frequency	0.07	0.11	[-0.11, 0.25]	[-0.07, 0.20]	2529
Black-headed grosbeak	Head Up:Sex	Sound Pressure Level	0.20	0.12	[0.02, 0.40]	[0.06, 0.35]	3042
Black-headed grosbeak	Head Up:Sex	Sex	0.07	0.06	[-0.04, 0.17]	[-0.02, 0.14]	5207
Black-headed grosbeak	Head Up:Sex	Hour	0.04	0.06	[-0.06, 0.15]	[-0.04, 0.12]	6538
Black-headed grosbeak	Head Up:Sex	Date	-0.12	0.08	[-0.25, 0.02]	[-0.22, -0.01]	3101
Black-headed grosbeak	Head Up:Sex	Frequency SPL Interaction	0.21	0.17	[-0.06, 0.50]	[0.00, 0.43]	4493
Black-headed grosbeak	Head Up:Sex	Frequency Sex Interaction	-0.01	0.13	[-0.23, 0.20]	[-0.18, 0.16]	4719
Black-headed grosbeak	Head Up:Sex	SPL Sex Interactions	-0.11	0.13	[-0.32, 0.10]	[-0.28, 0.06]	4421
Black-headed grosbeak	Head Up:Sex	(phi)	16.00	1.15	[14.17, 17.89]	[14.57, 17.48]	5106

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
Black-headed grosbeak	Mean Time Down	(Intercept)	-0.75	0.06	[-0.85, - 0.64]	[-0.83, -0.67]	1039
Black-headed grosbeak	Mean Time Down	Median Frequency	0.03	0.08	[-0.09, 0.16]	[-0.06, 0.13]	1437
Black-headed grosbeak	Mean Time Down	Sound Pressure Level	-0.17	0.09	[-0.32, - 0.03]	[-0.29, -0.06]	1328
Black-headed grosbeak	Mean Time Down	Hour	0.05	0.04	[-0.01, 0.11]	[0.00, 0.10]	4628
Black-headed grosbeak	Mean Time Down	Date	-0.04	0.06	[-0.13, 0.06]	[-0.11, 0.04]	1994
Black-headed grosbeak	Mean Time Down	Frequency SPL Interaction	-0.16	0.13	[-0.37, 0.05]	[-0.33, 0.00]	2117
Black-headed grosbeak	Mean Time Down:Sex	(Intercept)	-0.71	0.07	[-0.81, - 0.59]	[-0.79, -0.62]	1227
Black-headed grosbeak	Mean Time Down:Sex	Median Frequency	-0.03	0.08	[-0.16, 0.11]	[-0.14, 0.08]	1303
Black-headed grosbeak	Mean Time Down:Sex	Sound Pressure Level	-0.19	0.10	[-0.36, - 0.03]	[-0.32, -0.06]	1639

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
Black-headed grosbeak	Mean Time						
	Down:Sex	Sex	-0.09	0.04	[-0.16, -0.02]	[-0.14, -0.04]	5519
Black-headed grosbeak	Mean Time						
	Down:Sex	Hour	0.04	0.04	[-0.02, 0.11]	[-0.01, 0.09]	5611
Black-headed grosbeak	Mean Time						
	Down:Sex	Date	-0.04	0.06	[-0.14, 0.05]	[-0.12, 0.03]	1961
Black-headed grosbeak	Mean Time	Frequency SPL					
	Down:Sex	Interaction	-0.15	0.13	[-0.36, 0.06]	[-0.31, 0.01]	2204
Black-headed grosbeak	Mean Time						
	Down:Sex	Frequency Sex Interaction	0.14	0.08	[0.01, 0.27]	[0.04, 0.24]	4419
Black-headed grosbeak	Mean Time						
	Down:Sex	SPL Sex Interactions	0.01	0.08	[-0.12, 0.14]	[-0.09, 0.11]	4587
American goldfinch	Down	(Intercept)	2.67	0.05	[2.59, 2.76]	[2.61, 2.74]	2695
American goldfinch	Down	Median Frequency	0.05	0.10	[-0.11, 0.23]	[-0.08, 0.18]	3317
American goldfinch	Down	Sound Pressure Level	-0.12	0.10	[-0.29, 0.04]	[-0.25, 0.00]	3102

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
American goldfinch	Down	Hour	-0.11	0.09	[-0.25, 0.04]	[-0.22, 0.00]	4309
American goldfinch	Down	Date	0.05	0.10	[-0.12, 0.22]	[-0.08, 0.18]	3619
American goldfinch	Down	Frequency SPL Interaction	0.02	0.19	[-0.29, 0.32]	[-0.22, 0.25]	4760
American goldfinch	Down:Sex	(Intercept)	2.52	0.08	[2.39, 2.65]	[2.42, 2.62]	3133
American goldfinch	Down:Sex	Median Frequency	0.01	0.10	[-0.15, 0.18]	[-0.11, 0.14]	3815
American goldfinch	Down:Sex	Sound Pressure Level	-0.21	0.16	[-0.47, 0.05]	[-0.41, -0.01]	2816
American goldfinch	Down:Sex	Sex	0.23	0.09	[0.08, 0.38]	[0.11, 0.34]	4433
American goldfinch	Down:Sex	Hour	-0.06	0.09	[-0.21, 0.08]	[-0.17, 0.05]	5013
American goldfinch	Down:Sex	Date	0.03	0.10	[-0.13, 0.21]	[-0.10, 0.16]	3194

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
American goldfinch	Down:Sex	Frequency SPL Interaction	0.01	0.18	[-0.30, 0.30]	[-0.22, 0.24]	4926
American goldfinch	Down:Sex	SPL Sex Interactions	0.16	0.18	[-0.13, 0.45]	[-0.07, 0.39]	3528
American goldfinch	Scans	(Intercept)	3.57	0.12	[3.38, 3.74]	[3.43, 3.70]	1207
American goldfinch	Scans	Median Frequency	0.11	0.09	[-0.03, 0.25]	[0.00, 0.22]	2973
American goldfinch	Scans	Sound Pressure Level	0.03	0.15	[-0.21, 0.27]	[-0.16, 0.21]	2376
American goldfinch	Scans	Date	-0.22	0.09	[-0.37, -0.06]	[-0.34, -0.10]	2741
American goldfinch	Scans	Hour	-0.05	0.07	[-0.16, 0.07]	[-0.13, 0.04]	4340
American goldfinch	Scans	Frequency SPL Interaction	0.07	0.14	[-0.17, 0.31]	[-0.12, 0.26]	3473
American goldfinch	Scans:Sex	(Intercept)	3.62	0.13	[3.41, 3.82]	[3.46, 3.77]	1464

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
American goldfinch	Scans:Sex	Median Frequency	0.13	0.10	[-0.02, 0.29]	[0.01, 0.25]	2872
American goldfinch	Scans:Sex	Sound Pressure Level	-0.01	0.18	[-0.29, 0.28]	[-0.23, 0.21]	2111
American goldfinch	Scans:Sex	Sex	-0.08	0.08	[-0.21, 0.05]	[-0.18, 0.02]	3777
American goldfinch	Scans:Sex	Hour	-0.05	0.07	[-0.16, 0.07]	[-0.14, 0.04]	3961
American goldfinch	Scans:Sex	Date	-0.21	0.10	[-0.36, -0.05]	[-0.33, -0.09]	2979
American goldfinch	Scans:Sex	Frequency SPL Interaction	0.05	0.15	[-0.19, 0.29]	[-0.14, 0.24]	3533
American goldfinch	Scans:Sex	SPL Sex Interactions	0.06	0.14	[-0.16, 0.28]	[-0.11, 0.23]	3713
American goldfinch	Head Up	(Intercept)	1.14	0.09	[1.00, 1.27]	[1.04, 1.24]	1947
American goldfinch	Head Up	Median Frequency	0.02	0.14	[-0.21, 0.25]	[-0.16, 0.20]	2826

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
American goldfinch	Head Up	Sound Pressure Level	0.08	0.16	[-0.15, 0.35]	[-0.10, 0.27]	2340
American goldfinch	Head Up	Date	-0.23	0.15	[-0.47, 0.01]	[-0.42, -0.04]	2779
American goldfinch	Head Up	Hour	0.11	0.12	[-0.08, 0.31]	[-0.04, 0.26]	3633
American goldfinch	Head Up	Frequency SPL Interaction	0.08	0.24	[-0.31, 0.48]	[-0.22, 0.38]	3504
American goldfinch	Head Up	(phi)	14.29	1.90	[11.33, 17.58]	[11.89, 16.77]	3681
American goldfinch	Head Up:Sex	(Intercept)	1.32	0.13	[1.11, 1.52]	[1.16, 1.47]	2292
American goldfinch	Head Up:Sex	Median Frequency	0.08	0.15	[-0.17, 0.32]	[-0.11, 0.26]	2982
American goldfinch	Head Up:Sex	Sound Pressure Level	-0.03	0.23	[-0.39, 0.36]	[-0.31, 0.27]	2271

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
American goldfinch	Head Up:Sex	Sex	-0.26	0.13	[-0.47, -0.06]	[-0.42, -0.10]	4300
American goldfinch	Head Up:Sex	Date	-0.21	0.15	[-0.45, 0.03]	[-0.40, -0.02]	3197
American goldfinch	Head Up:Sex	Hour	0.09	0.13	[-0.11, 0.29]	[-0.07, 0.25]	3721
American goldfinch	Head Up:Sex	Frequency SPL Interaction	0.02	0.25	[-0.37, 0.43]	[-0.29, 0.33]	5071
American goldfinch	Head Up:Sex	SPL Sex Interactions	0.17	0.25	[-0.23, 0.58]	[-0.14, 0.49]	3447
American goldfinch	Head Up:Sex	(phi)	14.76	1.98	[11.74, 18.22]	[12.29, 17.29]	4815
American goldfinch	Mean Time Down	(Intercept)	-0.70	0.03	[-0.75, -0.65]	[-0.74, -0.67]	1685
American goldfinch	Mean Time Down	Sound Pressure Level	0.04	0.06	[-0.06, 0.12]	[-0.03, 0.11]	2514

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
American goldfinch	Mean Time Down	Median Frequency	-0.09	0.05	[-0.18, -0.01]	[-0.16, -0.03]	2870
American goldfinch	Mean Time Down	Date	0.16	0.05	[0.07, 0.25]	[0.09, 0.23]	2620
American goldfinch	Mean Time Down	Hour	0.01	0.04	[-0.06, 0.08]	[-0.04, 0.06]	3907
American goldfinch	Mean Time Down	Frequency SPL Interaction	-0.04	0.09	[-0.18, 0.10]	[-0.15, 0.08]	3812
American goldfinch	Mean Time Down:Sex	(Intercept)	-0.69	0.04	[-0.76, -0.63]	[-0.75, -0.64]	2728
American goldfinch	Mean Time Down:Sex	Median Frequency	-0.08	0.05	[-0.16, 0.00]	[-0.14, -0.02]	3092
American goldfinch	Mean Time Down:Sex	Sound Pressure Level	0.23	0.07	[0.11, 0.35]	[0.14, 0.33]	2434
American goldfinch	Mean Time Down:Sex	Sex	-0.02	0.04	[-0.09, 0.05]	[-0.07, 0.03]	4474
American goldfinch	Mean Time Down:Sex	Date	0.13	0.05	[0.05, 0.22]	[0.07, 0.20]	2551
American goldfinch	Mean Time Down:Sex	Hour	-0.02	0.04	[-0.09, 0.05]	[-0.08, 0.03]	3453

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
American goldfinch	Mean Time Down:Sex	Frequency SPL Interaction	0.03	0.09	[-0.12, 0.17]	[-0.08, 0.14]	3538
American goldfinch	Mean Time Down:Sex	SPL Sex Interactions	-0.32	0.08	[-0.46, - 0.18]	[-0.43, -0.22]	2765
Lazuli bunting	Down	(Intercept)	2.97	0.08	[2.84, 3.11]	[2.87, 3.08]	3300
Lazuli bunting	Down	Median Frequency	0.08	0.24	[-0.32, 0.47]	[-0.22, 0.39]	1748
Lazuli bunting	Down	Sound Pressure Level	-0.05	0.18	[-0.35, 0.23]	[-0.28, 0.17]	3241
Lazuli bunting	Down	Hour	-0.22	0.17	[-0.49, 0.06]	[-0.43, 0.00]	2489
Lazuli bunting	Down	Date	0.26	0.25	[-0.14, 0.68]	[-0.04, 0.58]	1794
Lazuli bunting	Down	Frequency SPL Interaction	0.25	0.41	[-0.43, 0.94]	[-0.28, 0.78]	2704
Lazuli bunting	Scans	(Intercept)	3.49	0.07	[3.38, 3.60]	[3.40, 3.57]	3325
Lazuli bunting	Scans	Median Frequency	-0.25	0.20	[-0.56, 0.08]	[-0.49, 0.00]	2227
Lazuli bunting	Scans	Sound Pressure Level	0.23	0.13	[0.02, 0.46]	[0.06, 0.40]	3256
Lazuli bunting	Scans	Hour	0.09	0.14	[-0.14, 0.32]	[-0.09, 0.27]	2731
Lazuli bunting	Scans	Date	-0.05	0.18	[-0.33, 0.24]	[-0.27, 0.18]	2396

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
Lazuli bunting	Scans	Frequency SPL Interaction	0.15	0.30	[-0.35, 0.62]	[-0.23, 0.53]	3178
Lazuli bunting	Head Up	(Intercept)	0.98	0.12	[0.78, 1.18]	[0.83, 1.13]	3009
Lazuli bunting	Head Up	Median Frequency	-0.18	0.32	[-0.71, 0.33]	[-0.60, 0.21]	2330
Lazuli bunting	Head Up	Sound Pressure Level	0.19	0.23	[-0.20, 0.57]	[-0.10, 0.48]	3086
Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
Lazuli bunting	Head Up	Date	-0.32	0.28	[-0.76, 0.15]	[-0.68, 0.04]	2677
Lazuli bunting	Head Up	Hour	0.27	0.24	[-0.12, 0.65]	[-0.03, 0.57]	2674
Lazuli bunting	Head Up	Frequency SPL Interaction	0.00	0.53	[-0.87, 0.86]	[-0.65, 0.66]	2866
Lazuli bunting	Head Up	(phi)	9.00	1.80	[6.29, 12.13]	[6.79, 11.36]	2759
Lazuli bunting	Mean Time Down	(Intercept)	-0.91	0.07	[-1.01, - 0.80]	[-0.99, -0.82]	3458
Lazuli bunting	Mean Time Down	Median Frequency	-0.06	0.17	[-0.36, 0.22]	[-0.28, 0.16]	2656
Lazuli bunting	Mean Time Down	Sound Pressure Level	-0.16	0.13	[-0.37, 0.04]	[-0.32, 0.00]	3159

Species	Model	Parameter	Mean	SD	CI 90%	CI 80%	ESS
Lazuli bunting	Mean Time	Hour	0.00	0.13	[-0.20, 0.21]	[-0.16, 0.17]	3103
	Down						
Lazuli bunting	Mean Time	Date	0.06	0.16	[-0.21, 0.33]	[-0.15, 0.27]	2687
	Down						
Lazuli bunting	Mean Time	Frequency SPL	-0.30	0.30	[-0.80, 0.21]	[-0.68, 0.08]	3386
	Down	Interaction					

Table A.2 Model summary of foraging point counts.

Foraging Point Count						
	Me	S	CI	CI	ES	
an		D	90%	80%		S
(Intercept)	-	0.	[-	0.48, -	[-	20
	0.26	17	0.55, 0.00]	0.05]		95
LEQ	-	0.	[-	[-		23
Median	0.24	34	0.81, 0.31]	0.68, 0.19]		24
Frequency	0.07	30	0.43, 0.55]	0.31, 0.44]		53
Hour	-	0.	[-	[-		37
	0.03	23	0.42, 0.35]	0.33, 0.27]		28
Julian Date	0.18	22	0.19, 0.54]	0.11, 0.46]		00
LEQ:Freque	-	0.	[-	[-		23
ncy	0.49	56	1.40, 0.43]	1.20, 0.22]		02

Table A.3 Model summary for proportion of time spent with head down in opportunistic videos.

Proportion of Head Down						
	Me	S	CI	CI	E	
an		D	90%	80%		SS
(Intercept)	-	0.	[-	[-		22
	0.99	27	1.41, -0.55]	1.30, -0.67]		21
LEQ	0.1	0.	[-	[-		34
Distance	5	42	0.52, 0.83]	0.37, 0.67]		93
to Observer	0.1	0.	[-	[-		35
Group	9	42	0.52, 0.84]	0.34, 0.71]		46
Size	-	0.	[-	[-		36
Perch	0.10	38	0.72, 0.51]	0.55, 0.37]		06
Height	0.6	0.	[-	[0.06		33
	0	42	0.11, 1.27]	, 1.12]		03
(phi)	5.3	1.	[3.26	[3.64		31
	3	45	, 8.04]	, 7.21]		89

Table A.4 Model summary for visual head scans in opportunistic videos.

Visual Scans						
	Me	S	CI	CI	E	
an		D	90%	80%		SS
(Intercept)	0.0	0.	[-	[-		10
	7	13	0.16, 0.26]	0.10, 0.23]		11
LEQ	0.0	0.	[-	[-		32
Distance	0	14	0.24, 0.23]	0.19, 0.18]		15
to Observer	-	0.	[-	[-		14
	0.22	18	0.51, 0.06]	0.45, 0.01]		36
Group	0.0	0.	[-	[-		41
Size	0	12	0.21, 0.20]	0.16, 0.15]		03
Perch	0.1	0.	[-	[-		32
Height	6	18	0.13, 0.45]	0.06, 0.38]		45

Table A.5 Model summary for movement number in opportunistic videos.

Movement Number						
	Me	S	CI	CI	E	
an		D	90%	80%		SS
(Intercept)	-	0.	[-	[-		28
	0.83	14	1.07, -0.60]	1.01, -0.66]		49
LEQ	-	0.	[-	[-		41
Distance	0.35	23	0.73, 0.03]	0.65, -0.06]		11
to Observer	-	0.	[-	[-		37
	0.43	24	0.83, -0.04]	0.73, -0.13]		12
Group	0.0	0.	[-	[-		43
Size	5	21	0.28, 0.40]	0.21, 0.32]		90
Perch	0.0	0.	[-	[-		39
Height	0	25	0.41, 0.42]	0.32, 0.32]		74

Table A.6 Model summary for proportion of time spent moving in opportunistic videos.

Proportion of Time Moving						
	Me	S	CI	CI	E	
an		D	90%	80%		SS
	-	0.	[-	[-		21
(Intercept)	1.76	25	2.17, -1.37]	2.07, -1.47]		11
	-	0.	[-	[-		40
LEQ	0.36	30	0.84, 0.12]	0.75, 0.01]		15
Distance	0.1	0.	[-	[-		30
to Observer	8	32	0.36, 0.70]	0.23, 0.58]		27
Group	0.1	0.	[-	[-		37
Size	8	29	0.30, 0.63]	0.18, 0.54]		73
Perch	-	0.	[-	[-		31
Height	0.54	36	1.16, 0.02]	1.01, -0.09]		28
	7.7	2.	[4.59	[5.11		13
(phi)	7	25	, 11.82]	, 10.87]		20

Table A.7 Bird feeder model RMSEs and means for each behavior

Species	Model Behavior	R MSE	R Mean	Behavior
Black-headed grosbeak	Down	.37	11.69	
Black-headed grosbeak	Down : Sex	.32	11.69	
Black-headed grosbeak	Scans	.89	34.54	
Black-headed grosbeak	Scans: Sex	.77	34.54	
Black-headed grosbeak	Head Up	.09	0.82	
Black-headed grosbeak	Head Up: Sex	.09	0.82	
Black-headed grosbeak	Mean Time Down	.37	0.48	
Black-headed grosbeak	Mean Time	.37	0.48	
American goldfinch	Down: Sex	.02	14.45	
American goldfinch	Down	.76	14.45	
American goldfinch	Scans	.78	35.90	
American goldfinch	Scans: Sex	.75	35.90	
American goldfinch	Head Up	.09	0.76	
American goldfinch	Head Up: Sex	.09	0.76	
American goldfinch	Mean Time Down	.20	0.50	
American goldfinch	Mean Time	.19	0.50	
Lazuli bunting	Down: Sex	.05	19.13	
Lazuli bunting	Down	.27	32.79	
Lazuli bunting	Scans	.10	0.73	
Lazuli bunting	Head Up	.35	0.44	
Lazuli bunting	Mean Time Down			