

**Anthropogenic noise and noise-adjusted signals influence
territorial-defense behaviors of male Baird's sparrows (*Centronyx bairdii*)**

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ABSTRACT

Anthropogenic noise can constrain the acoustic communication of wildlife species through acoustic masking. However, many species display noise-adjusted signals which are theorized to provide release from acoustic masking. Yet, noise-adjusted signals may alter how receivers perceive and respond to signalers or fail to improve acoustic detection under noisy conditions. Thus, noise and noise-adjusted signals could have consequences for species that rely on acoustic communication for breeding. Baird's sparrow (*Centronyx bairdii*) is a grassland bird species that displays noise-adjusted songs. To investigate the potential impacts of noise and noise-adjusted songs on the intrasexual behavior of this species, I conducted repeated measures playback studies ($n = 69$ dyads) on free-living male Baird's sparrows. My research took place in the mixed-grass prairies of Southern Alberta during the species breeding season (May to July 2018 and 2019). To simulate territory intrusions in 'noisy' and 'quiet' conditions, I used a playback design to broadcast unadjusted and noise-adjusted Baird's sparrow song and oil-well drilling noise to individual male birds. To determine if song or noise treatment influenced male behavior, I compared the number of songs, calls, flybys over the experimental speaker, and song latency for each trial type. Focal male song latency was longer for unadjusted songs broadcast with noise versus without noise, suggesting that noise constrained acoustic detection. However, song latency for noise-adjusted songs broadcast with noise was similar to unadjusted songs broadcast in quiet conditions, suggesting that noise-adjusted songs are easier to detect acoustically in noise. I concluded that noise-adjusted songs partially restore acoustic communication in noisy conditions. The remaining focal male responses did not differ significantly by song treatment, suggesting that the song types are functionally equivalent. However, responses differed significantly between noise treatments. Focal males sang fewer songs whilst increasing alarm call vocalizations and engaged in more flybys under noisy conditions. These results suggest that noise heightens aggression in individuals or that males use different strategies to determine the location and fighting ability of rivals in the presence of noise. While it is uncertain what mechanism(s) underly these behavioral changes, I concluded that anthropogenic noise acts as a disturbance to this species.

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DEDICATION

I dedicate my thesis to my father (Pep). Without his love, guidance, and unwavering support, my life's trajectory may have been very different. I'm glad he talked me out of pursuing a career in mortuary science.

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CHAPTER 1: BACKGROUND OF CONSERVATION BEHAVIOR

The field of conservation behavior represents the synergistic union of the fields of animal behavior and conservation biology; conservation behavior recognizes and promotes the application of knowledge pertaining to animal behavior as a valuable tool in addressing conservation issues (Blumstein and Fernández-Juricic 2004, Berger-Tal et al. 2011). While wildlife managers have long used basic behavioral knowledge to steer management decisions (Sutherland 1998), effort to unite the fields of animal behavior and conservation biology has mainly occurred over the past three decades (Clemmons and Buchholz 1997, Festa-Bianchet and Apollonio 2003, Buchholz 2007, Berger-Tal et al. 2011). This delay is thought to be a result of the two disciplines' disparate research focuses and objectives (Linklater 2004, Angeloni et al. 2008). For instance, behaviorists and conservation biologists tend to use different biological scales in research; behavioral ecologists often conduct research at the individual scale, whereas conservation biologists typically do research at larger biological scales (e.g., population, community) (Sutherland 1998, Gosling and Sutherland 2000). Furthermore, the field of animal behavior tends to emphasize the development of evolutionary theories, while conservation biology tends to have a more pragmatic and applied focus (Sutherland 1998, Blumstein and Fernández-Juricic 2004). Given these dissimilarities, it is perhaps no surprise that some have questioned the practical contribution of animal behavior to conservation biology (Caro 2007).

However, conservation biology stands to benefit from the inclusion of the knowledge of the principals governing animal behavior, particularly by integrating such knowledge into management plans or decisions (Berger-Tal et al. 2011). Specifically, knowledge of behavior can be manipulated to improve conservation outcomes (Swaisgood et al. 2003, Madliger 2012, Shier 2016). For example, conspecific decoys and playbacks of conspecific vocalizations have been used in tandem with other conservation actions to successfully re-establish once extirpated breeding colonies of Atlantic puffins (*Fratercula arctica*) and Arctic terns, (*Sterna paradisaea*) in the Gulf of Maine (Kress 1983, Kress and Nettleship 1988). This strategy was used because the above species display "conspecific attraction," whereby individuals make settlement decisions based on the presence of conspecifics cues (Ward and Schlossberg 2004, Nocera et al. 2006).

Behavioral indicators associated with wildlife can also be used to evaluate the effectiveness of current conservation actions (Berger-Tal et al. 2011, Berger-Tal and Saltz 2016). In a broader context, there is a call for the field of conservation to embrace a more evidence-based approach by chronicling the outcomes of current management practice (Pullin et al. 2004, Sutherland et al. 2004). This action would facilitate future management and decision making and learning through an iterative process (Pullin et al. 2004, Sutherland et al. 2004). To illustrate the above point, wildlife corridors are a widely used conservation tool aimed at improving functional connectivity in fragmented habitats (Chetkiewicz et al. 2006, LaPoint et al. 2013). Yet, wildlife corridors often lack evidence-based support that demonstrate their efficacy (Dunning et al. 1992, Davies and Pullin 2007). The extent to which species use or avoid wildlife corridors may be influenced by a variety of factors such as the composition (e.g., width or vegetation) of the corridor (Haddad 1999, Hilty and Merenlender 2004, Brodie et al. 2015). Therefore, the use of behavioral indicators, like animal movement data between habitat patches connected by wildlife corridors, can help shed light on the efficacy of a wildlife corridor to improve functional connectivity (Wikelski et al. 2007, LaPoint et al. 2013).

Behavioral indicators can also be used to identify anthropogenic disturbances to populations or species (Berger-Tal et al. 2011). When populations are faced with rapid environmental change, they may respond by dispersing away from the disturbance, or adjusting to the altered environment through behavioral flexibility (Sih 2013, Wong and Candolin 2015). Over the past decade, considerable research attention has focused on the prevalence of anthropogenic noise in aquatic and terrestrial habitats (Barber et al. 2010, Francis and Barber 2013, Williams et al. 2015, Higgs and Mickle 2018). Examining behavioral indicators, like species avoidance of habitats experiencing high anthropogenic noise conditions, has helped researchers characterize anthropogenic noise as a disturbance for a myriad of wildlife species across various taxa (Rheindt 2003, Tyack et al. 2011, Vargas-Salinas, Fernando Cunningham et al. 2014, Kleist et al. 2017, Injaian et al. 2018, Raboin and Elias 2019).

Other behavioral indicators, namely adjustments to acoustic-signaling behavior, are prevalent in species remaining in habitats experiencing anthropogenic noise (reviewed in Shannon et al. 2016b). A large portion of this research has focused specifically on avian species (reviewed in Roca et al. 2016). Signal adjustments such as increased amplitude or increased minimum frequency are thought to occur because these theoretically improve acoustic

communication in noisy conditions (reviewed in Shannon et al. 2016b, but see Ríos-Chelén et al. 2017). Briefly, noise can constrain acoustic communication through a variety of mechanisms, such as acoustic masking (Brumm and Slabbekoorn 2005). Acoustic masking occurs when vocalizations and ambient noise overlap in frequency, or when the amplitude of ambient noise is higher than that of the vocalization (Brenowitz 1982, Dooling and Blumenrath 2013). When acoustic masking by noise occurs, it may be difficult or impossible for receivers to detect or discriminate between acoustic signals (Lohr et al. 2003).

Research efforts exploring the impacts of anthropogenic noise on acoustic communication have disproportionately focused on signalers (reviewed in Shannon et al. 2016b). This is concerning as noise-adjusted signals may fail to restore acoustic detection in the presence of noise (Templeton et al. 2016). Alternatively, noise-adjusted signals may improve acoustic detection in the presence of noise but alter encoded information used by receivers to determine the signaler's identity, quality, or status (Halfwerk et al. 2011a, Luther and Magnotti 2014). For species reliant on acoustic communication for breeding behaviors or alerting conspecifics to the presence of predators, compromised communication networks could deleteriously impact individual survival or recruitment, and this could have population consequences (McGregor et al. 2013, Read et al. 2014). For these reasons, receiver response must be investigated in order to evaluate the efficacy of noise-adjusted signals to improve acoustic detection and preserve discrimination in the presence of noise. Receiver response can serve as another behavioral indicator used by conservation behaviorists to understand the severity of anthropogenic noise as a disturbance to a species or population.

RESEARCH OBJECTIVES

My research examined the behavioral responses of a grassland songbird to anthropogenic noise pollution. Baird's sparrow (*Centronyx bairdii*) is a species that displays noise-adjusted songs in response to oil-well drilling noise (Curry et al. 2017). However, it was unknown if the noise-adjusted songs of this species actually improve acoustic detection in the presence of noise or if noise-adjusted songs alter biologically important information encoded within signals. To investigate the potential impacts of noise and noise-adjusted songs on the intrasexual behavior of Baird's sparrows, I simulated territorial intrusions in 'noisy' versus 'quiet' conditions by broadcasting unadjusted and noise-adjusted Baird's sparrow song and oil-well drilling noise to males. This allowed me to compare the number of songs, calls, flybys over the speaker, and song latency (the amount of time elapsed from the start of a playback until the focal male sang) for each trial to determine if song or noise treatment influenced male behavior. Ultimately, my research objectives were to: (1) determine if territorial-defense behavior differed in response to unadjusted songs and noise-adjusted songs in quiet conditions, (2) determine if territorial-defense behavior differed in response to unadjusted songs and noise-adjusted songs in experimentally-elevated noise levels, and (3) determine if territorial-defense differed in quiet and experimentally-elevated noise levels.

DISTURBANCES CAUSED BY OIL AND GAS DEVELOPMENT

In recent decades, the extraction of oil and natural gas has become an increasingly common activity in the grasslands of North America (Askins et al. 2007, Copeland et al. 2011). Unsurprisingly, activity in this sector inflicts various forms of environmental change that threaten grassland-dependent species, particularly grassland birds (Nasen et al. 2011, Roch and Jaeger 2014). In Canada, grassland obligates have declined by 57% and are ranked as the second most threatened avian group (North American Bird Conservation Initiative Canada 2019). Oil and gas development results in direct habitat loss and fragmentation from the construction of primary (i.e., well pads) and supporting (i.e., roads) infrastructure (Sylvester et al. 2013, Ludlow et al. 2015, Green et al. 2017). Associated road traffic and tall structures can act as direct sources of mortality from collision events (Beck et al. 2006, Green et al. 2017). Functional habitat loss may occur for some species through the avoidance of remaining habitat that has been altered by the influx of non-native vegetation (Ingelfinger and Anderson 2004, Dale et al. 2007, Ludlow et al. 2015, Thompson et al. 2015). Furthermore, the construction and presence of tall infrastructure can serve as novel perches that alter the relative abundance of avian predators and brood parasites alike, which has the potential to jeopardize the reproductive success and survivorship of individuals (Degregorio et al. 2014, Bernath-Plaisted et al. 2017).

Oil and natural gas development also introduces sensory pollution to grasslands through the introduction of anthropogenic noise (Barber et al. 2010, Rosa et al. 2015). Noise generated by primary and supporting infrastructure can propagate over long distances; for example, the acoustic footprint of well pads containing noise-generating compressor engines can elevate ambient noise conditions for up to 650 m from its source (Francis et al. 2011b). As a result, functional habitat loss may occur when species avoid or leave otherwise suitable habitats inundated by anthropogenic noise (Rheindt 2003, Bayne et al. 2008, Francis et al. 2009, Drolet et al. 2016). There are several nonexclusive theories proposed to explain these behavioral patterns; for instance, noise may induce a physiological stress response (Blickley et al. 2012b, Kleist et al. 2018), or may constrain a receiver's ability to use acoustic information (i.e., signals or cues) essential for conspecific communication (Habib et al. 2007) or predator-prey detection (Mason et al. 2016). The potential impact of noise generated by oil and gas activities on wildlife is an increasing conservation concern; as a result, there is a steadily growing body of research

dedicated to investigating this topic (see Habib et al. 2007, Bayne et al. 2008, Drolet et al. 2016, Nenninger and Koper 2018).

CHAPTER 2: LITERATURE REVIEW

ACOUSTIC COMMUNICATION IN PASSERINES

Acoustic communication is widely used by songbirds to ensure survival and promote reproductive success (Kroodsmma and Byers 1991, Collins 2004). In many songbird species, song is used by males to deter potential intruders from territories (Peek 1972, Smith 1979, Falls 1988, McDonald 1989, Searcy et al. 1998). Keeping territories free from rivals increases an individual's reproductive success by minimizing the likelihood of cuckoldry or loss of territorial resources (Catchpole and Slater 2008). Early evidence for the territorial function of song comes from experiments where male songbirds were surgically muted and returned to territories; when compared to unmuted males, muted males tended to experience higher rates of territory loss (Peek 1972, Smith 1979, McDonald 1989). In somewhat less invasive experiments, the territorial function of song was illustrated by replacing males with silent loudspeakers or loudspeakers that broadcast conspecific songs (Falls 1988, Searcy et al. 1998). When compared to silent loudspeakers, territories that contained speakers broadcasting conspecific songs had a longer latency for territorial intrusions by rivals despite the physical absence of the territorial owner (Falls 1988, Searcy et al. 1998).

Songs can also convey information about the signaler, which is attended to by various receivers (Collins 2004). In the context of territorial interactions, the type of information encoded within a song might convey a rival's location (McGregor and Falls 1984, McGregor 1993, Naguib and Wiley 2001), identity (Brooks and Falls 1975, Briefer et al. 2008, Osiejuk and Manser 2014), fighting ability (Linhart et al. 2012) or aggressive motivation (Smith and Price 1973, Ripmeester et al. 2007). All of this encoded information can help an individual determine the threat level posed by a signaler (Gil and Gahr 2002, Collins 2004). Ultimately, individuals identified as representing greater threats to territorial holders tend to elicit more aggressive responses when compared to low-threat rivals (Illes et al. 2006, de Kort et al. 2009, DuBois et al. 2011, Moseley et al. 2013).

The "ranging hypothesis" (Morton 1986) states that receivers can estimate the distance and directionality of signalers, particularly conspecific rivals, by attending to the acoustic properties of a signal. To explain, as any long-distance signal propagates through space, local phenomena such as vegetation or weather cause signals to degrade (i.e., changes in a signal's

amplitude, spectral or temporal characteristics signal) via the scattering, absorption, refraction or reverberation of soundwaves (Morton 1975, Marten and Marler 1977, Heimann and Gross 1999). Generally, the farther apart a signaler and a receiver are, the greater the potential for signal degradation (Morton 1975, Marten and Marler 1977).

Evidence for the acoustic recognition of specific individuals has largely come from neighbor-stranger discrimination research (Brooks and Falls 1975, Briefer et al. 2008, Osiejuk and Manser 2014). In this body of research, the “dear-enemy phenomenon” (Fisher 1954) describes the trend for territory owners to display weaker aggressive responses to neighbors when compared to strangers (but see Molles and Vehrencamp 2001). Unlike a known neighbor, strangers theoretically represent a greater threat to territory owners (Temeles 1994). As the territory status of a stranger is unknown, a stranger might attempt to seize an individual’s territory in addition to attempting to engage in extrapair copulations (Temeles 1994). In contrast, because neighbors already occupy a territory, they may only jeopardize an individual’s paternity (Temeles 1994, Olendorf et al. 2004). In this way, diminished aggression towards neighbors helps individuals avoid costly territorial disputes and permits more time to be allocated to activities like vigilance or foraging (Getty 1987).

Signals may also encode and convey information about the fighting ability (Linhart et al. 2012) or aggressive motivation (Smith and Price 1973, Ripmeester et al. 2007) of individuals. In both of these instances, signal exaggeration (i.e., dishonesty) may be selected for (Smith and Price 1973). Signal reliability in agonistic communication is proposed to be maintained by two main mechanisms (Smith and Price 1973). With respect to fighting ability, signal reliability may be maintained through “index signals” (Smith and Price 1973, Smith and Harper 1995). In index signals, the acoustic properties of a signal are linked to the physical attributes of a signaler (Smith and Price 1973, Smith and Harper 1995). For example, individuals with larger body sizes tend to vocalize at lower pitches (i.e., size-pitch allometry) (Davies and Halliday 1978). In several taxa, body size appears linked to fighting ability, and larger individuals typically win fights (Clutton-Brock et al. 1979, Wells 1988). For avian species, size-pitch allometry has been demonstrated in only a limited number of species, such as purple-crowned fairy-wrens (*Malurus coronatus*) (Hall et al. 2013) and willow warblers (*Phylloscopus trochilus*) (Linhart and Fuchs 2015). Motor performance, as opposed to body size, is thought to be a more important variable in predicting fighting ability for avian species (Bradbury and Vehrencamp 2011, Searcy et al.

2014). With respect to acoustic signals, motor performance may be conveyed through the use of trills (Byers et al. 2010, Moseley et al. 2013) or other difficult-to-produce sounds (Illes et al. 2006, Cardoso and Hu 2011).

Unlike index signals, signals of aggressive motivation or other signals of intent are not physically constrained, and as a consequence, individuals may inflate their willingness to escalate to physical conflict (Caryl 1979, Gardner and Morris 1989, Reş and Osiejuk 2010, Searcy et al. 2013). One way the reliability of aggressive signals is proposed to be maintained is through receiver-dependent costs (Zahavi 1977, Guilford and Dawkins 1995). Game theory predicts that dishonest signals are selected against by means of receiver retaliation (Caryl 1979, Enquist 1985). In other words, individuals may have to pay the cost of physical injury inflicted by receivers if they are bluffing about their aggressive motivation. In the context of birds, intent signals differ by species and can include short-term behavioral adjustments such as soft-song (low amplitude song) (Dabelsteen et al. 1998, Ballentine et al. 2008, Templeton et al. 2012, Akçay and Searcy 2015) or song overlapping (Dabelsteen et al. 1997, Mennill and Ratcliffe 2004, Akçay et al. 2020).

CHALLENGES TO ACOUSTIC COMMUNICATION

As briefly discussed above, long-range acoustic signals propagating through space inevitably experience interference and distortion. For example, dense vegetation causes attenuation (i.e., decrease in signal intensity) through the absorption, scattering, and reflecting of a signal's soundwaves (Morton 1975, Marten and Marler 1977, Forrest 1994, Heimann and Gross 1999). The influence of vegetation on soundwave propagation is more pronounced for high-frequency signals or noise (< 2 kHz) (Martens and Michelsen 1981, Watanabe and Yamada 1996). Ultimately, when a signal's intensity is decreased, so is the active space or maximum distance that a receiver can detect a signal (Brenowitz 1982, Dooling and Blumenrath 2013). In addition to vegetation, weather can also influence the transmission of long-range acoustic signals; for example, wind and temperature gradients can cause fluctuations in signal amplitude (Rudnick 1947). Still, natural ambient noise (e.g., multispecies choruses, moving water) can also constrain the detection and discrimination of a signal through acoustic masking (Marten and Marler 1977, Wiley and Richards 1978, Brenowitz 1982, Forrest 1994, Langemann et al. 1998). Acoustic masking can occur when a signal and ambient noise overlap in frequency, or when the

amplitude of ambient noise is higher than that of a signal (Brenowitz 1982, Dooling and Blumenrath 2013). In this way, acoustic masking lowers the signal-to-noise ratio; as a result, a signal or its components are rendered inaudible to a receiver (Lohr et al. 2003).

EVOLUTION OF ACOUSTIC COMMUNICATION

Ecological features are thought to play a significant role in shaping the evolution of acoustic signals (Brown 1989, Ryan et al. 1990, Kopuchian et al. 2004, Boncoraglio and Saino 2007, Potvin et al. 2011). Morton (1975) first proposed the “acoustic adaptation hypothesis,” which states that organisms have evolved to use acoustic signals that are best suited for their structural habitat. These best-suited acoustic signals minimize degradation while maximizing transmission distance (Morton 1975). To illustrate this hypothesis, bird songs in structurally-complex habitats, such as forests, tend to use pure tones, low frequencies, and have wide spacing between notes (reviewed in Boncoraglio and Saino 2007). These acoustic properties are more robust to the degradation, blurring, and reverberation that inevitably occurs when sound waves encounter physical obstacles, like vegetation, during transmission (Richards and Wiley 1980, Ryan and Brenowitz 1985).

In addition to the structural habitat, ambient background noise has also been proposed to influence the evolution of acoustic signals (Brumm 2006, Schmidt et al. 2013, Krishnan and Tamma 2016, Chitnis et al. 2020). For example, the “Lombard effect” (Lombard 1911) describes the ability of birds and other taxa to cope with acute noise by temporarily and immediately increasing the amplitude of acoustic signals (Zollinger and Brumm 2011). By increasing the signal-to-noise ratio, the acoustic detection and discrimination of signals by receivers in competing noise is improved (Lohr et al. 2003, Luther and Gentry 2013). Another evolutionary strategy to avoid acoustic masking from low-frequency noise generated by features, such as wind or fast-moving bodies of water, includes vocalizing at frequencies that are not overlapped by background noise (Dubois and Martens 1984, Douglas and Conner 1999). Furthermore, longer syllables or song length can also improve the detection of a signal by a receiver in noise (Lengagne et al. 1999, Gough et al. 2014). As aforementioned, biotic noise also contributes to overall ambient noise. The “acoustic niche hypothesis” (Krause 1993) states that acoustically communicating species within a mature ecological community minimize acoustic overlapping by occupying distinct aural niches (Krause 1993). These niches may be partitioned by temporal,

spatial or spectral means (Schmidt et al. 2013, Hart et al. 2015, Krishnan and Tamma 2016, Chitnis et al. 2020).

Receivers are also thought to have evolved myriad strategies to cope with the challenges of signal detection and discrimination posed by the physical environment and the presence of noise (Wiley 2017). For example, receivers may optimize signal reception by selecting higher perches in forested habitats (Dabelsteen et al. 1993, Mathevon et al. 2005) as this may help alleviate signal distortion caused by ground effects (Embleton 1996, Holland et al. 1998, Nemeth et al. 2001). Additionally, receivers may be equipped with neurosensory mechanisms to facilitate signal detection and discrimination in the presence of noise (reviewed in Bee and Michey1 2008). For instance, the auditory continuity illusion describes the capacity for receivers to cognitively fill gaps of signals partially masked by ambient noise (Dannenbring 1976, Braaten and Leary 1999, Riecke et al. 2008).

ANTHROPOGENIC NOISE

Anthropogenic noise is an evolutionarily recent phenomenon that has the capacity to constrain and influence the acoustic communication of wildlife (Sih et al. 2011, Francis and Barber 2013, Roca et al. 2016). Generally, anthropogenic noise is characterized as low-frequency (i.e., ≤ 4 kHz) and as containing more acoustic-energy than biophony (e.g., wildlife vocalizations) or geophony (e.g., wind and rain) (Blickley and Patricelli 2010, Pijanowski et al. 2011, Luther and Gentry 2013, Gage and Axel 2014, Mullet et al. 2016). Such acoustic characteristics of anthropogenic noise facilitate long-distance propagation (e.g., ≥ 1 km) without substantial intensity loss (Luther and Gentry 2013). However, the spatial extent of noise differs between linear and point sources of noise due to the inverse distance law (i.e., the geometric spreading of sound waves) (Embleton 1996). If amplitude is held constant, linear sources of noise will have larger acoustic footprints when compared to point sources of noise (Forrest 1994, Luther and Gentry 2013). Anthropogenic noise may also differ from natural sources of noise temporally. For instance, wind passing through vegetation is the main contributor to ambient noise in natural open grassland habitats; as a result, ambient noise levels tend to peak midday when wind velocity is highest (Green 1992, Dodgin 2018). However, because of rapid oil and gas development in many grassland habitats, infrastructure, like compressor stations, introduce

novel sources of continuous low-frequency noise (Bayne et al. 2008, Francis and Barber 2013, Rosa et al. 2015).

ANTHROPOGENIC NOISE AND ACOUSTIC COMMUNICATION

Like natural sources of noise, anthropogenic noise has the potential to interfere with the acoustic communication of wildlife through acoustic masking. Acoustic masking caused by anthropogenic noise may result in fitness consequences; however, these fitness consequences are predicted to be signal-specific (Blickley and Patricelli 2012). For example, anthropogenic noise that acoustically masks anti-predator signals, such as alarm calls, could have dire consequences for survival. In a field experiment using superb fairy-wrens (*Malurus cyaneus*), individuals failed to flee to cover when conspecific alarm calls were broadcast with experimentally-introduced noise (Zhou et al. 2019). Similarly, parental communication of predation risk to nestling tree swallows (*Tachycineta bicolor*) was disrupted by noise, such that nestlings under experimentally-elevated noise conditions called for longer after alarm calls when compared to quiet conditions (McIntyre et al. 2014). In the context of anti-predator signals, the acoustic masking of alarm calls in one species could impact the survival of another species. Specifically, this might occur when individuals in one species regularly attends to the alarm calls of a heterospecific individuals. For example, northern cardinals (*Cardinalis cardinalis*) attend to the alarm calls of tufted titmice (*Baeolophus bicolor*), but when northern cardinals living in habitats impacted by traffic noise were presented experimentally-broadcast alarm calls of tufted titmice, many individuals failed to respond entirely (Grade and Sieving 2016). Failure to respond appropriately with vigilance behavior or hiding could result in individual mortality (Grade and Sieving 2016).

Anthropogenic noise that entirely or partially acoustically masks songs may have consequences for reproduction, such as decreased pairing success (Habib et al. 2007), weakened pair bonds (Swaddle and Page 2007), or diminished territory-defense behavior (Kleist et al. 2016, Zwart et al. 2016). Regarding the latter, weakened territory-defense behavior could cost a male cuckoldry or loss of territorial resources (Halfwerk et al. 2011b, Kleist et al. 2016). For example, spotted towhees (*Pipilo maculatus*) and chipping sparrows (*Spizella passerina*) were exposed to simulated territorial intrusions in habitats of natural ambient noise and habitats altered by low-frequency compressor noise (Kleist et al. 2016). When compared to simulated

territorial intrusions in habitats with natural ambient noise, focal males in noisy habitats displayed a greater response latency (to sing or approach the experimental speaker) (Kleist et al. 2016). In a similar experiment, Lenis and Guillermo-Ferreira (2020) presented simulated territorial intrusions to great kiskadees (*Pitangus sulphuratus*) in habitats of varying levels of urban noise. Their results corroborated the findings of the above experiment, with individuals displaying longer response latency in habitats experiencing higher ambient noise levels (Lenis and Guillermo-Ferreira 2020).

In general, when faced with rapid environmental change, populations or species may disperse away from the disturbance, or attempt to deal with the novel environment by modifying behaviors (Sih et al. 2011, Sih 2013, Wong and Candolin 2015). In regard to the former, evidence suggests that some avian species avoid habitats experiencing high anthropogenic noise (Rheindt 2003, Kleist et al. 2017, Injaian et al. 2018). Spatial avoidance of anthropogenic noise is often hypothesized to occur because of acoustic masking, which disproportionately threatens birds with low-frequency vocalizations (McGregor et al. 2013). Indeed, avian species with low-frequency vocalizations often occur at lower abundances in habitats impacted by noise (Rheindt 2003, Hu and Cardoso 2010, Kleist et al. 2017).

However, some avian species remain in habitats experiencing high anthropogenic noise, and many of these species display noise-induced alterations in acoustic signaling behavior (Fuller et al. 2007, Bermúdez-Cuamatzin et al. 2009, Hu and Cardoso 2010). Altering signal behavior and or signal structure is proposed to be adaptive, whereby signal detection and discrimination in the presence of noise are improved (Brumm and Zollinger 2013). These alterations appear to be species-specific, meaning even closely-related species may display starkly different strategies in response to the same form of anthropogenic noise (Francis et al. 2011a, Curry et al. 2017). Furthermore, strategies may be noise-specific such that a particular species display different strategies in response to varying forms of anthropogenic noise (Potvin and Mulder 2013, Lenske 2014, Warrington et al. 2018). This variation in response to noise and ultimately what strategy is employed by a species or individual might be a function of the extent of acoustic masking, physical limitations (e.g., physiological or biomechanical), the need to preserve encoded information, life history or prior experience (Brumm 2004, Brumm and Slater 2006, Podos et al. 2009, Lazerte et al. 2016, Curry et al. 2017, Warrington et al. 2018). Below I

discuss some of the common strategies employed by avian species in response to anthropogenic noise.

Amplitude Shifts

Laboratory and field experiments indicate that numerous mammalian (Hotchkin and Parks 2013) and avian species (Manabe et al. 1998, Brumm and Todt 2002, Pytte et al. 2003, Lowry et al. 2012, Kight and Swaddle 2015, Derryberry et al. 2017, Hardman et al. 2017) are capable of making noise-dependent changes to song or call amplitude. Known as the “Lombard effect” (Lombard 1911), this pattern entails individuals immediately increasing the amplitude of their acoustic signals in response to increasing background noise (Brumm and Todt 2002, Zollinger and Brumm 2011). A higher signal amplitude is proposed to be adaptive because it increases the signal-to-noise ratio and may help maintain the active space of the signal (Lohr et al. 2003). Indeed, in comparison to the below example of spectral adjustments, amplitude shifts are hypothesized to be a more effective strategy in improving acoustic communication under noisy conditions (Nemeth and Brumm 2010).

Spectral Shifts

Species may also alter the frequencies of an entire signal or particular signal elements in response to anthropogenic noise (Pytte et al. 2003, Gross et al. 2010, Verzijden et al. 2010, Montague et al. 2013, Curry et al. 2017). In some cases, higher frequency shifts may be a by-product of the aforementioned Lombard effect (Brumm and Todt 2002, Nemeth et al. 2013); however, evidence suggests that spectral shifts can occur independently of song amplitude (Potvin and Mulder 2013). In many examples, avian species have been found to raise the minimum frequencies of songs in response to low-frequency anthropogenic noise (Pytte et al. 2003, Gross et al. 2010, Verzijden et al. 2010, Montague et al. 2013); in theory, this would improve the contrast between the signal and the prevailing background noise (Lohr et al. 2003, Luther and Gentry 2013). Curiously, some species respond to noise by displaying signals with decreased signal frequency parameters (Potvin et al. 2014, Curry et al. 2017, Gentry et al. 2017, Wolfenden et al. 2019). In some instances, decreasing signal frequency parameters might be adaptive because lower-frequency signals have greater active spaces (Potvin et al. 2014). Still, increasing minimum frequency or decreasing maximum frequency may increase whole-signal or

signal-element tonality via decreased bandwidth, and more tonal signals may improve detectability and discrimination in the presence of noise (Lohr et al. 2003, Roca et al. 2016).

Temporal Shifts

Another means of avoiding acoustic masking is to shift singing activities to periods during the day when anthropogenic noise levels are lower (Fuller et al. 2007, Nordt and Klenke 2013, Cartwright et al. 2014, Gil et al. 2015, Dorado-Correa et al. 2016). The use of the “temporal overlap avoidance strategy” (Yang and Slabbekoorn 2014) appears to be mainly a response to long-term and predictable forms of noise from sources such as rush hour traffic and airports (Fuller et al. 2007, Dominoni et al. 2016). Unlike the aforementioned strategies, currently, there is no evidence to suggest that the temporal overlap avoidance strategy is an immediate form of signaling flexibility used by avian species in response to anthropogenic noise (Yang and Slabbekoorn 2014). However, at least two mammalian species have been found to avoid vocalizations during experimentally-introduced intermittent white noise and instead waited to vocalize during brief quiet windows (Egnor et al. 2007, Roy et al. 2011).

Multimodal Shifts

So far, this discussion has been restricted to adjustments in one sensory modality (i.e., hearing), yet avian and other wildlife species often employ and attend to signals across multiple sensory modalities (Higham and Hebets 2013). Improved communication in the presence of anthropogenic noise may occur through shifting effort to visual signals or increasing signal redundancy through the use of multiple modalities (Hebets and Papaj 2005, Partan and Marler 2005, Akçay and Beecher 2019). For example, male song sparrows (*Melospiza melodia*) displayed more wing waves and warbled soft songs in response to simulated territorial intrusions occurring in experimentally elevated noise levels when compared to quiet trials (Akçay and Beecher 2019). The researchers in this study concluded that, when faced with noisy conditions, males potentially preserved communication by employing a redundant signaling strategy across modalities (Akçay and Beecher 2019). Contrary to this study, Ríos-Chelén et al. (2015) found that red-winged blackbirds (*Agelaius phoeniceus*) did not increase the intensity of the visual displays in response to higher anthropogenic noise levels.

Are Noise-Induced Acoustic Adjustments Measurement Artifacts?

Many of the abovementioned studies used spectrograms in sound-analysis programs, such as Raven Pro, to measure the acoustic parameters of signals. Yet, the use of spectrograms in noise-adjusted signal research presents several issues (Zollinger et al. 2012, Brumm and Bee 2016, Brumm et al. 2017, Ríos-Chelén et al. 2017). For one, without a universally accepted standard for spectrogram settings (e.g., contrast, brightness and window size), variation in spectrograms settings may prevent comparisons among and between studies (Zollinger et al. 2012). A more central problem to noise-adjusted signal research, however, is when researchers use on-screen cursors or a “by-eye practice” (Ríos-Chelén et al. 2016, 2017) to measure the minimum frequency of a signal. The use of this technique is subjective and unreliable, particularly when attempting to measure the minimum frequency of a signal in a recording in the midst of loud, low-frequency sounds (Zollinger et al. 2012, Ríos-Chelén et al. 2017). Although contingent on the characteristics of the noise and the signal, low-frequency portions of recorded signals may become visually undetectable on spectrograms but still acoustically present; in this situation, researchers may make a Type I error (i.e., false-positive) (Zollinger et al. 2012, Brumm and Bee 2016, Brumm et al. 2017, Ríos-Chelén et al. 2017). To circumvent this problem in future studies, some researchers advocate the use of power spectra rather than spectrograms for more consistent minimum and maximum frequency measurements (Zollinger et al. 2012).

Are Noise-Induced Adjustments Adaptive?

In order for noise-induced adjustments to be adaptive, strategies must restore the ability of receivers to both detect and discriminate between signals in the presence of noise. Yet, few studies have examined if noise-adjusted signals actually improve reception in the face of anthropogenic noise (but see Pohl et al. 2012, Montague et al. 2013, Luther and Magnotti 2014, Lazerte et al. 2017, Curry et al. 2018). One study focusing on receivers was conducted by Templeton et al. (2016), who highlighted that noise-adjusted signals do not always restore communication in the presence of noise. In this study, great tits (*Parus major*), increased the amplitude of alarm calls under experimental traffic noise. Because of the presence of the Lombard effect, the researchers predicted that amplitude adjustments would restore anti-predator behavior in the presence of competing noise. Great tits were then exposed to playbacks of: (1) alarm calls only, (2) traffic-noise only, (3) amplitude-adjusted alarm calls paired with low traffic

noise, and, (4) amplitude-adjusted alarm calls paired with high traffic noise (Templeton et al. 2016). Playbacks of alarm calls only resulted in normal antipredator behavior, while playbacks of amplitude-adjusted alarm calls paired with low traffic noise resulted in weakened antipredator behavior (e.g., fewer alarm calls). However, when amplitude-adjusted alarm calls were paired with high traffic noise, individuals failed to respond to playbacks with antipredator behavior (Templeton et al. 2016).

Even if noise-adjusted signals improve detection in the presence of noise, discrimination of the signal may be impacted (Slabbekoorn and Ripmeester 2008, Halfwerk et al. 2011a). For example, frequency adjustments to signals may impact how receivers perceive and subsequently respond to the signal (Mockford and Marshall 2009, Montague et al. 2013, Luther et al. 2016, Curry et al. 2018). Luther and Magnotti (2014) investigated this topic by presenting northern cardinals (*Cardinalis cardinalis*) with simulated territorial intrusions of noise-adjusted and unadjusted songs (i.e., frequency adjusted) under a gradient of noise conditions. During low levels of background noise, focal males gave stronger responses (e.g., increased number of songs and flybys) to unadjusted songs relative to noise-adjusted songs. However, responses between the two song types became more similar with increasing background noise. The researchers concluded that because focal males gave different responses to noise-adjusted and unadjusted songs in quiet environments, the two song types were not functionally equivalent (Luther and Magnotti 2014).

In contrast to the above study, Curry et al. (2018) found evidence to suggest that noise-adjusted songs improved communication in noisy contexts. In this study, Savannah sparrows (*Passerculus sandwichensis*), were presented simulated territorial intrusions of noise-adjusted and unadjusted songs in three different acoustic environments. In low levels of background noise, focal males gave stronger responses (e.g., increased number of wing flicks and attacks) to unadjusted songs when compared to noise-adjusted songs (Curry et al. 2018). Yet, in high levels of background noise, agonistic responses to noise-adjusted songs were similar to unadjusted songs broadcast in low levels of background noise. Given these results, the researchers concluded that although noise-adjusted songs altered song meaning in quiet environments, noise-adjusted songs restored normal agonistic behavior in noisy contexts (Curry et al. 2018).

STUDY SPECIES

The Baird's sparrow (*Centronyx bairdii*) is a small grassland obligate that breeds in the northern Great Plains and overwinters in the southwestern part of the United States and northern Mexico (Green et al. 2020). The southern regions of Alberta, Saskatchewan, and Manitoba are important habitat for Baird's sparrow as they collectively contain ~45% of the species breeding range (COSEWIC 2012). Sexes are nearly identical in appearance, with females and males displaying cryptic plumage consisting of a buffy yellow head, white belly, and light brown and black streaks on the back (Green et al. 2020). Black streaking, reminiscent of a necklace, appears on the chest of Baird's sparrows (Green et al. 2020).

Breeding and Territorial Behavior

Baird's sparrows arrive at breeding sites in early May, and sometimes as late as June (Ahlering et al. 2006, Green et al. 2020). This species is characterized as semi-nomadic given evidence of low breeding site fidelity (Green et al. 2020). Baird's sparrows display clumped distribution patterns at breeding sites, potentially due to the species' selection of breeding habitat via conspecific auditory cues (Ahlering et al. 2006). During the breeding season, males demonstrate territoriality via displays (e.g., wing fluttering) and singing from perches or the ground in territory centers (Green et al. 2020). During territorial disputes, behaviors such as calling and chasing (on wing and by foot) increase (Cartwright et al. 1937). Playbacks of Baird's sparrow song within territories elicit agonistic responses from males and provokes neighboring males to sing (Green 1992, Ahlering et al. 2006).

Song Behavior

Singing is limited to male Baird's sparrows, and like many passerines, song is culturally learned (Green 1992, Wheelwright et al. 2008). Currently, 13 song types have been described for Baird's sparrows, and males only use one song type throughout their lifespan (Green 1992). All song types are high-frequency and typically contain introductory syllables, a trill, and a terminal note or syllable (Green et al. 2020) (Figure 1). Curiously, males on adjacent territories tend to use different song types (Green 1992; Waldinger, *personal observation*). Finally, song dialects have not been observed in Baird's sparrow, this suggests that song types are not geographically constrained (Green 1992, Green et al. 2020).

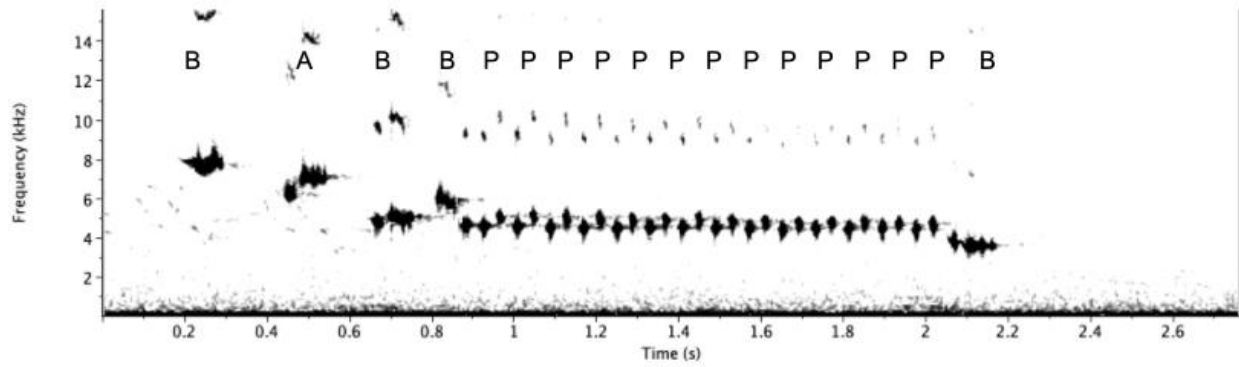


Figure 1. A spectrogram of a Baird's Sparrow song. Syllable classifications used in this spectrogram are consistent with Curry et al. (2017). Syllables include: (A) an introductory syllable, (B) an introductory or final syllable, and (P) an alternating frequency trill syllable. Spectrogram was generated in Raven Pro (v. 1.5) using spectrogram window size 512, brightness 50, and contrast 90.

Song Behavior in Anthropogenic Noise

Baird's sparrows display noise-adjusted songs in the presence of anthropogenic noise (Curry et al. 2017). Curry et al. (2017) found that when compared to quiet conditions, Baird's sparrows recorded in noisy conditions decreased the peak frequency of songs and altered five of the eight song syllables analyzed. Three of the five altered song syllables were introductory syllables, while the remaining two were trill syllables (Curry et al. 2017). Two introductory syllables had decreased frequencies, while the third introductory syllable was increased in frequency. One trill syllable displayed increased power, and the second trill syllable displayed decreased power and shorter duration (Curry et al. 2017). Alteration of introductory notes is significant as introductory notes are believed to be important for species recognition (Green 1992). However, it is unknown what function trill syllables play in Baird's sparrow. In other sparrow species, trills are believed to signal male quality (Ballentine et al. 2004, Sung and Handford 2020).

Population Trends, Threats, and Conservation Action

Population declines of the once common Baird's sparrow have been recorded in the United States and Canada since 1966 (Wilsey et al. 2019). In Canada, federal conservation actions began with the listing of Baird's sparrow as "Threatened" under the Species at Risk Act (SARA) in 1989 (Goossen et al. 1993 in Wiggins 2006). In the following year, the Baird's Sparrow Recovery Team was formed, and a species recovery plan was produced (Goossen et al. 1993 in Wiggins 2006). After a species assessment by The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 1996, the status of Baird's sparrow was downgraded to "Not at Risk" (SARA 2020). COSEWIC assessed the status of the species again in 2012 and elevated the status of Baird's Sparrow to "Special Concern" (COSEWIC 2012). Most recently, Baird's sparrow was added to Schedule 1 with the status "Special Concern" (SARA 2020). In Alberta, where my study system was located, Baird's sparrow is listed as Sensitive (Alberta Environment and Parks 2015).

The decline of Baird's sparrow populations is primarily attributed to the loss and degradation of its breeding habitat (Jones and Green 1998, COSEWIC 2012). Conversion to cropland is a major historical and ongoing threat to Baird's sparrow (Jones and Green 1998, Wiggins 2006). In addition, overgrazing by domestic livestock also negatively impacts Baird's

sparrow density and reproductive success (Owens and Myres 1973, Sutter et al. 1995). The physical expansion of the energy extraction sector may also threaten Baird's sparrow as well as other grassland birds (Ludlow et al. 2015, Thompson et al. 2015). Baird's sparrow density is impacted by forms of habitat alteration associated with oil and natural gas development including the encroachment of non-native plant species, creation of roads and the presence of vertical infrastructure (Sutter et al. 2000, Dale et al. 2007, Ludlow et al. 2015, Nenninger and Koper 2018). While other grassland obligate species appear to avoid habitat impacted by noise generated by oil and gas infrastructure (Blickley et al. 2012a), at least one study found that such noise did not explain well avoidance by Baird's sparrows (Nenninger and Koper 2018). Instead, this study attributed Baird's sparrow well avoidance to the physical footprint of infrastructure (Nenninger and Koper 2018).

CHAPTER 3: IMPACTS OF NOISE AND NOISE-ADJUSTED SIGNALS ON AGONISTIC BEHAVIORS OF MALE BAIRD'S SPARROWS

ABSTRACT

Anthropogenic noise can constrain the acoustic communication of wildlife species through acoustic masking. Yet, many wildlife species display noise-adjusted signals which are theorized to provide release from acoustic masking. However, noise-adjusted signals may alter encoded signal information attended to by receivers or fail to improve acoustic communication in noise. I examined the efficacy of noise-adjusted signals using Baird's sparrow (*Centronyx bairdii*), a species that displays noise-adjusted signals. I conducted repeated measures playback studies ($n = 69$ dyads) on free-living male Baird's sparrows in the mixed-grass prairies of Southern Alberta during their breeding season (May to July 2018 and 2019). I used a playback design to broadcast pre-recorded unadjusted and noise-adjusted male song in the presence and absence of oil-well drilling noise to simulate territorial intrusions in quiet and noisy conditions. To determine if song or noise treatment influenced male behavior, I compared the number of songs, calls, flybys over the experimental speaker, and song latency (time elapsed after the start of a playback for males to sing) for each trial type. Song latency for unadjusted songs was longer in the presence of oil-well drilling noise, suggesting that acoustic detection was constrained by noise. However, song latency for noise-adjusted songs broadcast with noise was similar to unadjusted songs broadcast in quiet conditions, indicating that noise-adjusted songs improve acoustic detection in the presence of competing noise. Overall, responses differed significantly by noise treatment; males sang less, called more, and did more flybys in noisy conditions. These results suggest that noise elicits more aggressive territorial-defense behavior or hinders the ability of individuals to locate or assess rivals.

INTRODUCTION

In grassland habitats, primary (i.e., well pads) and supporting (i.e., roads) non-renewable energy infrastructure are major contributors to anthropogenic noise (Bayne et al. 2008, Barber et al. 2011, Rosa et al. 2015). Noise emitted from these sources can impact avian species abundance (Blickley et al. 2012a), community composition (Francis et al. 2009), and pairing success (Habib et al. 2007). Acoustic masking of critical vocalizations used in breeding behavior

or survival is one proposed mechanism underlying these changes (Barber et al. 2010, McGregor et al. 2013). Acoustic masking can occur when a vocalization and ambient noise overlap in frequency, or when the amplitude of ambient noise is higher than that of a vocalization (Brenowitz 1982, Dooling and Blumenrath 2013). When acoustic masking occurs, the distance over which a receiver can detect a vocalization (i.e., the active space of a signal) is reduced (Lohr et al. 2003).

In the presence of anthropogenic noise, many avian species alter their vocalizations by means of amplitude (Brumm and Todt 2002, Lowry et al. 2012), frequency (Potvin and Mulder 2013, Luther and Magnotti 2014) or timing (Fuller et al. 2007, Dominoni et al. 2016). Alterations may involve the whole song or only specific syllables (reviewed in Brumm and Zollinger 2013). Furthermore, adjustments appear to be species-specific such that closely-related species may display disparate strategies in response to the same form of anthropogenic noise (Francis et al. 2011a, Curry et al. 2017). Adjustments may also be contingent on the noise source, such that a particular species may display different adjustments in response to different forms of anthropogenic noise (Potvin and Mulder 2013, Lenske 2014, Warrington et al. 2018). Ultimately, noise-adjusted songs may reduce the impact of acoustic masking by increasing the signal-to-noise ratio or increasing the contrast between a vocalization and competing background noise (Brumm and Slabbekoorn 2005, Wiley 2013).

However, noise-adjustments may fail to improve acoustic communication in the presence of noise. For example, although great tits (*Parus major*) increased the amplitude of alarm calls when exposed to traffic noise, these amplitude adjustments were not sufficient to counteract the masking effects of high-amplitude traffic noise (Templeton et al. 2016). Even if signal detection is improved, adjustments to vocalizations, like songs, may impact their perception by receivers (Halfwerk et al. 2011a). Briefly, the encoded information in songs is thought to be crucial in territory-defense behavior as songs can convey information regarding an individual's location (McGregor and Falls 1984, McGregor 1993, Naguib and Wiley 2001), identity (Brooks and Falls 1975, Briefer et al. 2008, Osiejuk and Manser 2014), fighting ability (Linhart et al. 2012) or aggressive motivation (Smith and Price 1973, Ripmeester et al. 2007). How territorial males perceive intruders is thought to influence the strength of their territory-defense behavior and intruders that are perceived as low-threat (e.g., low aggression or low fighting ability) tend to elicit weaker responses (Illes et al. 2006, de Kort et al. 2009, Brumm and Ritschard 2011,

Moseley et al. 2013). Therefore, noise-adjusted signals may alter how territorial males perceive and subsequently respond to intruders. For example, simulated territorial intrusions of noise-adjusted songs of northern cardinals (*Cardinalis cardinalis*) (Luther and Magnotti 2014) and great tits (Mockford and Marshall 2009) elicited weaker territorial responses from conspecifics when compared to unadjusted songs. If noise-adjusted signals distort the threat level posed by an intruder, weaker or slower territorial responses to truly threatening intruders could cost a male territorial takeovers or cuckoldry (Halfwerk et al. 2011a, Kleist et al. 2016).

Baird's sparrow (*Centronyx bairdii*) is a grassland-obligate songbird that breeds in the mixed-grass prairies of Canada and the United States (Green et al. 2020) and displays noise-adjusted songs in response to experimental playbacks of noise generated by oil-well drilling (Curry et al. 2017). The ability of Baird's sparrows to adapt to noise could have conservation implications. Population declines of Baird's sparrows have been recorded in the United States and Canada since 1966 (Wilsey et al. 2019). As a result, this species is federally listed as a species of Special Concern in Canada under the Species at Risk Act (SARA 2020). The decline of Baird's sparrow is mainly attributed to widespread historic habitat loss caused by conversion to cropland (Jones and Green 1998, Wiggins 2006). However, in recent years, new forms of habitat loss and degradation have been wrought by oil and gas development and may also contribute to the decline of Baird's sparrow (Ludlow et al. 2015, Green et al. 2017). In addition to the physical loss of habitat, oil and gas development generates substantial noise which leads to the avoidance of other grassland-obligate species (Blickley et al. 2012a). However, at least one study found that such noise did not explain oil well avoidance by Baird's sparrows (Nenninger and Koper 2018). This might suggest that the noise-adjusted signals of Baird's sparrows are effective in restoring acoustic communication in the presence of noise.

In this study, I broadcast pre-recorded unadjusted and noise-adjusted male song in the presence and absence of oil-well drilling noise to simulate territorial intrusions in quiet and noisy conditions. This allowed me to determine if the territorial-defense behavior of free-living male Baird's sparrow differed between song treatments (noise-adjusted vs. unadjusted songs), between noise treatments (quiet vs. and noisy) and if there was an interaction between these treatments. I predicted that if noise-adjusted songs improve acoustic detection in the presence of noise, then noise-adjusted songs will elicit quicker responses when compared to unadjusted songs in the presence of noise. If noise-adjusted songs improve detection in noise and do not compromise

signal content (i.e., change encoded information), then noise-adjusted songs and unadjusted songs should elicit similar responses in quiet conditions.

METHODS

Ethics

This research was conducted under University of Manitoba animal care protocols #F15-005/1/2/3 (AC11301) (2018) and #F19-003 (AC11449) (2019), Canadian bird banding permit #10840, Canadian Wildlife Service (CWS) permit #17-AB-SC001, and Alberta Environment and Sustainable Research Development Research Permit #18-347 (2018) and #19-258 (2019).

Site and Timing

My study took place in May-July 2018 and 2019 within a 50 km radius of Brooks, Alberta, Canada (50.56417°N, 111.8989°W, 760 meters above sea level). This area is located on the periphery of the prairie pothole region and exhibits limited topographical relief. Much of the land in this area is privately owned and managed by the Eastern Irrigation District (EID). EID manages land under a multiple-use philosophy and leases land for activities, including livestock grazing and energy extraction. On EID-leased grazing pastures, vegetation is mostly comprised of native mixed-grass prairie species like western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Hesperostipa comata*), blue grama (*Bouteloua gracilis*), and junegrass (*Koeleria macrantha*). Additionally, exotic plant species, such as goatsbeard (*Tragopogon dubius*) and crested wheatgrass (*Agropyron cristatum*) occur, but in low abundances. In my study area, the size of leased grazing pastures tends to be 1.6 x 1.6 km or larger, and pastures are divided by three-wire fences or range roads. Pastures and energy extraction lease sites are often adjacent to one another. The size of energy extraction lease sites is typically 100 m x 100 m. A lease site for energy extraction often consists of a bare or gravel footprint, primary infrastructure (to extract or distribute oil or natural gas), technical cattle fences surrounding the primary infrastructure, and a three-wire fence at the perimeter of the lease site. Dirt or gravel service roads extending from energy extraction lease sites connect to the rural road system. On energy extraction lease sites, primary infrastructure often produces high amplitude and broadband sound; however, the majority of energy tends to be concentrated within the lower frequency ranges (i.e., $\leq 3\text{kHz}$)

(Rosa et al. 2015, Antze and Koper 2018). For example, generator-powered screw pumps, used to extract oil, may produce noise at $79 \pm \text{SD } 3.5$ dBc at 10 m; meanwhile, gas compressor stations, which distribute oil through pipeline networks, can produce noise $82 \pm \text{SD } 3.1$ dBc at 10 m (Antze and Koper 2018).

My study sites (i.e., focal male territories and locations of playback experiments) were all located on annually-grazed native mixed-grass pastures owned by EID. These sites were all ≥ 600 m from noise-producing infrastructure and ≥ 100 m from low-traffic dirt service roads. As a result, ambient noise on my study site was mostly generated by natural sources (e.g., wind, birdsong). On these sites, I searched for territorial male Baird's sparrows by attending to behavioral cues such as singing. Once located, I used a 6-m mist net, decoy, and a small Bluetooth speaker broadcasting conspecific songs to capture individuals. After extraction from the mist net, I verified the sex (using cloacal protuberance) and the age of the individual (using molt limits and feather quality) (Pyle et al. 2008). I also took morphometric measurements (e.g., bill height, width, length, tarsus length, flattened wing-chord) of the individual using calipers, a wing ruler, and a digital scale. I banded individuals with a CWS metal band and a unique combination of two or three plastic color bands (red, yellow, dark blue, light blue, orange, green, light green, gray, pink, purple, and brown). To reduce the chance of color bands reopening and injuring birds, I used a portable soldering iron to seal the bands shut. In an effort to minimize stress on the individuals, I processed and released all birds within 20 min. Lastly, I took a GPS waypoint using an eTrex 10 (Garmin Ltd., Olathe, Kansas, USA) at the location of the banding event. I referenced the banding event GPS waypoint when attempting to re-sight the focal male for subsequent playback experiments.

Playback Trials

My playback experiments sought to determine if the territory-defense behavior of focal males differed between song treatments (noise-adjusted vs. unadjusted songs), noise treatments (ambient noise (hereafter 'quiet') vs. experimentally introduced noise (hereafter 'noise')) and if there were interactions between these treatments. To accomplish this, I presented matched-stimuli playback trials (dyads) ($n_{\text{noise-adjusted}} = 35$; $n_{\text{unadjusted}} = 34$) to focal males ($n_{\text{color-banded}} = 62$, $n_{\text{unbanded}} = 7$). Dyad halves were ~ 17 min long and were separated by 1.3 – 2.2 h (median = 1.5 h). Each dyad half consisted of three 5 min trials separated by 1 min (Table 1).

I began dyads with a priming trial that entailed broadcasting a standardized conspecific song exemplar for 5 min. The purpose of the priming trial was to ensure that I had placed the speaker in the focal male's territory and confirm his color bands (when applicable). Additionally, the priming trial helped me ensure the sex of unbanded individuals as only males sing (Green et al. 2020). After the priming trial came the noise-control trial, which entailed broadcasting oil-well drilling noise only (Table 1). The purpose of the noise-control trial was to ensure that the experimental noise would not cause the focal male to flee the area. The main trial followed the noise-control trial (Table 1). In the main trials, I presented each focal male with a song exemplar (noise-adjusted or unadjusted song exemplar). This song exemplar was presented in one of two noise treatments (quiet or noise). As my study used a matched-stimuli playback design, a focal male's song exemplar remained the same for the second main trial. However, in the second trial, I used the opposite noise treatment of the first main trial (Table 1). In this way, focal males were exposed to a song exemplar in both quiet and noisy conditions. In each trial, I narrated the behaviors (e.g., total number of songs, total number of calls, total number of flybys past the song speaker) of focal males into a Zoom H4n Pro Digital Recorder (Zoom, Tokyo, Japan) which I later transcribed and tallied.

To control for potential effects of song or noise exemplar quality, I randomly assigned each focal male a unique stimuli combination (i.e., one song exemplar and one noise exemplar) to be used in noise-control trials and main trials across dyad halves (McGregor 2000, Grava et al. 2013). I controlled for effect order by randomly assigning each focal male one of two treatment orders for noise presentation in main trials: (1) noise then quiet, (2) quiet then noise. These random assignments were constrained, such that treatments were balanced (Milinski 1997). To control for potential effects of seasonal variation, I conducted each focal male's dyads on the same day. Playbacks of Baird's sparrow song cause males on adjacent territories to sing (Green 1992, Ahlering et al. 2006), so I did not test neighbors on the same day. Finally, I conducted playbacks under standardized conditions (≤ 6 h after sunrise, average wind speed ≤ 15 km/h, and temperature $> 0^\circ\text{C}$ (Celsius)).

Table 1. Experimental playback design. This table depicts an example of a focal male's stimuli assignment with a Treatment Order of 1 (i.e., noise then quiet).

Dyad	Event	Description of Event	Time
1	Priming trial	Standardized priming exemplar broadcast	5 min
	No stimulus	No stimulus	1 min
	Noise-control	Noise exemplar broadcast <i>Example: Noise exemplar # 1 broadcast</i>	5 min
	No stimulus	No stimulus	1 min
	Main trial	Song exemplar and noise exemplar broadcast simultaneously <i>Example: Song exemplar # 24 broadcast with noise exemplar # 1</i>	5 min
	No Stimulus	Bird returns to normal behavior between dyad halves	~ 1.5 h
2	Priming trial	Standardized priming exemplar broadcast	5 min
	No stimulus	No stimulus	1 min
	Noise-control trial	Noise exemplar broadcast <i>Example: Noise exemplar # 1 broadcast</i>	5 min
	No stimulus	No stimulus	1 min
	Main trial	Song exemplar broadcast <i>Example: Song exemplar # 24 broadcast</i>	5 min

Experimental Setup

To simulate a male intruder, I broadcast song exemplars at ~88 dBc SPL at 1 m (reference level dBc 34.2 SPL) from a Traynor TVM50 portable amplifier (Yorkville Sound, Pickering, Ontario, Canada) (hereafter ‘song speaker’). This amplitude was used because it is comparable to the natural amplitude of broadcast songs of Baird’s sparrows (Koper et al. 2016). To simulate a noise disturbance on a focal male’s territory, I broadcast oil-well drilling noise at ~87 dBc SPL at 1 m (reference level dBc 34.2 SPL) from a Mackie SRM350 v2 (LOUD Technologies, Woodinville, Washington, USA) (hereafter ‘noise speaker’) powered by a 12-volt deep-cell battery and portable inverter. Other similar studies broadcast oil-well drilling noise at an average of 88 dBc SPL at 10 m (Curry et al. 2017). However, I broadcast noise at the above amplitude to simulate an oil-well at a distance (Curry et al. 2017) and minimize potential observer error (Ortega and Francis 2010, Koper et al. 2016). I transported all experimental equipment to focal male territories using a modified bike cart. I observed all focal males prior to the playback setup to determine song perches and territorial boundaries. This was done because speaker placement, if outside of a male’s territory, can influence results (Phillips and Derryberry 2018). After observing the focal male, I placed the song speaker at the approximate center of the focal male’s territory. I then placed the noise speaker ~50 m from the song speaker; the speakers were oriented so that they faced one another (Figure 2). To aid in distance estimates, I placed ropes marked at 5-m and 10-m intervals at the base of the song speaker and in four directions (Figure 2). I minimized disturbance during trials by connecting each speaker to an iPhone 5s (Apple Inc., Cupertino, California, USA) via XLR cables. This permitted me to control the devices at a crouched location ~20 m from the song speaker and 70 m from the noise speaker.

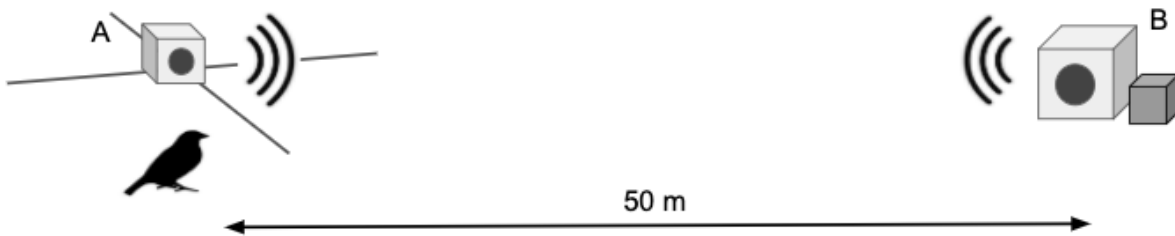


Figure 2. Schematic of experimental equipment used in playbacks (not to scale). In this figure, (A) represents the speaker used to broadcast song exemplars and ropes used to assist in distance estimates; (B) represents the speaker and battery used to broadcast oil-well drilling noise exemplars. Speakers were placed ~50 m apart. The location of all experimental equipment remained constant across a focal male's dyad halves.

Playback Files

Noise exemplars

To create noise exemplars, I used existing high-quality audio files of oil-well drilling noise. These audio files were originally made in September-October 2013 by recording different active drilling rigs with Zoom H4n Digital Recorders (Zoom, Tokyo, Japan; WAV files at 48-kHz sample rate, 24-bit resolution) (Curry et al. 2017). I made three noise exemplars from three different oil-well drilling recordings in the program Audacity (Audacity Team 2018). To make a noise exemplar, I selected 5 min of oil-well drilling noise from one recording. This was done to ensure that the selection was free from sudden noises such as truck horns. Next, I edited the selection to create a 30-s fade-in to full volume, 4 min of full volume noise and 30-s fade-out. This step was done to preclude startling focal males with a sudden introduction of noise. Finally, to control for peak amplitudes across exemplars, I standardized the peak amplitude of the noise exemplar (Grabarczyk et al. 2019).

Song exemplars

To create song exemplars, I used existing recordings of free-living male Baird's sparrow songs made in May-July 2014 in the same region as my experiments (Curry et al. 2017). In these recordings, different individuals were recorded using Zoom H4n Digital Recorders with built-in stereo microphones angled at 90 degrees at maximal recording volume (WAV files at 48-kHz sample rate, 16-bit resolution). Songs were recorded by pointing the recorder directly at singing males (Curry et al. 2017). Baird's sparrows were recorded under two different acoustic treatments: (1) when background noise was limited to natural sounds (e.g., bird song and wind) (hereafter 'unadjusted songs'), and (2) within 400 m of experimental playbacks of recorded oil-well drilling noise broadcast at an average 88 dBc SPL at 10 m (hereafter 'noise-adjusted songs') (Curry et al. 2017). Unadjusted and noise-adjusted songs differed significantly for several acoustic parameters (Curry et al. 2017). When compared to recordings made under natural ambient noise conditions, Baird's sparrows recorded in the presence of noise decreased the peak frequency of their songs and altered five out of eight song syllables. Three of the five altered song syllables were introductory syllables, while the remaining two were trill syllables (Curry et al. 2017). Two introductory syllables displayed decreased frequency parameters, while one

introductory syllable displayed increased frequency. One trill syllable displayed increased power, and the second trill syllable displayed decreased power and shorter duration (Curry et al. 2017).

From these song recordings, I made 28 song exemplars ($n_{noise-adjusted} = 14$, $n_{unadjusted} = 14$) from 28 different individuals in the program Audacity (Audacity Team 2018). To make a song exemplar, I used three different songs from the same focal male. Next, I spaced these songs at ~ 10 s (natural spacing) for 5 min (Cartwright et al. 1937). To reduce background and wind noise, I filtered each exemplar below 1000 Hz with a roll-off of 48 dB. Finally, to control for peak amplitudes across exemplars, I standardized the peak amplitude of the song exemplar (Grabarczyk et al. 2019).

Ambient Noise

To characterize ambient noise levels, I recorded ≥ 20 s of ambient noise using a Zoom H4n Pro Digital Recorder (Zoom, Tokyo, Japan) immediately after each main trial. I made these ambient noise recordings by holding the device directly upwards at the location of the song speaker. I ensured that the device microphones were angled at 90° and that the maximal recording volume was used for each ambient noise recording. I made these ambient noise recordings as uncompressed audio (WAV files at 48 kHz sampling rate, 16-bit resolution). I used Raven Pro (v. 1.5) to extract the Average Power (dB) and Peak Power (dB) of four different frequency bands for each ambient noise recording using a Hann window function with a fast Fourier transformation length of 512 samples, 3 dB bandwidth set at 135 Hz and overlap of 50% (Table A3). Frequency band one included all possible frequencies in the ambient noise recording (0-24 kHz). Frequency band two included the frequency range below Baird's sparrow song (0-2 kHz). Frequency band three included the approximate frequency range of Baird's sparrow song (2-12 kHz). Finally, frequency band four included the approximate frequency range above Baird's sparrow song (12-24 kHz).

I collected and extracted ambient noise values because I intended to use those as independent variables in subsequent analyses. However, I found that average wind speeds of > 5 km/h 'peaked' the microphone, leading to truncated measurements in Raven Pro. Given that 64% of trials occurred in conditions where average wind speeds exceeded 5 km/h, ambient noise values were not included in subsequent analyses (Table A3).

STATISTICAL ANALYSES

Fixed and Random Factors

My playback experiments sought to determine if the territory-defense behavior of focal males during main trials differed between song treatments (noise-adjusted vs. unadjusted songs), between noise treatments (quiet vs. and noisy) and if there was an interaction between these treatments. To accomplish this I fitted generalized linear mixed-effects models to analyze four focal male responses: (1) “songs,” total number of songs per trial, (2) “calls,” total number of calls per trial, (3) “flybys,” total number of flybys per trial and, (4) “song latency” the time elapsed from the start of the trial until the focal male’s first song (s). To account for the repeated measures design, I used the focal male’s identity as a random factor. I used the categorical variables of song treatment (0 = unadjusted and 1 = noise-adjusted) and noise treatment (0 = quiet and 1 = noisy) as fixed effects. I also explored the influence of five independent variables on focal male responses so that I could control for their effects if necessary. These independent variables included: (1) “Julian date,” Julian date of playback experiment, (2) “start-time,” start time of the trial (min), (3) “average wind speed,” average wind speed recorded immediately after the trial (km/h), (4) “starting distance,” focal male’s distance from the song speaker at the beginning of the trial (m), and (5) “treatment order,” treatment order of noise presentation (0 = quiet first and 1 = noise first). Variables 1-3 were centered around the mean.

Model Selection

I began by fitting each response variable with three different distributions, (1) Poisson, (2) nbinom1 (negative binomial distribution, linear parameterization) and, (3) nbinom2 (negative binomial distribution, quadratic parameterization) (Brooks 2020). This resulted in a total of twelve models, all of which included the five aforementioned independent variables. Next, to determine the best distribution for each response variable, I used Akaike’s Information Criterion (AIC_c) for small sample sizes to compare a response variable’s three models. The lowest-scoring models for each response variable were selected as the best distribution, and these distributions were used in subsequent models.

After this, I inspected the lowest scoring models of each response variable for significant independent variables. Independent variables were considered significant at $\alpha = 0.05$. Any independent variables identified as significant were included in subsequent models.

Next, I fitted each model with an interaction term between the categorical fixed effects of song treatment and noise treatment. Because count data often include more zeros than what is expected for Poisson or negative binomial distributions (Heilbron 1994), I assessed my three count data variables for zero-inflation. This was done by building two additional models for each of these response variables. These models included: (1) a model with constant zero-inflation (a single zero-inflation parameter applying to all observations), and (2) a model with complex zero-inflation (zero-inflation predicted by the interaction term) (Brooks et al. 2017). I inspected models that converged for significant interaction terms.

If the interaction term was non-significant, I deleted it from the model to decrease problems resulting from collinearity (Quinn and Keough 2002). If the interaction term was removed, I reassessed my data for zero-inflation by building three models for each response variable. Each model included the categorical fixed effects of song treatment and noise treatment. The three models included: (1) a non-zero inflated model, (2) a constant zero-inflation (an intercept-only) model, and (3) a complex zero-inflation (zero-inflation predicted by fixed effects) model (Brooks et al. 2017). As above, I then compared a response variable's three models using AIC_c and selected the lowest scoring model for interpretation.

R Packages Used

I completed all analyses using R Statistical software (R Core Team 2020), and effects were considered significant at $\alpha = 0.05$. To develop generalized linear mixed-effects models, I used the package `glmmTMB` 1.0.1 (Brooks 2020). To compare models using AIC_c , I used the package `bblme` 1.0.23.1 (Bolker 2020). To graph focal male responses, I used the package `ggplot2` 3.3.1 (Wickham 2020).

RESULTS

Total songs produced by focal males in trials ranged from 0 to 37 (mean = 11.59, SD = 10.03, songs/trial). AIC_c model selection among preliminary models supported a negative binomial (`nbinom1`) distribution (For detailed results see Appendix; Table A4, Table A5). There

was no interaction between song treatment and noise treatment on the total songs ($P = 0.379$, non-zero-inflated model, Table A6). AIC_c model selection among main effects models supported the non-zero-inflated model (Table A7; Table A8). In this model, song treatment (noise-adjusted or unadjusted songs) did not influence the total number of songs (Table 2; Figure A4). There was a significant effect of noise on total songs, such that focal males sang less in response to simulated territorial intrusions in noisy trials when compared to quiet trials (Table 2; Figure A4). Although the focal male's starting distance was identified as an influential variable in the preliminary analysis (Table A5), this variable did not have a statistically significant effect in the final model selected for analysis (Table 2).

Total calls produced by focal males in trials ranged from 0 to 56 (mean = 6.79, SD = 11.40, call/trial). AIC_c model selection among preliminary models supported a negative binomial (nbinom1) distribution (Table A4; Table A5). There was no interaction between song treatment and noise treatment on total calls ($P = 0.564$, non-zero-inflated model, Table A6). AIC_c model selection among main effects models supported the non-zero-inflated model. In this model, song treatment did not have an influence on the total number of calls (Table 2). When compared to quiet trials, focal males tended to call more in noisy trials, however this result fell short of statistical significance ($P = 0.065$, Table 2; Figure A5). There was a significant effect of start time and average wind speed on calls (Table 2). Fewer calls were produced with earlier start times (Table 2). Meanwhile, more calls were produced with higher wind speeds (Table 2).

Total flybys over the song speaker by focal males in trials ranged from 0 to 15 (mean = 1.18, SD = 2.28, flyby/trial). AIC_c model selection among preliminary models supported a Poisson distribution (Table A4; Table A5). There was no interaction between song treatment and noise treatment on the number of total flybys ($P = 0.267$, non-zero-inflated model, Table A6). AIC_c model selection among main effects models of flybys supported the constant zero-inflation model (Table A8). In this model, song treatment did not influence the total number of flybys (Table 2). However, focal males did more flybys over the song speaker in noisy trials (Table 2; Figure A6). There was also a significant effect of focal male's starting distance and Julian date on total number of flybys; When focal males had a closer starting distance and when playbacks occurred earlier in the season, individuals engaged in more flybys (Table 2).

In 83% of trials, focal males responded to simulated intrusions by singing. Of these main trials, song latency ranged from 10-300 s per trial (mean = 71.36, SD = 76.79, song latency

(s)/main trial). AIC_c model selection among preliminary models supported a negative binomial (nbinom2) distribution (Table A4; Table A5). Unlike other models, there was a significant interaction between song treatment and noise treatment on song latency ($P = 0.028$, Table 2). Focal males took longer to respond with song when presented unadjusted songs broadcast in conjunction with noise (Table 2; Figure 3). However, when main trials consisted of noise-adjusted songs broadcast with noise, song latency returned to normal (i.e., unadjusted songs broadcast without noise) (Figure 3). Lastly, there was a significant effect of treatment order such that song latency decreased when noise was presented first (Table 2).

Table 2. Final models of focal male responses selected for interpretation. All categorical variables were dummy coded: song treatment (0 = unadjusted vs. 1 = noise-adjusted), noise treatment (0 = quiet vs. 1 = noise), and treatment order (0 = quiet then noise vs. 1 = noise then quiet). Bold font represents statistical significance ($P < 0.05$).

Analysis	Distribution	Parameter	Estimate	SE	P value
Songs	Negative Binomial (Nbinom1)	(Intercept)	2.30	0.23	P < 0.001
		Song Treatment (Noise-Adjusted)	0.34	0.24	0.156
		Noise Treatment (Noise)	-0.28	0.12	0.018
		Starting Distance	-0.00	0.00	0.114
Calls	Negative Binomial (Nbinom1)	(Intercept)	1.06	0.31	0.001
		Song Treatment (Noise-Adjusted)	0.00	0.32	0.998
		Noise Treatment (Noise)	0.36	0.19	0.065
		Start Time	-0.01	0.00	P < 0.001
		Average Wind Speed	0.09	0.04	0.014
Flybys	Zero-Inflated Poisson with constant zero inflation	Conditional Model			
		(Intercept)	-0.25	0.41	0.541
		Song Treatment (Noise-Adjusted)	0.00	0.41	0.992
		Noise Treatment (Noise)	0.33	0.17	0.057
		Julian Date	-0.04	0.01	0.005
		Starting Distance	-0.02	0.01	0.004
		Zero-inflation model			
		(Intercept)	-3.18	1.03	0.002
Song Latency	Negative Binomial (Nbinom2)	(Intercept)	4.10	0.21	P < 0.001
		Song Treatment (Noise-Adjusted)	0.13	0.27	0.627
		Noise Treatment (Noise)	0.70	0.24	0.003
		Treatment Order (1)	-0.50	0.21	0.020
		Song Treatment (Noise-Adjusted) * Noise Treatment (Noise)	-0.74	0.34	0.028

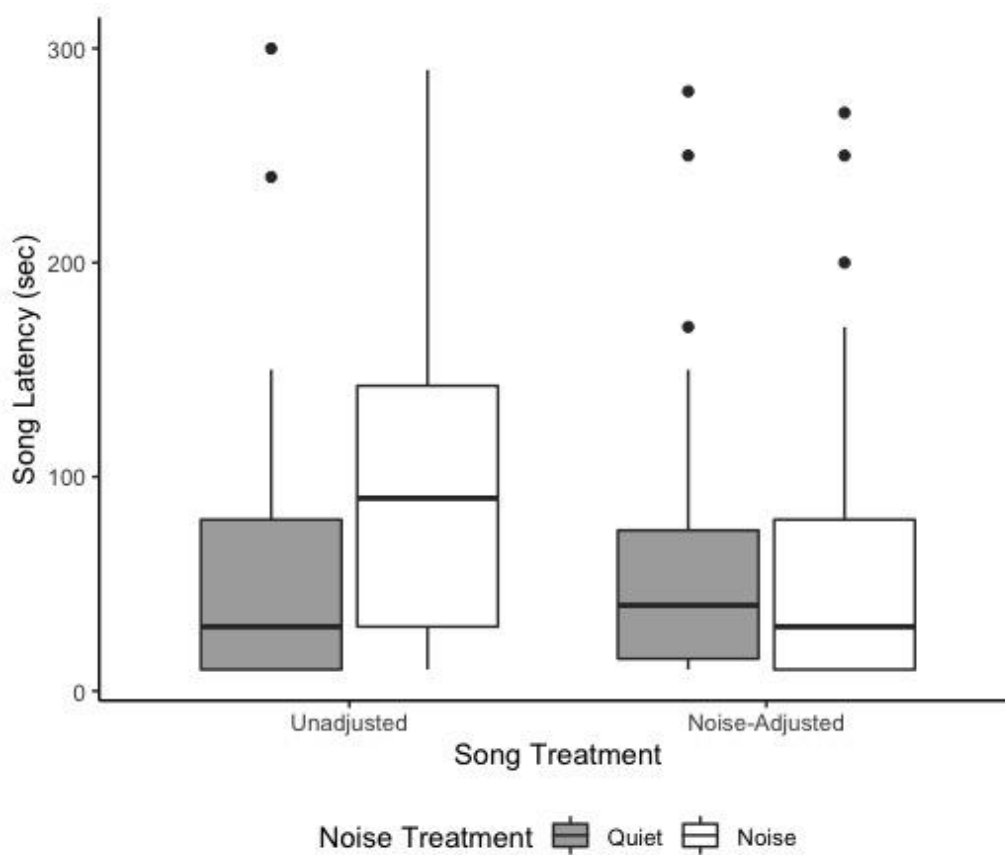


Figure 3. Song latency (s) of focal males ($n_{\text{individuals}} = 63$) in trials ($n_{\text{trials}} = 115$) by song treatment ($n_{\text{unadjusted-trials}} = 57$; $n_{\text{noise-adjusted-trials}} = 58$), and noise treatment ($n_{\text{quiet-trials}} = 60$; $n_{\text{noise-trials}} = 55$). Boxes represent the Inter-Quartile Range (IQR), and horizontal lines within boxes represent medians. Vertical lines (whiskers) denote upper and lower quartile ranges. Black dots represent outliers.

DISCUSSION

I found that song latency differed between noise-adjusted songs and unadjusted songs broadcast with noise. Focal males responded by singing sooner to noise-adjusted songs when compared to unadjusted songs in the presence of oil-well drilling noise. This suggests that in Baird's sparrows, noise-adjusted songs are easier to acoustically detect than unadjusted songs in noisy conditions. Therefore, noise-adjusted songs may partially restore acoustic communication in noise. In general, however, responses to noise-adjusted and unadjusted songs were similar. This suggests that noise-induced adjustments to songs do not alter the information encoded within. In other words, song types appear to be functionally equivalent in terms of information conveyed. However, territory-defense behaviors were strongly influenced by noise treatment. In noisy conditions, males sang less, called more, and engaged in more flybys over the song speaker. As discussed below, several mechanisms could be responsible for these behavioral changes.

Noise-Adjusted Songs Improve Detection and Maintain Song Content

My results indicate that song latency was mediated by an interaction between song treatment and noise treatment. Focal males took longer to respond with song to unadjusted songs in the presence of noise when compared to ambient noise conditions. Indeed, other studies have found agonistic responses to be delayed under noisy conditions (Kleist et al. 2016, Lenis and Guillermo-Ferreira 2020). This result suggests that the acoustic detection of unadjusted songs is constrained by competing noise, potentially due to acoustic masking. In contrast, when individuals were presented noise-adjusted songs broadcast with noise, their song latency was similar to that of unadjusted songs broadcast without noise. These results suggest that the song adjustments made by Baird's sparrows were effective in allowing songs to be heard better in the presence of noise, as has been reported in black-capped chickadees (*Poecile atricapillus*) (Lazerte et al. 2017) and great tits (*Parus major*) (Pohl et al. 2012). Thus, noise-adjusted songs might be considered adaptive in the sense that such signals can facilitate resident males to more quickly acoustically detect an intruder on their territory under noisy conditions.

Surprisingly, however, the remaining focal male responses did not vary with song treatment. This may suggest that male Baird's sparrows could not discriminate between song types, or that the differences in noise-adjusted songs and unadjusted songs are not biologically

important in male-male competition. This lack of discrimination is surprising because these song types differ significantly across several acoustic parameters (Curry et al. 2017) and because my above results suggest that the acoustic detection of song types differs. The lack of discrimination between song treatments in my research contrasts with findings from similar studies which have reported that focal male response differs when presented noise-adjusted and unadjusted songs in quiet conditions (Luther and Magnotti 2014, Curry et al. 2018). For example, Curry et al. (2018) concluded that because male Savannah sparrows displayed weaker responses (e.g., fewer attacks, wing flicks) to playbacks of noise-adjusted songs when compared to unadjusted songs in quiet environments, encoded information likely differed between unadjusted and noise-adjusted songs. In this way, noise-adjusted songs may have been perceived by focal males as less threatening.

Noise Alters Territorial-Defense Behavior

In this study, the presence or absence of noise significantly influenced focal male territory-defense behavior. The number of flybys increased significantly, as did the number of calls (although not statistically significant) in the presence of noise. These results suggest that focal males became more aggressive or were more willing to escalate to physical conflict under noisy conditions. Indeed, in other sparrow species, an increased number of flybys past experimental speakers broadcasting conspecific songs has been determined as a reliable predictor of attack and an unequivocal sign of aggression (Searcy and Beecher 2009). In Baird's sparrows, calls are thought to increase during intense territorial conflicts (Green et al. 2020). If increased flybys and calls indeed represented increased aggression in the presence of noise, perhaps elevated stress levels induced by the noise is the causal mechanism underlying these results. Corticosterone is a glucocorticoid hormone involved in the endocrine stress response of birds (Romero et al. 2009), and research has found that individuals have higher corticosterone levels in habitats inundated with anthropogenic noise (Blickley et al. 2012b, Davies et al. 2017, Curry et al. 2018, Kleist et al. 2018). Additionally, several studies have found that individuals in noisy territories have more aggressive responses to simulated territorial intrusions (Phillips and Derryberry 2018, Grabarczyk et al. 2019, Wolfenden et al. 2019). Although not explicitly measured, some studies have suggested that elevated stress levels induced by anthropogenic noise may contribute to more aggressive responses (Phillips and Derryberry 2018, Wolfenden et al. 2019).

Although focal males sang fewer songs in the presence of noise, this may not conflict with the above interpretation of heightened aggression in the midst of noise. Song rate is a reliable predictor of aggression in some species (Baker et al. 2012) but not others (Searcy et al. 2006, Akçay et al. 2013). Other forms of signaling behavior, such as song-overlapping (Dabelsteen et al. 1997) or low-amplitude soft songs (Templeton et al. 2012), might convey aggressive motivation in Baird's sparrows. However, my study did not measure these additional song behaviors.

In a different interpretation, fewer songs but increased flybys past the experimental speaker might indicate that focal males were behaving in a manner that would allow for more information to be gleaned about the simulated rivals (Phillips and Derryberry 2018, Grabarczyk et al. 2019, Wolfenden et al. 2019). In general, ambient background noise reduces the active space of acoustic signals and moving closer to the signal source would allow receivers to better attend to the encoded information in signals (Brenowitz 1982, Lohr et al. 2003, Kleist et al. 2016). Furthermore, movement-based responses might allow focal males to spot the simulated rival if one was present. In this way visual information could be used as an additional means to determine the threat level posed by the intruder (McGregor and Falls 1984, Anderson et al. 2013). Lastly, focal males singing fewer songs during simulated territorial intrusions would prevent the creation of additional acoustic interference caused by their own signals (Akçay et al. 2020).

It is also possible that males sang less and increased the number of calls during noisy trials because the presence of noise altered individuals' perceived predation risk (Frid and Dill 2002). In other studies, anthropogenic noise has been implicated with increased perceived risk of predation in a variety of taxa (Quinn et al. 2006, Rabin et al. 2006, Shannon et al. 2016a). In a more general sense, perceived predation risk is a key shaper of behavior as the consequences of ignoring potential danger can be lethal (Lima and Dill 1990, Stanford 2002). Thus, individuals are predicted to temporarily halt or modify behaviors (e.g., foraging, attempting to attract mates) in exchange for vigilance or alarm calling in scenarios where perceived predation risk is acutely elevated (Ferrari et al. 2009, Engqvist et al. 2015). In avian studies, individuals often decrease song rate or amplitude when a real or experimentally simulated predator is near (Abbey-Lee et al. 2016, Akçay et al. 2016). This response is thought to occur because predators may eavesdrop on the songs of signalers to determine their location (Mougeot et al. 2000, Krams 2001). Indeed,

in the context of Baird's sparrows, individuals tend to cease singing when aerial predators are present (Cartwright et al. 1937, Waldinger, *personal observation*).

Regardless of the reason for them, these results suggest that noise-adjusted signals can partially, but not completely, compensate for the challenges presented by anthropogenic noise to acoustic communication. Additionally, the presence of noise appears to strongly influence male territory-defense behavior. These behavioral changes might contribute to the decline of this species in a variety of ways. For example, if the presence of noise increases aggression or requires males to get closer to rivals to assess their threat-level, the potential for physical conflicts would likely increase (Grabarczyk et al. 2019). When individuals engage in physical conflict, they may incur physical injuries (Clutton-Brock et al. 1979) or be more vulnerable to predation (Jakobsson et al. 1995, Brick 1998). In the context of the latter, predation risk may increase because physical conflicts can be visually conspicuous to predators (Jakobsson et al. 1995, Brick 1998). Furthermore, individuals in conflict may also experience greater predation risk because fighting can reduce an individual's vigilance due to distraction (Jakobsson et al. 1995, Brick 1998). Anthropogenic noise is also hypothesized to act as a cognitive distraction in species (Chan and Blumstein 2011, Grade and Sieving 2016). Therefore, engaging in physical conflict in habitats inundated with anthropogenic noise might exacerbate predation risk due to mechanisms related to distraction. Furthermore, all proposed interpretations of the results result in trade-offs among behaviors. If individuals spend more time searching for rivals or vigilant because of increased perceived predation risk, a likely outcome is less time spent foraging (Quinn et al. 2006, Klett-Mingo et al. 2016). This trade-off between behaviors could jeopardize an individual's ability to gain mass essential for homeostasis or successful fall migration (Kölzsch and Blasius 2008, Huey et al. 2012, Ware et al. 2015).

Finally, while my results do not readily indicate that focal males were able to distinguish between song types, intersexual interactions may be impacted by noise-adjusted signals (Halfwerk et al. 2011a). In some avian species, females select mates based on song characteristics such as trill performance because it likely is an honest signal of male quality (Ballentine et al. 2004, Caro et al. 2010). Females are expected to be more discriminating than males with respect to attending to information encoded in song as mating with a low-quality male could jeopardize a female's reproductive success (Catchpole and Slater 2008). As previously detailed, the noise-adjusted songs of Baird's sparrows display alterations to song trills

(Curry et al. 2017). However, additional research is required to determine what, if any, role song plays in mate selection in this species and if noise-adjusted songs influence mate selection.

Still, it is possible that these interpretations inflate the impacts of noise on Baird's sparrow agonistic behavior. Individuals may habituate or become less reactive towards noise with repeated exposure (Dong and Clayton 2009, Nedelec et al. 2016). Therefore, the impacts of noise on territory-defense behavior may wane over time. Additionally, my study design examined only focal male responses to acoustic signals and did not include the use of a decoy or taxidermic mount. As a result, this study design may not have produced results representative of real territorial conflicts in this species. For example, visual cues, particularly for avian species living in open habitats, may be used in conjunction with acoustic cues to determine the location or threat level of potential rivals (McGregor and Falls 1984). Thus, attending to visual signals may safeguard communication in the presence of anthropogenic noise (Brumm and Slabbekoorn 2005, Hebets and Papaj 2005, Partan and Marler 2005, Akçay and Beecher 2019). Furthermore, in the absence of a decoy or taxidermic mount, the interpretation of more flybys past the experimental speaker during noisy trials as more aggressive is speculative as focal males did not have an item to attack (Searcy and Beecher 2009, Searcy et al. 2014).

CONCLUSION

My study contributes to the limited body of research dedicated to investigating how anthropogenic noise and noise-adjusted signals influence receiver behavior. Noise-adjusted Baird's sparrow songs may partially improve acoustic detection in the presence of noise. Yet, unlike other studies, territorial-defense behavior did not differ between unadjusted and noise-adjusted songs. This may suggest that focal males could not discriminate between song types or that the differences between noise-adjusted songs and unadjusted songs are not biologically meaningful in the context of male-male competition. Instead, focal male responses were most strongly influenced by the presence or absence of noise. While it is uncertain what mechanism(s) caused these behavioral changes, it seems reasonable to conclude that anthropogenic noise constitutes a disturbance to this species.

SUMMARY AND MANAGEMENT IMPLICATIONS

The field of conservation behavior advocates the use of behavioral indicators to help pinpoint anthropogenic disturbances for populations or species (Berger-Tal et al. 2011). Identifying specific anthropogenic disturbances can facilitate the development of targeted management techniques (Sutherland 1998, Berger-Tal et al. 2011, Madliger 2012). In my study, I used territorial-defense behavior as a behavioral indicator and found that the noise-adjusted songs of Baird's sparrows may partially restore acoustic communication in noise. However, I found that the presence of anthropogenic noise significantly altered individual behavior, potentially in ways that could negatively impact the fitness of males living in noisy environments.

Behavioral changes displayed by Baird's sparrows in the presence of noise could be resolved by reducing noise. Noise reduction can be accomplished by implementing structural mitigation measures, like noise barriers, around infrastructure (Blickley and Patricelli 2010). However, additional vertical infrastructure may negatively impact Baird's sparrow abundance. Indeed, evidence suggests that Baird's sparrows, as well as other grassland songbird species, tend to avoid sites with vertical anthropogenic structures (Nenninger and Koper 2018). Alternatively, noise reduction can be accomplished by implementing operational mitigation measures, like restricting oil and gas development and operations to months when migratory birds, such as Baird's sparrows, are not present (Blickley and Patricelli 2010). However, this form of mitigation might be logistically or economically untenable.

Perhaps the best way to manage noise and other forms of habitat disturbance to Baird's sparrow is to do so indirectly through landscape-scale planning (Dumyahn and Pijanowski 2011). Generally, Baird's sparrow abundance is impacted most severely by habitat loss and fragmentation as this can minimize patch size and introduce habitat edges (Davis 2004, Dale et al. 2007). To minimize habitat loss and fragmentation caused by the construction of new oil and gas infrastructure, the creation of new infrastructure should be restricted to already degraded sites while avoiding intact habitat cores (Kight et al. 2012, Thompson et al. 2015, Raynor et al. 2017). This action would be further optimized if it occurred in conjunction with the gradual decommissioning of infrastructure and reclamation of roads located in better quality habitat (Bernath-Plaisted and Koper 2016, Nenninger and Koper 2018). Additionally, because Baird's sparrow may also be sensitive to non-native plant species, reclaimed areas should be re-seeded

with a native seed to prevent the colonization of non-native plant species (Dale et al. 2007, Fansler and Mangold 2011). My recommended management approach is conceptually similar to the land-sparing approach found in agricultural literature where discrete purposes (i.e., conservation or intense agricultural production) are assigned to specific land parcels (Green et al. 2005, Fischer et al. 2008, Phalan et al. 2011). The strength of this approach is that it addresses the cumulative impacts of oil and gas development (Daniel and Koper 2019). Finally, although my research focused exclusively on Baird's sparrow, this management approach would stand to benefit multiple imperiled grassland species.

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APPENDIX

Table A3. Average Power (dB) and Peak Power (dB) values measured for four frequency bands from ambient noise recordings using Raven Pro (v. 1.5). This table displays only the values of ambient noise recordings when wind was < 5 km/h (50 of 135 dyads). The values from the right and left channels were averaged.

Parameter	Frequency band	Average	Min.	Max.	Range	SD
Average Power (dB)	Frequency Band 1 (0-24 kHz)	57.13	45.50	72.90	27.40	6.67
	Frequency Band 2 (0-2 kHz)	67.43	55.90	83.60	27.70	6.87
	Frequency Band 3 (2-12 kHz)	41.99	27.40	66.50	39.10	6.99
	Frequency Band 4 (12-24kHz)	28.69	20.90	43.80	22.90	2.52
Peak Power (dB)	Frequency Band 1 (0-24 kHz)	95.49	79.80	112.70	32.90	7.73
	Frequency Band 2 (0-2 kHz)	95.29	79.80	112.70	32.90	7.86
	Frequency Band 3 (2-12 kHz)	77.66	57.60	103.50	45.90	9.45
	Frequency Band 4 (12-24kHz)	45.82	33.60	80.70	47.10	8.19

Table A4. AIC_c selection results from preliminary independent variable models. Selection occurred between *nbinom1*, *nbinom2*, and Poisson distributions.

Analysis	Model	ΔAIC_c	AIC_c	df
Songs	Nbinom1	935.4	0.0	8
	Nbinom2	966.6	31.2	8
	Poisson	1069.8	134.5	7
Calls	Nbinom1	699.8	0.0	8
	Nbinom2	716.7	16.9	8
	Poisson	906.2	206.4	7
Flybys	Poisson	358.8	0.0	7
	Nbinom2	360.7	1.9	8
	Nbinom1	360.7	1.9	8
Song Latency	Nbinom2	1242.1	0.0	8
	Nbinom1	1246.3	4.3	8
	Poisson	3928.6	2686.5	7

Table A5. Preliminary models of independent variables inspected for significance. The categorical variable “Treatment Order” was dummy coded: (0 = quiet then noise vs. 1 = noise then quiet). Bold font represents statistical significance ($P < 0.05$).

Analysis	Distribution	Parameter	Estimate	SE	<i>P</i> value
Songs	Negative Binomial (Nbinom1)	(Intercept)	2.27	0.21	<i>P</i> < 0.001
		Julian Date	-0.00	0.01	0.825
		Start Time	0.00	0.00	0.357
		Average Wind Speed	-0.03	0.03	0.272
		Starting Distance	-0.01	0.00	0.055
		Treatment Order (1)	0.29	0.23	0.213
Calls	Negative Binomial (Nbinom1)	(Intercept)	1.61	0.33	<i>P</i> < 0.001
		Julian Date	-0.01	0.00	0.509
		Start Time	-0.01	0.00	<i>P</i> < 0.001
		Average Wind Speed	0.09	0.04	0.015
		Starting Distance	-0.01	0.00	0.313
		Treatment Order (1)	-0.21	0.31	0.491
Flybys	Poisson	(Intercept)	-0.09	0.35	0.806
		Julian Date	-0.04	0.01	0.004
		Start Time	-0.00	0.00	0.069
		Average Wind Speed	-0.02	0.03	0.620
		Starting Distance	-0.01	0.01	0.021
		Treatment Order (1)	-0.48	0.39	0.221
Song Latency	Negative Binomial (Nbinom2)	(Intercept)	4.45	0.20	<i>P</i> < 0.001
		Julian Date	-0.01	0.00	0.312
		Start Time	-0.00	0.00	0.906
		Average Wind Speed	0.02	0.03	0.534
		Starting Distance	-0.00	0.00	0.536
		Treatment Order (1)	-0.48	0.22	0.028

Table A6. Preliminary models inspected for significant interactions. Models selected for interpretation (see Table 2) and models that failed to converge are not displayed. All categorical variables were dummy coded: song treatment (0 = unadjusted vs. 1 = noise-adjusted), noise treatment (0 = quiet vs. 1 = noise), and treatment order (0 = quiet then noise vs. 1 = noise then quiet). Bold font represents statistical significance ($P < 0.05$).

Analysis	Distribution	Parameter	Estimate	SE	P value
Songs	Negative Binomial (Nbinom1)	(Intercept)	2.36	0.24	$P < 0.001$
		Song Treatment (1)	0.24	0.26	0.346
		Noise Treatment (1)	-0.40	0.18	0.028
		Starting Distance	-0.01	0.00	0.089
		Song Treat. (1) * Noise Treat. (1)	0.21	0.24	0.379
Songs	Zero-Inflated Negative Binomial (Nbinom1) with constant zero inflation	Conditional Model			
		(Intercept)	2.36	0.24	$P < 0.001$
		Song Treatment (1)	0.24	0.26	0.346
		Noise Treatment (1)	-0.40	0.18	0.028
		Starting Distance	-0.01	0.00	0.089
		Song Treat. (1) * Noise Treat. (1)	0.21	0.24	0.379
		Zero-inflated Model			
(Intercept)	-20.66	4833.30	0.997		
Calls	Negative Binomial (Nbinom1)	(Intercept)	1.13	0.33	0.001
		Song Treatment (1)	-0.13	0.39	0.739
		Noise Treatment (1)	0.25	0.27	0.362
		Start Time	-0.01	0.00	$P < 0.001$
		Average Wind Speed	0.09	0.04	0.017
		Song Treat. (1) * Noise Treat. (1)	0.23	0.39	0.564
Calls	Zero-Inflated Negative Binomial with constant zero inflation	Conditional Model			
		(Intercept)	1.13	0.33	0.001
		Song Treatment (1)	-0.13	0.39	0.739
		Noise Treatment (1)	0.25	0.27	0.362
		Start Time	-0.01	0.00	$P < 0.001$
		Average Wind Speed	0.09	0.04	0.017
		Song Treat. (1) * Noise Treat. (1)	0.23	0.39	0.564
		Zero-inflated Model			
(Intercept)	-20.34	6032.35	0.997		
Flybys	Poisson	(Intercept)	-0.65	0.42	0.127
		Song Treatment (1)	0.27	0.45	0.549
		Noise Treatment (1)	0.62	0.25	0.015
		Julian Date	-0.04	0.01	0.004
		Starting Distance	-0.01	0.01	0.017
		Song Treat. (1) * Noise Treat. (1)	-0.36	0.33	0.267

Table A7. Preliminary main effects models. Models selected for interpretation (see Table 2) and models that failed to converge are not displayed. All categorical variables were dummy coded: song treatment (0 = unadjusted vs. 1 = noise-adjusted), noise treatment (0 = quiet vs. 1 = noise), and treatment order (0 = quiet then noise vs. 1 = noise then quiet). Bold font represents statistical significance ($P < 0.05$).

Analysis	Distribution	Parameter	Estimate	SE	P value
Calls	Zero-Inflated Negative Binomial with constant zero inflation (Nbinom1)	Conditional Model			
		(Intercept)	1.06	0.31	0.001
		Song Treatment (1)	-0.00	0.32	0.998
		Noise Treatment (1)	0.36	0.19	0.065
		Start Time	-0.01	0.00	$P < 0.001$
		Average Wind Speed	0.09	0.04	0.014
		Zero-Inflated Model			
		(Intercept)	-20.03	5182.52	0.997
Flybys	Poisson	(Intercept)	-0.50	0.40	0.208
		Song Treatment (1)	0.05	0.40	0.892
		Noise Treatment (1)	0.41	0.17	0.014
		Julian Date	-0.04	0.01	0.004
		Starting Distance	-0.01	0.01	0.014

Table A8. AIC_c selection of preliminary main effects models. Selection occurred between: (1) non-zero inflated models, (2) zero-inflated models with constant inflation, and (3) zero-inflated models with complex zero inflation.

Model	AIC _c	Δ AIC _c	df
Song (1)	926.2	0.0	6
Song (2)	NA	NA	7
Song (3)	NA	NA	9
Call (1)	696.1	0.0	7
Call (2)	698.4	2.3	8
Call (3)	NA	NA	10
Flyby (2)	358.9	0.0	7
Flyby (1)	360.5	1.6	6
Flyby (3)	NA	NA	9

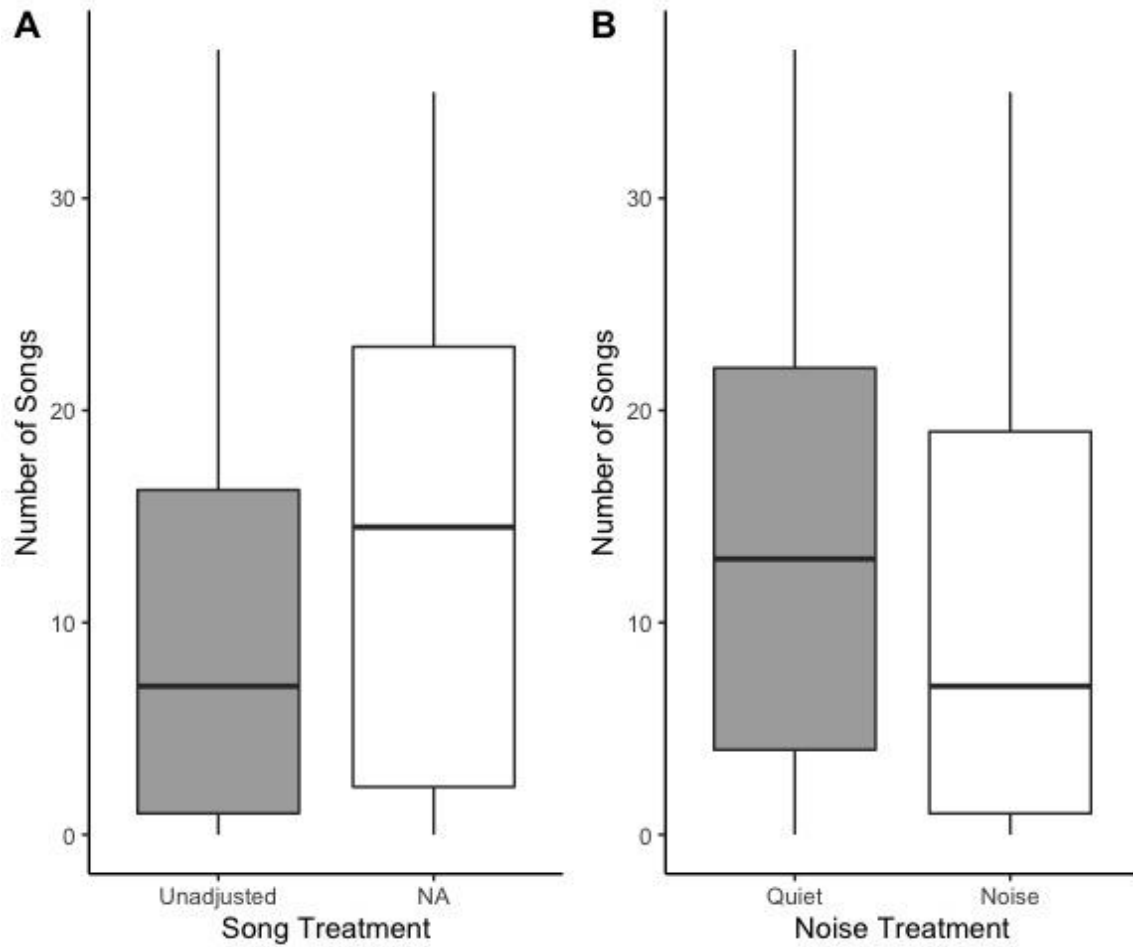


Figure A4. Number of songs by focal males ($n_{\text{individuals}} = 69$) in trials by (A) Song treatment ($n_{\text{unadjusted-trials}} = 68$; $n_{\text{noise-adjusted-trials}} = 70$), and (B) noise treatment ($n_{\text{quiet-trials}} = 69$; $n_{\text{noise-trials}} = 69$). Boxes represent the Inter-Quartile Range (IQR), and horizontal lines within boxes represent medians. Vertical lines (whiskers) denote upper and lower quartile ranges. Black dots represent outliers.

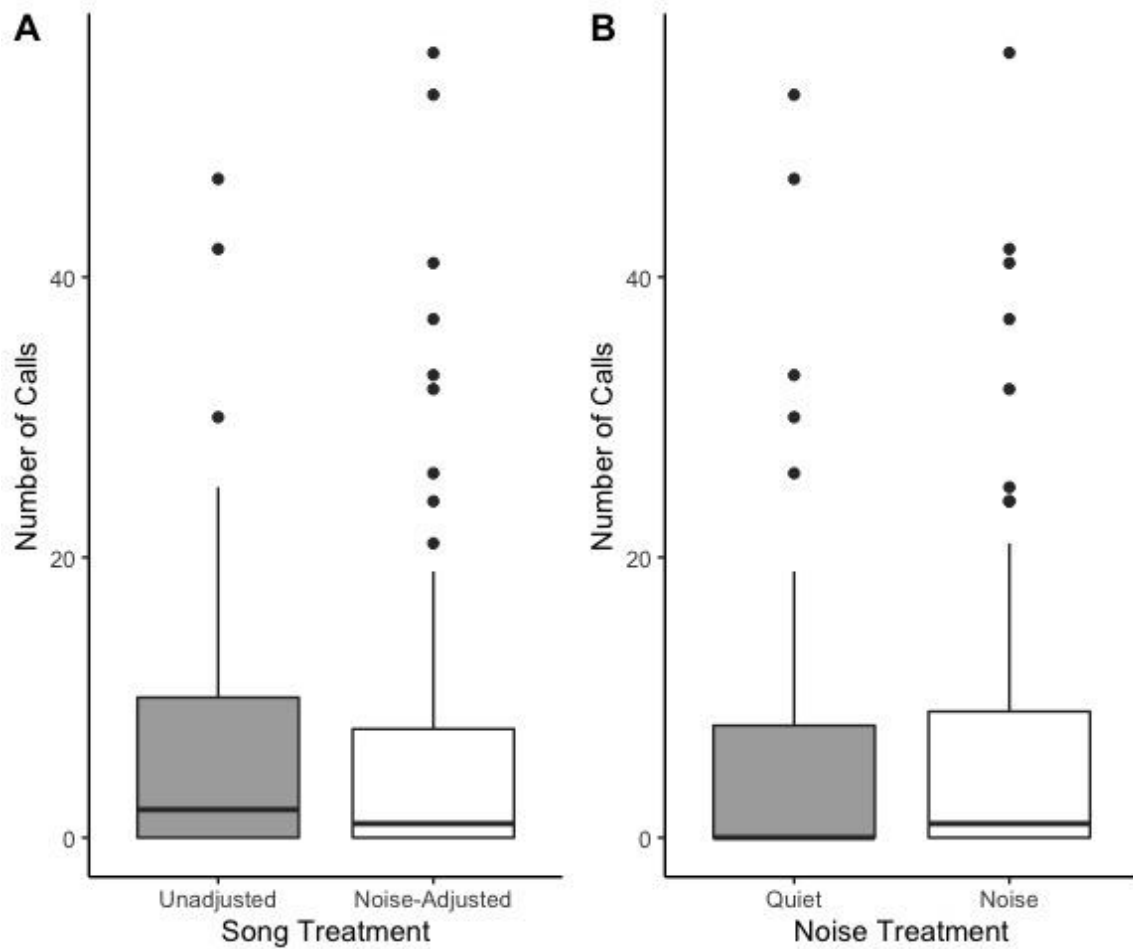


Figure A5. Number of calls by focal males ($n_{\text{individuals}} = 69$) in trials by (A) Song treatment ($n_{\text{unadjusted-trials}} = 68$; $n_{\text{noise-adjusted-trials}} = 70$), and (B) noise treatment ($n_{\text{quiet-trials}} = 69$; $n_{\text{noise-trials}} = 69$). Boxes represent the Inter-Quartile Range (IQR), and horizontal lines within boxes represent medians. Vertical lines (whiskers) denote upper and lower quartile ranges. Black dots represent outliers.

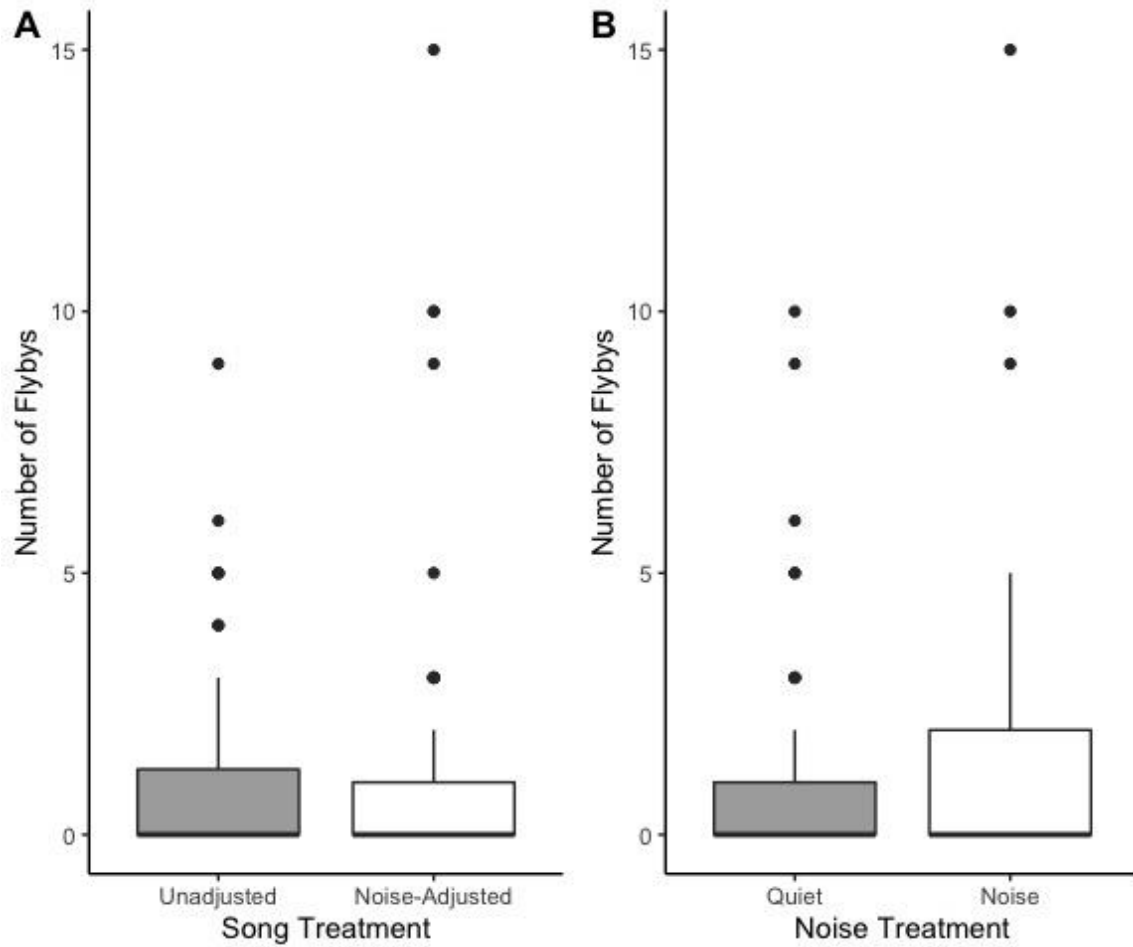


Figure A6. Number of flybys by focal males ($n_{\text{individuals}} = 69$) in trials by (A) Song treatment ($n_{\text{unadjusted-trials}} = 68$; $n_{\text{noise-adjusted-trials}} = 70$), and (B) noise treatment ($n_{\text{quiet-trials}} = 69$; $n_{\text{noise-trials}} = 69$). (A) Song treatment and (B) noise treatment. Boxes represent the Inter-Quartile Range (IQR), and horizontal lines within boxes represent medians. Vertical lines (whiskers) denote upper and lower quartile ranges. Black dots represent outliers.