

Song Discrimination Between Two Subspecies of Vesper Sparrow:
Pooecetes gramineus affinis and *Pooecetes gramineus confinis*

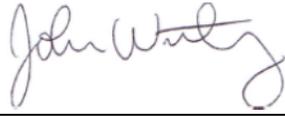
by
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A Thesis Submitted in partial fulfillment
of the requirements for the degree
Master of Environmental Studies
The Evergreen State College
June, 2021

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This Thesis for the Master of Environmental Studies Degree
by Timothy Leque

has been approved for
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A handwritten signature in cursive script, reading "John Withey". The signature is written in black ink and is positioned above a horizontal line.

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Abstract

Song Discrimination Between Two Subspecies of Vesper Sparrow: *Pooecetes gramineus affinis* and *Pooecetes gramineus confinis*

Timothy Leque

Vesper sparrows (*Pooecetes gramineus*) are grayish-brown songbirds of the family Passerellidae, found in open spaces such as prairies, meadows, and sagebrush steppe. Like other songbirds, male vesper sparrows sing throughout the breeding season to attract mates, as well as to delineate and defend territories. The Oregon vesper sparrow (*Pooecetes gramineus affinis*) is a subspecies endemic to the Pacific Northwest that has been identified as a species of conservation concern throughout its range. There is little research on the Oregon vesper sparrow, with some uncertainty regarding taxonomic status due to a lack of genetic analysis. Western vesper sparrows (*Pooecetes gramineus confinis*) occur east of the Cascade Mountains and are common and widespread throughout the western United States. The degree to which the boundary of the Cascades affects speciation among vesper sparrows is unknown, as wintering ranges for the two subspecies overlap in California. Differences in territorial response to conspecific song playbacks are often associated with evolutionary divergence between subspecies. This study involved exposing individual male vesper sparrows of two subspecies to playback of conspecific and heterospecific songs. The vesper sparrows in this study demonstrated some discrimination between subspecific song with differences in flight behavior between playback treatments. There were also differences in behavioral responses to playback, with Oregon vesper sparrows responding to playback with more singing, and western vesper sparrows responding to playback with more flights.

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Acknowledgements

This project would not have been possible without the help from numerous individuals, I apologize if I have left anyone out of my acknowledgements.

First, I would like to thank my friends and colleagues with the Avian Conservation Program, who all contributed to this project with their support and ornithological knowledge. Specifically, I would like to thank Veronica Reed because her expertise in the execution and analysis of playback experiments improved the quality of this thesis tremendously. I also would like to thank Gary Slater, who proposed the idea of a subspecific playback experiment involving the Oregon vesper sparrow, advised on study design, and assisted with the logistics of field work. Without Gary's consistent support in and out of the field this project simply would not have happened. Also, thanks to Karla Kelly who helped conduct playback experiments and whose expertise on the vesper sparrows of the Rainier Training Areas was a major contribution.

Several people from Joint Base Lewis-McChord's Fish and Wildlife Program also made essential contributions to this project. Jim Lynch facilitated access to the Artillery Impact Area and Rainier Training Areas and advised on locations of vesper sparrows. Jim was especially supportive of my thesis and engaged me in some great discussions on the Oregon vesper sparrow. Dan Grosboll provided his explosive ordinance expertise to ensure my safety while collecting data in the Artillery Impact Area. Dan also recommended several state wildlife areas for recording vesper sparrows that I would end up using as backup study areas.

Thanks to John Withey, my thesis reader who helped me with the statistical analysis of this project and provided substantive feedback on my thesis document.

I would also like to thank several other people who helped me along the way: Emily Lind from Klamath Bird Observatory provided song recordings of vesper sparrows in Oregon and advised me on equipment and protocol for recording birds in the field. Alison Styring of The Evergreen State College advised me on song recording and sampling design very early on when I was first planning my thesis and got me started in the right direction. Sanders Freed from the Center for Natural Land Management provided access to Tenalquot Preserve.

And a special thank you to my partner, Gabriela Santiago, who assisted with field work in eastern Washington and was patient and supportive throughout this time-consuming project.

Chapter 1: Introduction

Washington State is home to two subspecies of vesper sparrow (*Pooecetes gramineus*): the western vesper sparrow (*Pooecetes gramineus confinis*), which inhabits shrub-steppe and pine savannah habitats in eastern Washington, and the Oregon vesper sparrow (*Pooecetes gramineus affinis*), which is limited to remnant coastal prairies in western Washington. The breeding ranges for these subspecies do not overlap, and they are somewhat different morphologically. The Oregon vesper sparrows are slightly smaller on average, and with darker upperparts and a buff-tinged belly (King, 1968a, 1968b; Pyle, 1997; Rising, 1996). This study aimed to determine whether the two subspecies of vesper sparrow are able to discriminate between each other's song, and whether they exhibit any other differences in territorial response behavior.

The two subspecies of vesper sparrow that occur in Washington also differ considerably in population size and distribution. *P. g. confinis* is widespread in the Columbia Basin, Great Basin, and Great Plains while *P. g. affinis* is limited to remnant grassland habitat in the Puget Lowlands in Washington; and in the Willamette Valley, Umpqua Valley, Klamath Mountains, and Rogue Basin in Oregon (Altman, Stinson, & Hayes, 2020). While *P. g. confinis* is among the most abundant breeding birds found in sagebrush steppe habitat east of the Cascades, *P. g. affinis* is a rare breeder within grassland habitats of coastal Washington and Oregon. In recent decades *P. g. affinis* has experienced population decline, enough that they have been listed as endangered in Washington and U.S. Fish and Wildlife service has been petitioned to list them under the Endangered Species Act (Altman et al., 2020; American Bird Conservancy, 2016).

The subspecies designations for *Pooecetes gramineus* are accepted by most authors, but there has never been a genetic analysis to confirm their distinctiveness. Rising (1996) asserts that the subspecies of *Pooecetes gramineus* are indistinguishable in the field, and that *P. g. affinis* and *P. g. confinis* cannot be reliably distinguished in the hand. The variable and individualistic nature of *Pooecetes gramineus* songs make it impossible for human observers to distinguish the subspecies by ear. While humans may not be able to distinguish the song syllables and sequences unique to a particular subspecies, it is possible that the birds themselves have this ability, and that these differences contribute to reproductive barriers.

Most Passerines use song as a territorial signal, and this plays a key role in both reproductive selection as well as the defense of resources. Among the oscines, these signals are learned by juvenile birds (Baptista & Petrinovich, 1986). Cultural transmission of songs within isolated bird populations over time can result in song divergence, which likely contributes to genetic divergence and speciation (Mason et al., 2017; Podos & Warren, 2007). When divergent populations meet again in secondary contact zones, these diverged signals can act as reproductive barriers between subspecies or even smaller populations (Toews, 2017). Male songbirds may not perceive a foreign song or dialect as an immediate threat, whereas the song of a local bird indicates a confirmed competitor.

One common method for determining territorial response to birdsong used by ornithologists is the playback experiment. Exposing subjects (birds) to different stimuli (song recordings), researchers can tally territorial responses given by subjects to each treatment. Statistical analysis can then be used to determine whether the sample of individual birds exposed to stimuli differed in their responses to one stimulus type over another. Review of multiple playback studies show that birds typically respond more aggressively to songs of their own

subspecies over songs from a foreign subspecies (T. H. Parker, Greig, Nakagawa, Parra, & Dalisio, 2018). However, birds also react more aggressively to local songs versus those of a disjunct population, and therefore results from playback experiments must be carefully examined before drawing any conclusions regarding apparent discrimination.

The essence of this thesis is the use of song playback to help determine whether *P. g. affinis* and *P. g. confinis* are able to discriminate between each other's songs. The results of these playback trials can provide evidence supporting or contradicting the current subspecies designations of *Pooecetes gramineus* in western North America. Due to the limited research on *Pooecetes gramineus* taxonomy, and the imperiled status of *P. g. affinis*, any additional information on distinctions between *P. g. confinis* will assist in listing determinations of *P. g. affinis*. The hope for this document is to provide additional evidence informing the taxonomic status of *P. g. affinis*. This thesis has been written in four chapters. Chapter one (this introduction) outlines the research question and methods, as well as the context for why this research is important. Chapter two includes the literature review, which provides background on the biological function of birdsong, the history and applications of playback experiments, and summarizes subspecies descriptions of *Pooecetes gramineus*. Chapter three describes the field and analysis methods that were used to address the research questions. Chapter four concludes this thesis with a discussion of the biological meaning that could be interpreted from the results of the experiment.

Chapter 2: Literature Review

The purpose of this thesis is to determine whether two subspecies of vesper sparrow (*P. g. affinis* and *P. g. confinis*) can discriminate between each other's songs. Answering this question requires comprehension of the role that signaling plays in the life histories of songbirds. One must also understand how avian signaling has evolved into the behavior we observe today, and how it continues to change. The spatial extent of this study is the Pacific Northwest region of North America, as well as geographic features within the region such as the Cascade Mountains. The primary method of this study is the use of audio playbacks, a popular experimental method that has contributed considerable knowledge on the communication of animals (Falls, 1992). This method has been used to infer the degree of speciation among populations of numerous avian taxa (T. H. Parker et al., 2018). As for the subjects of this research, the taxonomy of *Pooecetes gramineus* is based on a variety of sources, including several dating back to the 19th century. There has never been a genetic analysis of *P. g. affinis*, and Jones and Cornely (2002) describe the subspecies designation of the vesper sparrow as “weakly defined to moderately distinct.” The song of *Pooecetes gramineus* has been characterized as variable and individualistic (Kroodsma, 1972; Ritchison, 1981), having implications on the designs, results, and discussion of this study.

Bird Song: Function and Evolution

Birds produce sound as a means of communication, broadcasting signals throughout their environment to be received by conspecifics sharing the same habitat. Simple calls are often used to communicate information of immediate importance such as the location of individuals (Marler, 2004) or the presence of predators (Smith, 1965), but more complex ‘songs’ are

primarily produced by males and are usually associated with breeding behavior. It is widely accepted that the main functions of birdsong are for sexual selection, and for the defense and sorting of territorial boundaries (Collins, 2004). While other bird groups extensively produce sound as a means for communication and often ‘sing’, complex singing behavior is most developed in the Passerines, or songbirds, the largest and most diverse order of birds. Singing is essential to the breeding ecology of nearly all passerine birds and can determine reproductive success (Potvin, Crawford, MacDougall-Shackleton, & MacDougall-Shackleton, 2015).

Nearly all birds possess syrinxes, noise producing organs believed to have developed in an extinct common ancestor. These organs serve no apparent purpose besides the production of noise signals and are therefore believed to provide an essential biological purpose. Birds have evolved to utilize a wide variety of social strategies, ranging from solitary to highly communal, and sound communication often plays a vital role in these interactions. Aural communication in birds is highly variable, not only between orders and species, but also phenologically. This variability is demonstrated by the contrast between winter flocking behavior, when contact and alarm calls are used to locate conspecifics as well as evade predators, and spring breeding territoriality, when these same species will partition themselves separately within the environment and compete for mates and resources.

Sexual Selection

Behaviors associated with sexual selection and breeding are incredibly diverse in birds. Examples of variable mating strategies include the coordinated ‘dances’ of Clark’s grebes (*Aechmophorus clarkii*), the lekking of the greater sage-grouse (*Centrocercus urophasianus*), building and presentation of decorative structures by bowerbirds (Ptilonorhynchidae), and food gifting, or ‘tidbitting’ among gallinaceous birds (Stokes & Williams, 1971). In the Passerines,

song appears to serve a primary role in the selection of reproductive partners. The time of the year when passerines sing is concurrent with the breeding season, when birds are selecting mates and partitioning resources within their habitat.

Important traits determining mate selection in birds are thought to include some measures of evolutionary fitness, and these can be physical, such as diet-influenced plumage ornaments (G. E. Hill, 1990) or acoustic, such as fast trill rates or wide frequency bandwidths (Ballentine, Hyman, & Nowicki, 2004; Collins, 2004). These characteristics often reflect higher-quality males who are more successful in the acquisition and defense of resources. Certain structural characteristics of a bird's song can be associated with differences in body mass, virility, and other measures of sexual fitness (Moseley & Podos, 2014). Projecting vocalizations requires sophisticated motor function and stamina, and a strong singer indicates good physical condition and strong motor skills to nearby conspecifics, advertising the survivability of that individual (Moseley & Podos, 2014). The ability to perform well is vital to a male bird's breeding success, as higher quality performances are more likely to solicit a response from a female (Ballentine et al., 2004). Stress or lack of food during the developmental stages of a bird's life can be reflected in weaker vocal performance as a breeding adult, negatively influencing reproductive success (Moseley & Podos, 2014).

Another metric of birdsong that communicates an individual's fitness is repertoire size. Song repertoires are defined as the variety of syllables a bird is capable of performing, as well as the number of combinations in which those syllables are vocalized. Repertoire size is often associated with male survivorship, and females of several bird species have shown preferences for large song repertoires in both laboratory settings and in the field (Collins, 2004; Potvin et al., 2015). In a study of song sparrows (*Melospiza melodia*), large repertoires were associated with

territory possession and reproductive success, while birds with small repertoires were more likely to lose their territories (Hiebert, Stoddard, & Arcese, 1989). Another study of song sparrows found that repertoire size was more indicative of reproductive success than territory location (Potvin et al., 2015). Despite this research, the ways in which repertoire size is related to reproductive success is overall poorly understood. Some have hypothesized that the ability to learn more songs is related to the size of certain areas in the avian brain, which can be affected by developmental stress early in life (Collins, 2004). A reduced song repertoire may act as an indicator of poor overall fitness, rendering that male an undesirable partner (Nowicki, Searcy, & Peters, 2002). Song repertoire is undoubtedly an important function in sexual selection of many bird species, however the ways in which song repertoire conveys biological fitness to potential mates is poorly understood.

Male Territoriality

Territoriality is a common trait throughout the animal kingdom, and in migratory birds, territoriality is exhibited during the spring and summer when birds have migrated to their Northern breeding grounds. Passerine species often flock together for safety while on their wintering grounds but compete over space and resources during the breeding season. Animal territories can generally be defined as a large area in which breeding, nesting, and raising fledglings occurs. Territory boundaries, along with the resources within them are defended from neighboring conspecifics (Hinde, 1956). During the breeding season many passerines will restrict themselves to their territories, habitually signaling their ownership to others by singing and confronting any trespassers along territory boundaries (Hinde, 1956). Birdsong is widely considered to serve the dual function of attracting sexual partners while simultaneously repelling rival conspecifics competing for the same limited space and resources. The purpose of acoustic

signals among birds is therefore largely based on the identity of the receiver: a female seeking to mate or a competing male of the same species. In the same way that a song might communicate physical condition to a potential mate, this information is also received by male conspecifics that must determine whether to engage in a territorial dispute. A song that communicates physical prowess through increased vocal performance may deter weaker males from intruding into the territory (J. N. Phillips & Derryberry, 2017). For example, Moseley et al. (2013) found that swamp sparrows (*Melospiza georgiana*) responded less aggressively to songs with artificially weakened trill rates than to control songs. Those same birds also responded less aggressively to artificially strengthened trills, unless the subject was a strong vocal performer, in which case they responded more aggressively. Repertoire size is also associated with higher male performance, and males with smaller repertoires are often ejected from their territories (Hiebert et al., 1989).

Male vocal performance is not the only factor influencing territorial response to songs from conspecifics. Proximity of breeding territories also influences the strength of a male's response. The 'dear enemy phenomenon' is common throughout the animal kingdom, in which territorial (usually) males respond less aggressively to individuals from neighboring territories (Ydenberg, Giraldeau, & Falls, 1988). Among birds, these types of interactions are most common in breeding territory situations, with males responding less aggressively the closer a neighboring territory is to their own (Temeles, 1992). In other words, an individual might exhibit a weakened response to a song from a bird they are more familiar with, such as a male from an adjacent territory.

As male birds are the primary signalers during breeding, most studies of birdsong have focused on the responses of territorial males. Across the numerous studies of avian communication, these responses have been measured in a variety of ways. Songbirds will often

approach speakers broadcasting songs from conspecifics, and will even attack mounts coupled with song playback (Akçay, Tom, Holmes, Campbell, & Beecher, 2011). Distance to speaker has been a primary territorial response measure in many studies. ‘Soft’ or low frequency singing is a lesser known territorial behavior, but has been observed in many passerines and has been measured as a response in several studies (Searcy & Beecher, 2009). Another infrequent measure of territoriality is ‘wing waves’, in which a bird usually puffs itself and flutters its wings (Akçay et al., 2011; J. N. Phillips & Derryberry, 2017). Increased rate of birdsong is also commonly used as a response measure, but song type matching/switching and overlapping are less reliable responses, as research on their importance have produced variable results (Kolesnikova, Liu, Kang, & Opaev, 2019; Searcy & Beecher, 2009). Recent literature analyzing song as a response measure have focused on adjustments to the receiver’s signal in response to the original signaler (Illes, Hall, & Vehrencamp, 2006). ‘Latency,’ or the time elapsed between signal broadcast and the aforementioned responses, is another way territorial response can be quantified (McGregor, 1992). While distance to speaker or ‘signaler’ is considered the most reliable territorial response measure, many researchers choose to use a combination of behaviors to quantify how breeding birds react to competitive signaling, allowing for a more robust analysis.

Vocal Tutoring, Cultural Transmission and Evolution

Among the passerines, song is transmitted to offspring either innately or culturally, and these different learning mechanisms are exemplified by two distinct groups within the order. The suboscines, or Tyranni, have innate songs that young birds are able to produce even with the absence of a vocal tutor (Kroodsma & Konishi, 1991). In contrast, oscine species including the sparrows, thrushes, larks and finches have learned songs that are mimicked by young birds exposed to conspecific vocal tutors (Slater, 1986). Members of this group may even have an

innate preference for learning songs of their own subspecies (D. A. Nelson, 2000), but can also mimic other species songs when deprived of songs from their own (Kroodsma, 1972). Song learning often occurs on natal grounds, when young and developing birds are exposed to songs of their own species (Baptista & Gaunt, 1994), and later begin practicing their ‘plastic’ song during dispersal (Marler & Tamura, 1964). Studies of some species have concluded that vocal learning ceases once a bird is past the early developmental stage (Hiebert et al., 1989), while others suggest that birds continue to learn songs from neighbors into their first breeding season (D. A. Nelson, 2000).

For many birds, geographic isolation of breeding grounds can result in not only allopatric speciation, but also differences in culturally transmitted songs. These culturally transmitted songs can change over time due to imprecise copying by juveniles (Podos & Warren, 2007; Slater, 1986), but also through selection influenced by structural and temporal differences in the birds environments (Derryberry et al., 2018; Karin, Cicero, Koo, & Bowie, 2018; Slabbekoorn & Smith, 2002; Wilkins, Seddon, & Safran, 2013). Consequently, populations of a species geographically isolated in different ecosystems over an extended period would develop distinct differences in song traits. These effects are apparent in comparisons of historical and current song types from urban versus rural populations (Derryberry, 2011; Moseley, Phillips, Derryberry, & Luther, 2019), and rapid song divergence among small isolated groups of translocated individuals (K. A. Parker, Anderson, Jenkins, & Brunton, 2012). Species with high site fidelity often develop dialects between isolated populations (Baker & Cunningham, 1985), and if these dialects become different enough may act as breeding barriers, eventually leading to speciation (Toews, 2017). There are several examples contradicting this theory particularly in

hybrid zones (Kenyon, Alcaide, Toews, & Irwin, 2017), indicating that the link between cultural evolution and genetic isolation could be weak in some species.

While differences in culturally transmitted behavior cannot necessarily be equated to genetic differences, the former does seem to be a reliable indicator of the latter (Mason et al., 2017). It would be expected however, that the birds themselves, cuing into aspects of the signals not immediately apparent to humans (frequencies, song length), would be able to discriminate between the song of a closely related competitor and a more benign foreign individual (Mason et al., 2017). Recent studies continue to provide evidence of the correlation between genetic and acoustic differences between oscines at the species and subspecies levels (Demko, Sosa-López, & Mennill, 2019; Pegan et al., 2015; Sosa-López, Martínez Gómez, & Mennill, 2016). Summary of published literature on song recognition appears to support the assertion that genetically isolated bird populations can discriminate between each other's songs (Freeman & Montgomery, 2017; T. H. Parker et al., 2018).

Avian Biogeography of the Pacific Northwest

While birds are able to disperse and colonize new areas more easily than other terrestrial animals, geographic barriers do contribute to speciation among many populations by restricting movement and by producing stark climatic differences. In North America, large mountain ranges mostly running north to south, are massive physical barriers to animal dispersal and produce distinct climatic regions. It is no coincidence that mountain ranges often coincide with the boundaries of speciation for many organisms (Swenson & Howard, 2005). These geographic variations have resulted in elaborate species diversification among many families of birds. The dynamics of speciation across geographic barriers within the intermountain west are incredibly

complex (Behle, 1978; Stein, Kutner, Hammerson, Master, & Morse, 2000), and the ability of birds to disperse to desirable habitat adds further difficulty in generalizing these processes. Reconstructing the evolutionary histories of migratory birds is further complicated by differences in geographic area of breeding versus wintering ranges (Barker, Burns, Klicka, Lanyon, & Lovette, 2015). This section of the literature review focuses on the geographic extent of the study area, contrasting between coastal and interior habitats on either side of the Cascade mountain range.

The mountains along the Pacific Crest of North America act as a boundary between numerous endemic coastal bird species or subspecies and those of the interior west (Behle, 1978). While the avian endemism of coastal California west of the Sierra-Nevada mountains is well known, similar dynamics in the Pacific Northwest are present, with coastal Washington harboring more breeding and wintering bird species than in the interior of the state (Stein et al., 2000). Several endemic or near-endemic avian species of the Pacific Northwest include the red-breasted sapsucker (*Sphyrapicus ruber*), chestnut-backed chickadee (*Poecile rufescens*), and sooty grouse (*Dendragapus fuliginosus*); as well as numerous endemic subspecies such as the streaked horned lark (*Eremophila alpestris strigata*), Puget Sound white-crowned sparrow (*Zonotrichia leucophrys pugetensis*), and black merlin (*Falco columbarius suckleyi*). The Cascade Mountains act as a high-elevation barrier between coastal and interior habitats, despite a relatively short distance of just over 100 miles. The climatic and vegetative differences across this distance is remarkable with temperate forests of the Puget Lowlands on one end of the spectrum and the sagebrush steppe of the Columbia Plateau on the other, divided by the Pacific cordillera.

Despite the geographic barriers and climatic contrasts, there is still considerable gradation in ecotones within the Pacific Northwest, allowing for clinal zones among a variety of closely related bird species and subspecies. Well-studied examples of clines include the hybridization zone in Western Washington and Oregon between Townsend's warblers (*Setophaga townsendi*) and hermit warblers (*Setophaga occidentalis*) (Krosby & Rohwer, 2010), and hybrid zones among *Sphyrapicus* woodpeckers (Seneviratne, Davidson, Martin, & Irwin, 2016). While hybridization between different species might be the most visible example of this phenomenon, it also occurs between subspecies within secondary contact zones, where previously isolated population segments begin to overlap (Short, 1969). Hybridization between formerly isolated populations has been documented in a number of bird species, with a considerable amount of research on subspecies of white-crowned sparrows (Brooks & Wimberger, 2018; Lipshutz, Overcast, Hickerson, Brumfield, & Derryberry, 2017).

These clinal zones can be particularly dynamic in mountain environments, where habitat conditions are variable from year to year. Coupling this fact with the ability of birds to shift their breeding ranges based on annual habitat conditions produces a serious taxonomic challenge for scientists attempting to designate subspecies boundaries across mountain gradients. North American mountain ranges, including the Cascades, are known to be hotspots of hybridization due to their cooccurrence with species and subspecies boundaries (Swenson & Howard, 2005). The presence of intergradation between population segments occurring in these areas means that morphological traits can be an unreliable indicator of species status. Researchers wishing to determine the locations of boundaries may need to take into account genetic and behavioral differences as well.

Playback Experiments

Song playback is a tool most commonly known for its practical applications but has also been a popular experimental method in the fields of animal behavior and bioacoustics, particularly for birds. Playback is used by biologists, wildlife enthusiasts and hunters alike for drawing wildlife close enough to survey, view, photograph and kill; as well as by land managers for repelling certain animals from airfields, livestock and crops (Falls, 1992). Experimental playback conducted by researchers usually involves exposing animal subjects to recordings of audio stimuli broadcast through a speaker, either in the field or in laboratories. Often animal subjects are exposed to several different “treatments” in the forms of artificially manipulated animal signals, or more often, signals from conspecifics varying by geographic location. Avian playback experiments have contributed to knowledge on the pertinent structural characteristics of signals used in communication (Illes et al., 2006; Moseley et al., 2013), effects of anthropogenic noise on signaling (Luther & Magnotti, 2014; Moseley et al., 2019), parallels between species and song divergence (T. H. Parker et al., 2018), and determining taxonomic statuses (Alström & Olsson, 1999; Alström, Rasmussen, Olsson, & Sundberg, 2008; Randler et al., 2012). The number of playback studies testing differences in geographically separated populations of birds has allowed for meta-analyses attempting to generalize the cumulative results of these experiments (Freeman & Montgomery, 2017; T. H. Parker et al., 2018).

Playbacks have been used in numerous experiments involving a variety of taxa including mammals, reptiles, amphibians, insects, and fish but not unexpectedly, these methods have been utilized most frequently with birds. Although the use of playback on birds can be found in literature dating back to the 1930s, the first study employing experimental playback treatments was Dilger’s (1956) comparison of thrush (*Hylocichla* and *Catharus spp.*) responses to songs of

other species versus their own (Falls, 1992). Some of these early playback studies informed ornithologists on neighbor/stranger discrimination (Weeden & Falls, 1959), vocal tutoring (Thorpe, 1958), repertoires (Hinde, 1958), and important structural components of songs (Abs, 1963; Falls, 1992). While many playback studies test the responses of males actively defending territories, experiments measuring female response to playback are far more scarce (Falls, 1992). A large portion of these studies compare responses of territorial males to intrusions from different types of signals, what the subject believes to be other birds. These can be digitally manipulated versions of the original signal to determine structural characteristics subjects are responding to like trill rate (Illes et al., 2006) or frequency (Luther & Magnotti, 2014).

In 1984, Hulbert published *Pseudoreplication and the Design of Ecological Field Experiments*, a critical piece that spurred debate among practitioners of song playback experiments. Hulbert identified pseudoreplication as a common design flaw in many of the published studies involving ecological field experiments. Donald Kroodsma published several papers discussing the design of animal playback experiments, with a particular focus on pseudoreplication in the wake of Hulbert's work (Kroodsma, 1986, 1989). Many of the early playback studies had committed pseudoreplication (Kroodsma, 1989), and recent analysis of these studies found that they produce more variable results than experiments that adequately sampled stimuli (T. H. Parker et al., 2018). In many of these experiments, only one or a few songs would be selected as stimuli and explanatory variables. If the song selected happened to be from an individual with a below or above average song performance, this could in turn weaken or strengthen the response to one of the playback treatments. In 1992, *The Thornbridge Hall NATO ARW Consensus* was published summarizing best study design and execution practices recommended by practitioners throughout the field. Essentially, the authors argue for the

sampling of stimuli along with the sampling of subjects to accurately measure the response to the song types being tested. Several of the authors of the consensus revisited this work about a decade later (Kroodsma, Byers, Goodale, Johnson, & Liu, 2001; McGregor, 2000). Research published since the pseudoreplication debate have generally adopted these better study design practices, although there are still examples of recent studies committing this kind of sampling error (T. H. Parker et al., 2018).

Frequently the different types of signals used as test stimuli are chosen to represent individuals sourced from a finite geographic area. A large body of research on the role of song in the evolutionary divergence of passerines includes numerous studies employing playback experiments as the primary methodology. Male territorial responses have been tested for differences in subspecies (Liu, Lohr, Olsen, & Greenburg, 2008; Matessi, Dabelsteen, & Pilastro, 2001; Petrinovich & Patterson, 1981), regional dialects (D. A. Nelson, 1998; Petrinovich & Patterson, 1981), and simply local versus non-local birds (Searcy, Nowicki, & Hughes, 1997). In most of these studies, results suggest that birds can discriminate between songs of their own and those of 'foreign' individuals (Freeman & Montgomery, 2017). A meta-analysis of local versus foreign song discrimination found that treatments between subspecies produced the most convincing examples of vocal discrimination by subjects (T. H. Parker et al., 2018). Observing differences in male territorial response between songs of separate subspecies may indeed serve as an appropriate indicator of speciation.

Vesper Sparrow (*Pooecetes gramineus*)

Species Description

Pooecetes gramineus or the Vesper Sparrow, previously known as the “bay-wing bunting” and “grass finch”, is a member of the family Passerellidae, which includes towhees, sparrows, buntings and longspurs. The only member of their genus, *Pooecetes gramineus* are relatively large sparrows, colored grayish brown to light tan, with dark brown streaking (Jones & Cornely, 2002; Pyle, 1997). They can be differentiated from other similarly drab sparrows by a white eye-ring, white outer retrices, and chestnut-brown lesser coverts (Jones & Cornely, 2002; Pyle, 1997). There is little sexual dimorphism within the species, with female measurements averaging slightly smaller than males (Pyle, 1997).

Pooecetes gramineus is a Nearctic migratory passerine confined to North and Central America, with four recognized subspecies (Jones & Cornely, 2002). *Pooecetes gramineus gramineus*, or “Eastern vesper sparrow” occurs from along the east coast of North America to the western edge of their range, Minnesota down through Texas (Berger, 1968; Pyle, 1997).

Pooecetes gramineus confinis, also known as “Western vesper sparrow” or “Great Basin vesper sparrow” can be found from western Nebraska all the way to the eastern slopes of the Cascade mountains, and south into Mexico during winter (King, 1968b; Pyle, 1997). *Pooecetes*

gramineus affinis, the Oregon Vesper Sparrow can be found along the Pacific coast, west of the Cascade and Sierra Nevada mountain ranges (Altman, 2011, 2017; King, 1968a; Pyle, 1997).

Pooecetes gramineus altus, the “mountain vesper sparrow” has the most limited range, confined to parts of Arizona, New Mexico, Utah, and Colorado (Johnson & Dickerman, 2006; A. R. Phillips, 1964; Pyle, 1997).

Pooecetes gramineus received their common name “vesper sparrow” due to the fact they are often the last bird heard singing into the evening, with “vesper” translating to “evening” in Latin (Jones & Cornely, 2002). The males often sing from elevated perches, while females select nest sites on the ground, building small grass cups at the base of clumps of vegetation, sticks or sod (Jones & Cornely, 2002). *Pooecetes* forage on the ground, eating a mix of grass and forb seeds, but mostly insects during the breeding season. Mothers feed the young of the year primarily insects (Jones & Cornely, 2002).

Habitat used by *Pooecetes gramineus* can be generally characterized as dry open spaces dominated by short and sparse vegetation, with some shrub or tree cover and bare ground (Camp & Best, 1993; Dechant et al., 2002; Jones & Cornely, 2002). Wiens (1969) and Harrison (1974) both described *Pooecetes gramineus* microhabitat preferences as being “xeric, sparsely vegetated” (p. 40, p. 37). *Pooecetes gramineus* breed in a variety of ecosystems, including sagebrush steppe, montane meadows, cropland, sandplain grasslands, reclaimed surface mines, coastal prairie and desert shrub and grasslands (Dechant et al., 2002; Jones & Cornely, 2002; Vickery, Hunter, & Wells, 1999; Wray, Strait, Whitmore, & Sparrow, 1982). Historically, *Pooecetes gramineus* likely used early successional habitats created by natural disturbances such as wildfires, erosion, grazing and trampling by bison (Best & Rodenhouse, 1984; Jones & Cornely, 2002). Many of the current habitats used by *Pooecetes gramineus* can be described as edges of anthropogenic openings, with artificial disturbance regimes tied to human land management practices such as grazing, crop production, mowing, and prescribed burning. This preference for disturbed areas can lead *Pooecetes gramineus* to breed in less than ideal habitats, such as in active agricultural land (Rodenhouse & Best, 1983), mowed airports, and reclaimed surface mines (Wray et al., 1982). *Pooecetes gramineus* habitat preferences have been

characterized as ecotonal (Owens & Myres, 1973), breeding along fencerows adjacent to cropland (Roadhouse & Best, 1983) and within grassland-woodland transitions (Dechant et al., 2002; Finzel, 1964).

During the breeding season, male *Pooecetes gramineus* spend a large portion of their time singing from elevated perches to delineate and defend their territories (Jones & Cornely, 2002). Multiple studies have identified perches as an important factor during breeding territory selection (Berger, 1968; Best & Rodenhouse, 1984; Castrale, 1983; Dechant et al., 2002; Rodenhouse & Best, 1983; Schaid, Uresk, Tucker, & Linder, 1983; Wiens, 1969). Berger (1968) observed that *P. g. gramineus* preferred perches greater than seven and a half meters tall in territories along edges of woodland. Best and Rodenhouse (1984) found associations with *P. g. gramineus* territory selection and pairing success to proximity of fencerows and shrub cover in Iowa cropland. In this study the authors attributed this association to the availability of singing perches along fencerows in a landscape otherwise devoid of perches. Castrale (1983) found *P. g. confinis* perch selection was related to intershrub distance and shrub density across several breeding sites in Utah.

Structure seems to be the most important characteristic of adequate perches, as *Pooecetes gramineus* apparently have no preference for live versus dead shrubs (Best, 1972; Castrale, 1983). A variety of reported perch heights suggests that *Pooecetes gramineus* probably do not select from a fixed range of heights but utilize perches that contrast structurally from the dominant vegetation height across a site, as well as the heights and volumes of other available perches (Castrale, 1983). Similarly, Harrison (1977) found no height preference by *P. g. gramineus* using artificial perches in Michigan. Although perches are an important habitat

requirement of *Pooecetes gramineus*, they prefer low densities of elevated perches within a sparse grassland landscape.

Oregon Vesper Sparrow (*Pooecetes gramineus affinis*)

Miller provided the first formal description of *P. g. affinis* in 1888, although J. G. Cooper noted the presence of vesper sparrows in the Puget lowlands nearly 30 years prior (Suckley & Cooper, 1860). Miller (1888, pp. 404-405) differentiated *P. g. affinis* from neighboring subspecies by its smaller size, and "... having the ground color above buffy-brown rather than grayish-brown. All the lighter areas of the plumage (including crissum, under wing-coverts and lining of wings) suffused with pinkish buff." (Figure 1). Pyle's (1997) measurements of *P. g. affinis* were consistent with Miller's as being smaller than other subspecies of vesper sparrow and describes plumage characteristics as well: "upperparts medium-dark grayish brown; underparts white with a buff tinge" (p. 558). *P. g. affinis* has since been accepted as a distinct subspecies due to these physical differences as well as their geographic isolation from other vesper sparrows, west of the Pacific crest (Altman, 2017; King, 1968a; Pyle, 1997).

P. g. affinis spend April through July on their breeding grounds in Washington and Oregon, migrating in August and September to spend the remainder of the year on their wintering grounds in California (Altman, 2017). The current known *P. g. affinis* breeding range extends north into Washington, with the majority of birds breeding on the South Sound Prairies within Joint Base Lewis-McChord (JBLM), and a few occasionally spotted on the eastern side of the Olympic Peninsula, San Juan Islands, and along the lower Columbia River (Altman, 2017). In 1860, Suckley and Cooper wrote that *P. g. affinis* was "[r]ather abundant on the Nisqually plains, Puget Sound" (p. 200). This passage suggests that the current breeding sites of *P. g. affinis* on JBLM are likely within the core of their historical range in Washington. In Oregon, *P.*

g. affinis breed in the Willamette Valley, Umpqua Valley and Rogue Basin (Altman, 2017). *P. g. affinis* migrate to California during winter, where they are found at low elevations from the Central Valley to Northern Baja California (Erickson, 2008). During winter, *P. g. affinis* range overlaps with *P. g. confinis*, which makes monitoring the wintering habits of these subspecies difficult (Altman, 2017; Erickson, 2008). *P. g. affinis*' breeding range historically extended into Northern California as well as Southwest British Columbia and Northwest Washington, but the species has been extirpated from most of their former breeding locations in these areas (Altman, 2011, 2017; Beauchesne, 2002; Roger, 2000). As Altman (2017) points out, the northward and



Figure 1. Oregon vesper sparrow (*Pooecetes gramineus affinis*) on Joint Base Lewis-McChord, Washington.

southward range retractions experienced by *P. g. affinis* populations are consistent with common extirpation patterns among bird communities. Curnutt, Pimm & Maurer (1996) found that peripheral sites with variable abundance of sparrows had populations that were likely less resilient to random environmental factors than those sparrow populations in the cores of their ranges. This pattern parallels that of the *P. g. affinis* range contractions. Massive habitat loss and degradation, especially within the northern extent of *P. g. affinis*' former range (Chappell, Gee, Stephens, Crawford, & Farone, 2001), would explain the pattern of local extirpations on small, isolated remnant prairies. In this respect, the decline of *P. g. affinis* resembles that of other coastal prairie obligate species listed under the Endangered Species Act, such as the streaked horned lark (*Eremophila alpestris strigata*), Mazama pocket gopher (*Thomomys Mazama*), and Taylor's checkerspot butterfly (*Euphydryas editha taylori*).

Poocetes gramineus affinis range retraction also parallels those of other prairie-oak associated birds once more widespread across the Pacific Northwest, such as western meadowlark (*Sturnella neglecta*), western bluebird (*Sialia mexicana*), and slender-billed white-breasted nuthatch (*Sitta carolinensis aculeate*) (Altman, 2011). Similar trends of grassland bird habitat loss, habitat fragmentation and habitat degradation due to residential and agricultural development have been documented across the continent (Brennan & Kuvlesky Jr., 2005; Vickery & Herkert, 2001). These effects have been more pronounced in the Pacific Northwest, where available habitat was historically limited and of which only a small fraction remains (Chappell et al., 2001).

Current breeding sites of *P. g. affinis* include restored prairie, airports, river dredge deposits, Christmas tree farms, and grazed pastureland (Altman, 2017). Vickery, Hunter & Melvin (1994) found that *P. g. gramineus* reached a 50% rate of occurrence on grassland patches

20 hectares (50 acres) or more in area, and that in general, presence of *P. g. gramineus* was positively correlated with patch size; current breeding sites in Washington range in the hundreds of acres. In Washington, known *P. g. affinis* breeding populations occur on sites with artificial disturbance regimes. JBLM's prairies frequently burn due to artillery sparked wildfires as well as an active prescribed burn program. Airports throughout the region adhere to FAA mowing standards, and Columbia River dredge deposits are frequently covered with new material (U.S. Army, 2014). The largest populations of *P. g. affinis* in Washington (150-200 birds; Altman, 2017) occur on JBLM, where available habitat is regularly burned, approximately every three to five years (Hill, Kronland, & Martin, 2017; Tveten & Fonda, 1999). These burned areas are then seeded with native forbs and grasses to meet the installation's habitat restoration goals. JBLM's Fish and Wildlife program also manages perch structure in occupied and potentially occupied training areas to promote favorable conditions for *P. g. affinis* (Jim Lynch, personal communication). On JBLM, most *P. g. affinis* nests have been found at the base of native bunchgrasses, especially Roemer's Fescue (*Festuca roemeri*), the dominant plant species seeded onto restoration prairies (Kronland, Hill, & Martin, 2018). *P. g. affinis* regularly perch and sing from man-made structures such as tanks, signs, and airfield lights.

Sparsely vegetated habitat associated with regular exposure to fire was once widespread across the Southern Puget Sound's fescue-dominated prairies (Chappell & Crawford, 1997). Prairie-oak habitat throughout the Puget Sound region had been maintained through burning by Indigenous peoples, who burned tracts of land to aid in the production of root and berry crops as well as providing openings for hunting (Boyd, 1999; Deur & Turner, 2005; Norton, 1979). Indigenous people did not limit fires to the prairies; they also allowed them to carry into the forest (Deur & Turner, 2005), resulting in a much broader transitional edge between grassland

and prairie than what can now be found on the remaining prairies of JBLM. *P. g. affinis* breeding locations in Washington, are generally found along forest-prairie transitions on JBLM (Jim Lynch, personal communication). The colonization of the region by European and American settlers brought Indigenous burning practices to an end, which led to loss of prairie habitat to widespread conifer and shrub encroachment, particularly by Douglas fir (*Pseudotsuga menziesii*) and Scotch broom (*Cytisus scoparius*) (Foster & Shaff, 2003; Tveten & Fonda, 1999). The lack of fire and the colonization of open land by exotic pasture grasses introduced by homesteaders (White, 1980) has increased the height and density of vegetation on what were historically prairies (Dennehy et al., 2011). These changes have been especially dramatic in the northern reaches of *P. g. affinis*' former range in British Columbia and northern Puget Sound, resulting in extirpation of those populations (Altman, 2011; Beauchesne, 2002; White, 1980). Removal of regular disturbance, introduction of exotic plant species and the resulting change of vegetation structure, has most likely degraded habitat in *P. g. affinis*' former range to a degree that most of those prairie remnants have been rendered unusable.

In the Willamette Valley of Oregon, home to a population of *P. g. affinis*, modern agricultural burning has replaced historical indigenous burning (Johannessen, Davenport, Millet, & McWilliams, 1971). Many of the other *P. g. affinis* breeding sites in Oregon are ranches and ranges subject to cattle grazing, which may also mimic natural disturbances (Altman, 2017). These anthropogenic disturbance regimes are likely creating and sustaining the open, sparse areas of patchy vegetation that *P. g. affinis* favor for breeding, somewhat resembling the natural disturbances of the past.

In recent years, *P. g. affinis* have become increasingly rare in the Pacific Northwest, with current estimates at 300 individuals left in Washington State (Altman et al., 2020). This

subspecies currently holds state protected status throughout its entire breeding and wintering ranges, and the U.S. Fish and Wildlife Service has been petitioned to list *P. g. affinis* under the federal Endangered Species Act (ABC, 2016). Limited published literature is available on this subspecies, so there is a need for additional research to inform conservation efforts. Altman (2017) states “[t]he highest priority research need is to understand the role of demographic parameters on population status. Two other important research needs include genetic evaluation of the boundaries of subspeciation, and determination of factors influencing populations on the wintering grounds.”

Western Vesper Sparrow (*Pooecetes gramineus confinis*)

The Western vesper sparrow (*Pooecetes gramineus confinis*), also known as the Great Basin vesper sparrow, was first described by Baird in 1858, and is the largest of the *Pooecetes gramineus* subspecies (Jones & Cornely, 2002; King, 1968b; Pyle, 1997; Rising, 1996). Compared with *P. g. gramineus*, *P. g. confinis* also has a thinner bill, slender streaking and paler gray coloration, but can be difficult to distinguish from *P. g. affinis*, even in hand (Rising, 1996). Plumage differences between the subspecies are also apparent in juvenile birds, with young *P. g. confinis* exhibiting lighter edging and buff along the back and crown (Figure 2; King, 1968b). Pyle (1997) offers a similar description of bill and coloration, adding that the tail of *P. g. confinis* average relatively longer than other subspecies. He also notes that the *P. g. confinis* of the Columbian Plateau average darker in plumage, leading to the designation of these birds as a separate subspecies by Jewett et al. (1953). However, this is the only source that separates the Columbian *P. g. confinis* as a distinct subspecies and Pyle attributes the darker coloration to intergradation with nearby populations of *P. g. affinis* (Pyle, 1997; Roger, 2000). The vesper sparrows of the Columbia Basin are widely considered synonymous with *P. g. confinis* across



Figure 2. Western vesper sparrow (*Poocetes gramineus confinis*) in Wenas Wildlife Area near Ellensburg, Washington.

authors (AOU, 1957; Jones & Cornely, 2002; King, 1968b; Pyle, 1997; Rising, 1996; Roger, 2000).

The Northern extent of *P. g. confinis*' range reaches into eastern British Columbia (K. J. Nelson & Martin, 1999), with the southern extent of their wintering range in Mexico (Pulliam & Mills, 1977). *P. g. confinis* breeds as far west as the eastern slopes of the Sierra-Nevada mountains and as far east as western Nebraska (Pyle, 1997). Throughout western North America, *P. g. confinis* is a common species associated with sagebrush (*Artemisia spp.*) steppe habitats across a wide altitudinal range, although they can also be found in open juniper and ponderosa

pine woodlands as well as montane meadows (Dechant et al., 2002; Finzel, 1964; King, 1968b; Schaid et al., 1983). Due to the large availability of these habitats in the intermountain west, *P. g. confinis* is far more widespread and numerous than *P. g. affinis*, whose suitable habitat is scarce within their already limited range.

The general habitat characteristics of *Poocetes gramineus* are consistent with the preferences of *P. g. confinis*: sparse and open grasslands with scattered perches. In Wyoming, for example, *P. g. confinis* were found to be common in grasslands that were transitioning to forest, characterized as grassland with a few scattered conifers, early successional trees and moderate shrub cover (Finzel, 1964). In the Northern Great Plains, presence of sagebrush was a limiting factor for *P. g. confinis* on reclaimed surface mines, suggesting that available perches are a habitat requirement of *P. g. confinis* (Schaid et al., 1983). Castrale (1983) found that in Utah, *P. g. confinis* showed a preference for the most prominent perches available, and showed an association with intermediate shrub densities relative to the other species present. While strongly associated with sagebrush, *P. g. confinis* showed no preference for living versus dead shrubs in Montana, suggesting the structural characteristics the plants provided was more important than any species-dependent characteristic (Best, 1972). Cumulatively these studies show that *P. g. confinis* can be found in sparse, open habitats with scattered perches across Western North America, and are particularly abundant in sagebrush steppe as this ecosystem is often characterized by their preferred habitat structure.

Although *P. g. confinis* is not of immediate conservation concern, as a species *Poocetes gramineus* have been declining since the 1960s across North America (Altman, 2017; Sauer et al., 2014). *P. g. confinis* is a common native of the grassland bird communities found across the intermountain west, with an affection for sagebrush steppe habitat. Across North America

scientists are alarmed by losses in biodiversity, with avifauna experiencing population declines over the last several decades. North America has seen the loss of nearly 3 billion birds, with sparrows and grassland species experiencing some of the greatest loss in numbers (Rosenberg et al., 2019). Conservation of grassland birds has been described as an “unfolding conservation crisis” (Brennan & Kuvlesky Jr., 2005), and *P. g. confinis* is one of many species that make up these communities. In Washington, the sagebrush steppe of the Columbia plateau is host to several state endangered and threatened species such as the Columbian sharp-tailed grouse (*Tympanuchus phasianellus*), pygmy rabbit (*Brachylagus idahoensis*), and ferruginous hawk (*Buteo Regalis*). This region historically was dominated by sagebrush, and although sizable tracts of native sagebrush steppe is still intact, about a quarter of the plateau’s land is used for agriculture (Groves et al., 2000). While much of the remaining sagebrush communities occur on publicly owned lands, very little (4%) has been set aside for biodiversity protection, and resource extraction is allowed across most of it (Groves et al., 2000). So, while *P. g. confinis* is not currently threatened, the species is likely declining along with grassland bird communities in general, and especially in Washington, the sagebrush habitat on which it depends is increasingly fragmented and degraded.

Song of the Vesper Sparrow

The song of the vesper sparrow was originally described in detail by Borror (1961), and is generally characterized as a series of two to four introductory whistles followed by one to two seconds of variable trills (Kroodsma, 1972; Rising, 1996; Sibley, 2003). Several authors have noted that the repertoires of the vesper sparrow are highly variable and individualistic (Hing, 2014; Kroodsma, 1972; Ritchison, 1981). Kroodsma (1972) found that *P. g. affinis* had remarkably large repertoires, noting that one individual sang 218 different song variations among

a sample of 400 songs. These large repertoire sizes may be important for sexual selection, similar to other sparrow species (Hiebert et al., 1989). Kroodsma (1972) suggested that juvenile vesper sparrows in the Willamette Valley learned songs from adults while on their natal grounds and noted weak dialects in the introductory notes of *P. g. affinis* songs. In Minnesota, Ritchison (1981) found no evidence of dialects among *P. g. gramineus* and attributed the differences from Kroodsma's (1972) findings to high dispersal rates related to occupancy of regularly disturbed breeding habitats. Ritchison (1981) also noted very little sharing of song syllables between individual vesper sparrows and no instances of shared song sequences. Hing (2014) found that in Montana, male *P. g. confinis* did not share song characteristics among neighboring territories, but with birds an intermediate distance away. Hing (2014) suggested these results could be attributed to vesper sparrows using song complexity as a mechanism for mating selection, with individual males attempting to differentiate themselves from their neighbors. These similarities in songs of intermediate distances could be explained by fidelity to the general location of natal sites. In published literature there have been no studies comparing songs between subspecies of vesper sparrows, and the species has not been the subject of playback experiments.

Several descriptions of an extended flight song can also be found in the limited literature on *Pooecetes gramineus* songs. Wells & Vickery (1994) described the extended flight song in detail, and discussed some possible functions of this signal. During the 1993 breeding season, the extended songs were mostly heard on one day in late July. Wells & Vickery suggested that the extended flight song might serve the purpose of rounding up juvenile birds together, possibly as a warning of nearby predators. This behavior was also mentioned by Burroughs (1905) who gave a colorful description of the song:

“One summer, up in the Catskills, I added another name to my list of ecstatic singers—that of the vesper sparrow. Several times I heard a new song in the air, and caught a glimpse of the bird as it dropped back to the earth. My attention would be attracted by a succession of hurried, chirping notes, followed by a brief burst of song, then by the vanishing form of the bird. One day I was lucky enough to see the bird as it was rising to its climax in the air, and to identify it as the vesper sparrow. The burst of song that crowned the upward flight of seventy-five or one hundred feet was brief; but it was brilliant and striking, and entirely unlike the leisurely chant of the bird while upon the ground. It suggested a lark, but was less buzzing or humming. The preliminary chirping notes, uttered faster and faster as the bird mounted in the air, were like the trail of sparks which a rocket emits before its grand burst of color at the top of its flight.”

J. Burroughs, *The Ways of Nature* (1905).

Listing Considerations for the Oregon Vesper Sparrow

The subjects of this study were chosen because of the need for better understanding of the subspecies boundaries for the rare and declining *P. g. affinis*. Controversy inevitably follows the listing of a new species under the Endangered Species Act (Wilde, 2014), and with the ability to list “species, subspecies, and distinct population segments” the distinction between significant population segments and genetically distinct taxonomic units can be contentious (Haig & Elia, 2010). What constitutes a distinct population segment is left unclear by the Endangered Species Act, and so it is left to taxonomists and conservationists to debate which species and populations deserve legal protection and finite resources. While North American birds are some of the most well studied in the world, there is still taxonomic uncertainty among many subspecies (Zink, 1996), with some listed species having relatively low genetic distinctiveness (Zink & Barrowclough, 2008). Some argue for a holistic approach to species designation, taking into account genetic, morphological, distributional and cultural factors (Alström et al., 2008).

The results of this study could have potential impacts on current land use taking place on sites hosting remnant populations of *P. g. affinis*. Evidence supporting the designation *P. g.*

affinis as a distinct population segment of *Pooecetes gramineus* would strengthen the argument that protection of this subspecies under the Endangered Species Act is warranted. In Washington, nearly all remaining *P. g. affinis* occur on JBLM's artillery impact area and Rainier training areas. Listing of *P. g. affinis* could have the consequence of restricting training exercises on JBLM, an indispensable military installation and part of the United States defense apparatus. Several other listed species occur on JBLM, some of which share habitat with *P. g. affinis*, such as the Mazama pocket gopher (*Thomomys mazama*), Taylor's checkerspot butterfly (*Euphydryas editha taylori*) and streaked horned lark (*Eremophila alpestris strigata*). The fact that *P. g. affinis* breed within priority habitat of endangered species with training restrictions already in place would mean that listing of the subspecies might not have a profound impact on military exercises.

Conclusion

The songs of vesper sparrows are highly variable and individualistic (Kroodsma, 1972; Ritchison, 1981), and therefore are difficult to discriminate by ear. Two western subspecies, *P. g. affinis* and *P. g. confinis* are morphologically similar, impossible to differentiate at a distance and even difficult up close (Rising, 1996). The degree to which Pacific cordillera boundary affects speciation among vesper sparrows is unknown as wintering ranges for *P. g. affinis* and *P. g. confinis* overlap in southern and central California (Altman, 2017; Erickson, 2008). Altman (2017) also notes uncertainty regarding subspecies boundaries within the Klamath Mountains of Oregon, and Pyle (1997) suggests intergradation with *P. g. affinis* among the *P. g. confinis* of the Columbian Plateau. Furthermore, it is unclear to what degree differences in song culture act as a boundary to gene flow between the two subspecies. While differences in habitat associations and geographic distributions may not be adequate in themselves to constitute subspecies

designations, considering morphological and behavioral differences can provide a more robust set of evidence in the absence of genetic analysis. To answer the question of whether vesper sparrows distinguish individuals of another subspecies, we can ‘ask’ this question to the birds themselves through playback experiments.

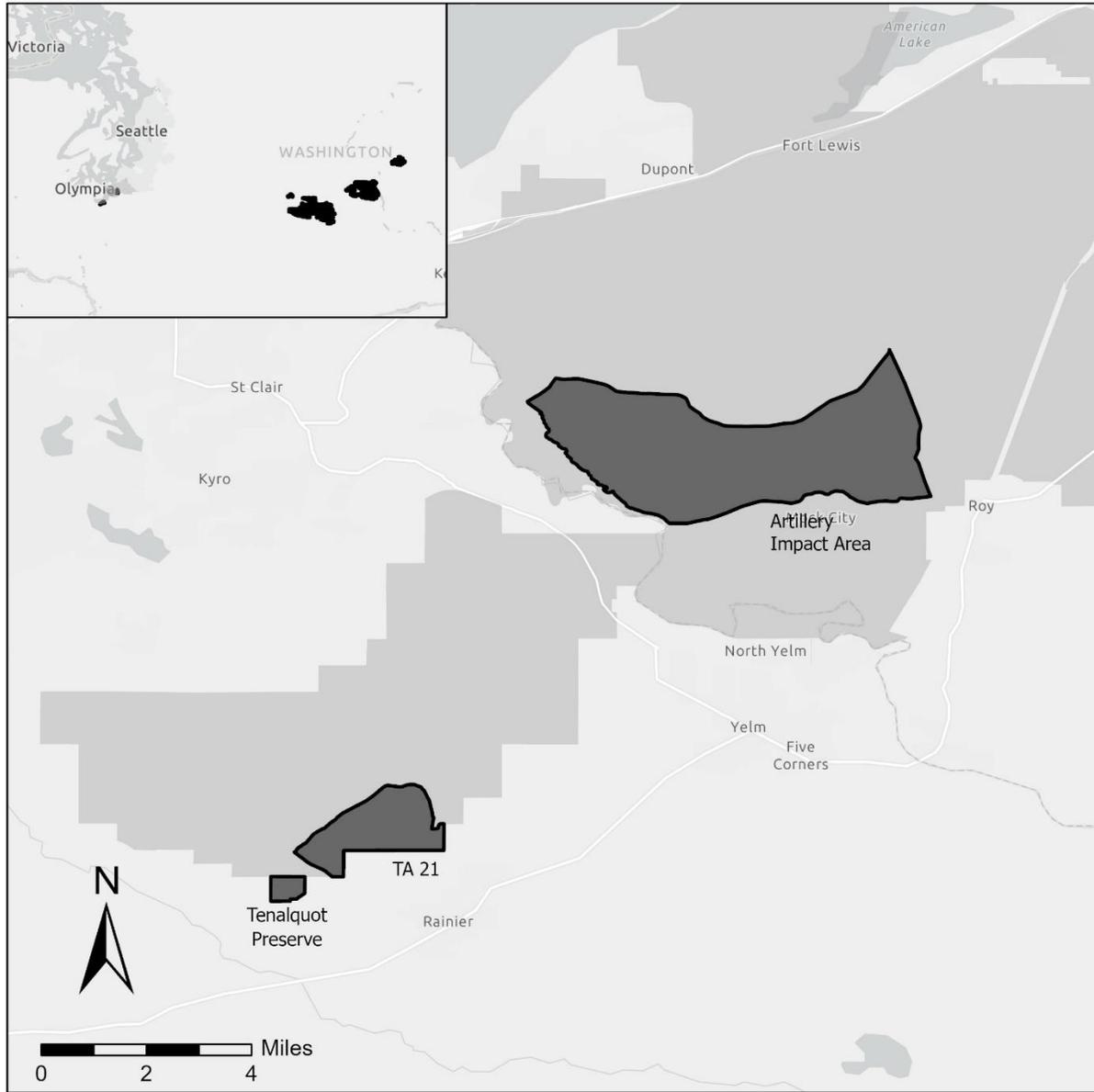
Chapter 3: Methods

Study Area

Oregon vesper sparrow

The last place in Washington where *P. g. affinis* breeds in numbers is on Joint Base Lewis McChord (JBLM), an 86,000-acre military installation in the South Puget Lowlands of Washington. The base encompasses the largest remaining patches of glacial outwash prairie and oak-savannah habitat left in western Washington. The song recording and playback trials for *P. g. affinis* took place within the two areas of the installation where *P. g. affinis* is known to breed: the Artillery Impact Area (AIA) and the Rainier Training Areas (RTAs; Figure 3). Access to the Artillery Impact Area is highly restricted due to the presence of unexploded ordnance, and work in this area required support by an explosive ordnance disposal specialist. The Rainier Training Areas have far less restrictions, so there was consistent access to that site throughout the breeding season. Several pairs also breed on Tenalquot Preserve, a private nature reserve owned and managed by the Center for Natural Lands Management. Tenalquot Preserve shares a border with the southernmost portion of the RTAs, and the birds that breed there contribute to the RTA population of *P. g. affinis*. Breeding territories were typically located in the ecotonal habitat between prairie and Douglas fir forest.

P. g. affinis Study Area



■ Study Area
■ Joint Base Lewis-McChord

Figure 3. *P. g. affinis* study sites within the South Puget Sound region of western Washington State. Two training areas on Joint Base Lewis-McChord support the majority of breeding pairs of *P. g. affinis* left in Washington.

Western vesper sparrow

East of the Cascade crest, *P. g. confinis* is a common and widespread breeding species found in a variety of open upland habitats throughout the Columbia Basin. Study areas were located using the vesper sparrow species map from eBird.org (eBird, 2019), and were selected based on high frequencies of vesper sparrow observations, proximity to *P. g. affinis* study areas, and public access. Recordings and playback trials with *P. g. confinis* as the focal subspecies occurred on state and private land in Yakima, Kittitas, and Douglas counties. State public lands included Wenas, Quilomene, and Whiskey Dick state wildlife areas, all located in the foothills outside of Ellensburg, Washington (Figure 4). These wildlife areas are all co-owned and managed by Washington Department of Fish and Wildlife and Washington Department of Natural Resources. In one instance, a private landowner offered access to his property for song recordings. Some song recordings also took place on publicly accessible portions of The Nature Conservancy's Beezley Hills Preserve outside of Ephrata, Washington. Habitat within the *P. g. confinis* study areas can generally be described as sagebrush steppe, with a few sites in the transitional zone to ponderosa pine (*Pinus ponderosa*) forest.

P. g. confinis Study Area

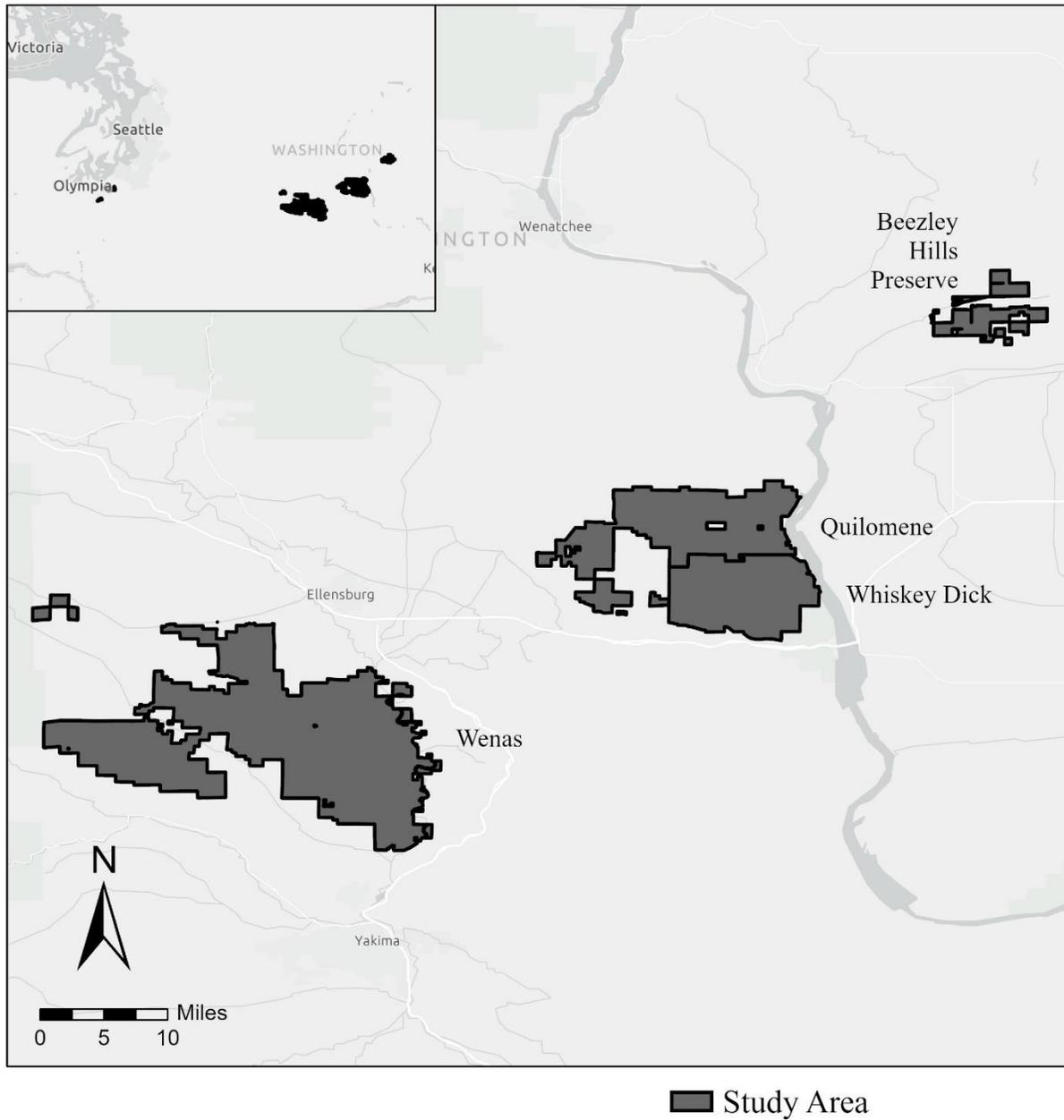


Figure 4. *P. g. confinis* study sites within the Columbia Basin region of eastern Washington State. Playback trials were conducted at two WDFW-managed wildlife areas in 2020, with some songs recorded at a Nature Conservancy-owned site near Ephrata.

Song Recordings

The songs that sourced the playback stimuli were recorded from unprovoked wild vesper sparrows in the spring of 2019. *P. g. affinis* songs were recorded in the AIA and RTAs of JBLM from April 29th until June 10th. Songs of *P. g. confinis* were recorded at Beezley Hills Preserve and at Wenas Wildlife Area from May 11th until June 9th. Recording efforts were staggered between subspecies, site, and spread out across the breeding season. Singing male vesper sparrows were located by ear, approached within a distance of approximately 30 meters and recorded singing for up to 15 minutes. Songs were recorded with 44.1 kHz sampling rate in 16-bit wav format with an Olympus LS-100 Multi-track PCM recorder and a Sennheiser ME62 microphone with a parabolic reflector. Two stimuli used in the trials were sourced from a colleague who recorded *P. g. confinis* songs at Wright's Meadows in Klamath County, Oregon during spring of 2018 using a Marantz PMD-660 solid-state recorder and Sennheiser ME62 microphone with a parabolic reflector. Those songs were also recorded in 16-bit wav format but with a 48.0 kHz sampling rate.

Songs of both subspecies consistently matched descriptions by Sibley (2003) and Rising (1996) of two to four introductory whistles followed by a series of 4-7 musical trills. While the types of syllables are highly variable between individual vesper sparrows, they only have one primary song-type. During bouts of singing, vesper sparrows will broadcast this primary song-type repeatedly, each time using a different variation of syllables. Kroodsma (1972) for example, found 218 variations out of 400 songs analyzed from a single vesper sparrow.

Raven Pro (ver. 1.6.1) software was used to normalize amplitude of the song recordings as well as remove background noise with band filters (Center for Conservation Bioacoustics, 2019). Songs were spaced out at 10-second intervals throughout each playback recording using

Audacity ® (2019) software. This spacing was based on the mean inter-song interval within the raw song recordings of both subspecies. Playback stimuli were constructed using the maximum number of possible song variations available from each source recording. Songs were edited into six-minute wav files to be used in the field as playback stimuli. Thirty-six playback stimuli were produced in total, 18 from each subspecies, with each recording sourced from a unique individual to avoid pseudoreplication (Kroodsma, 1989).

P. g. affinis

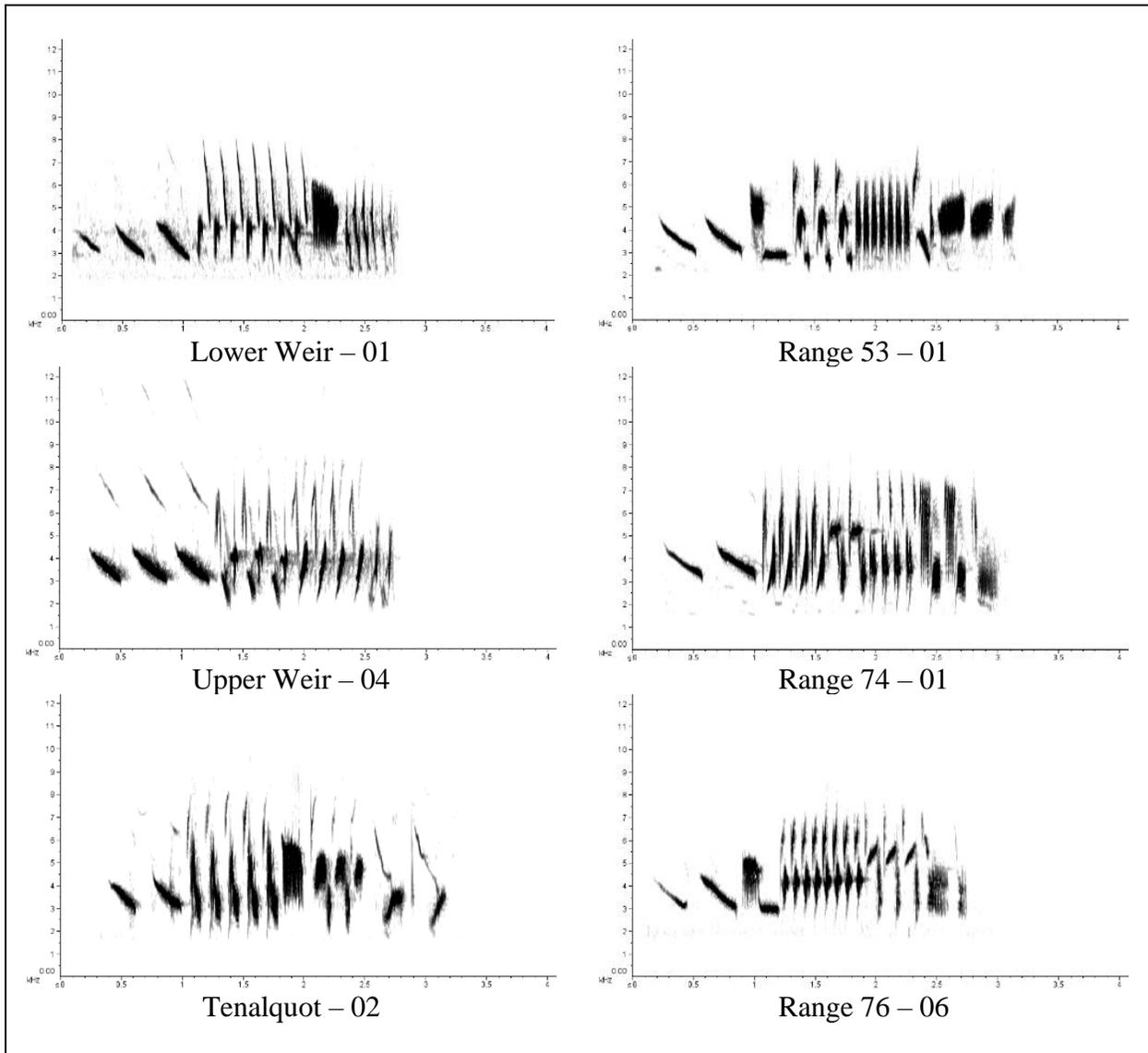


Figure 5. Spectrograms of six song exemplars, each from a unique individual *P. g. affinis* occurring at different sites in the Puget Lowlands.

P. g. confinis

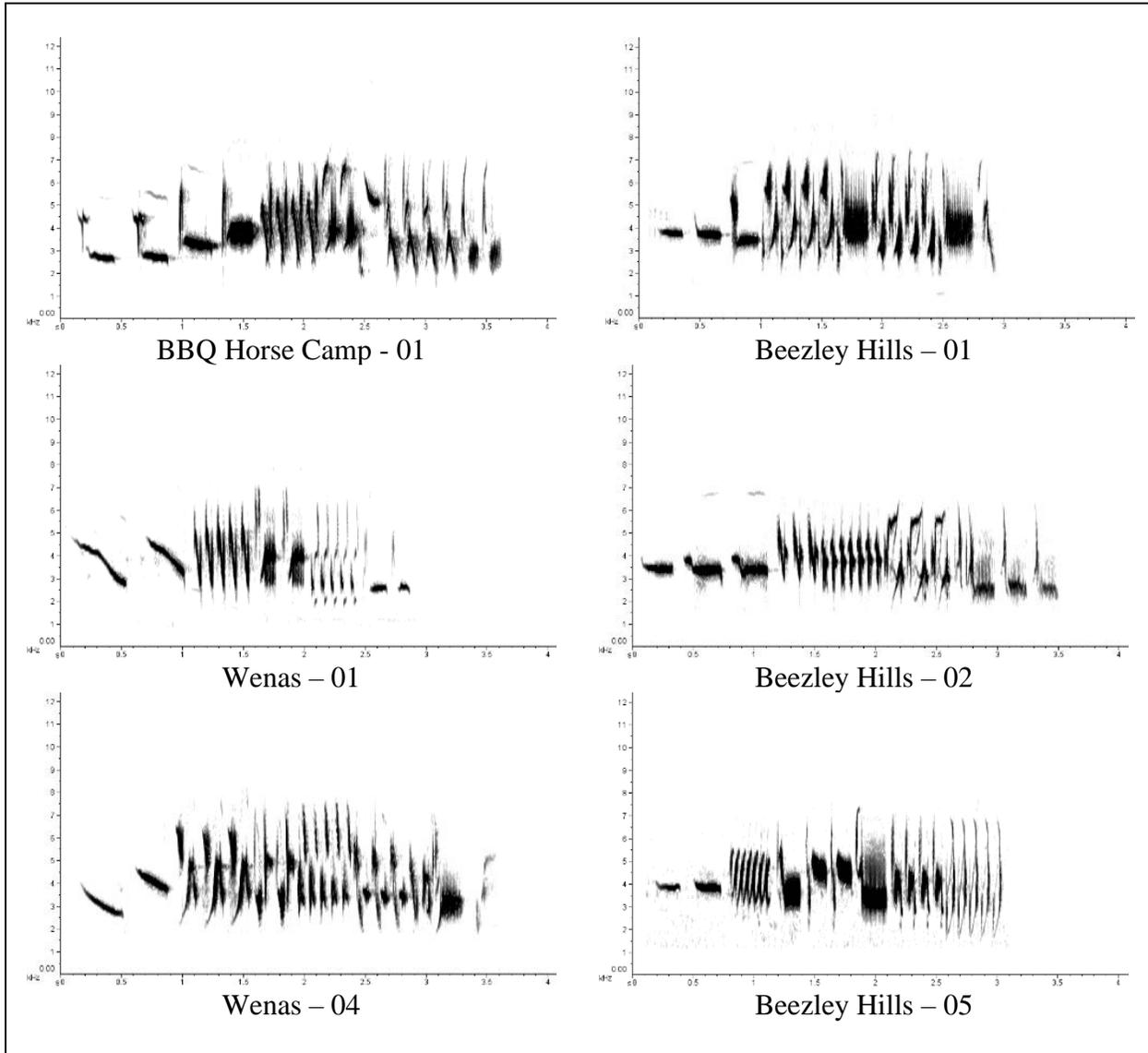


Figure 6. Spectrograms of six song exemplars, each from a unique individual *P. g. confinis* occurring at different sites in the Columbia Basin.

Playback Experiment

Playback trials for *P. g. affinis* were conducted on JBLM from May 14th through July 10th, 2020. Seventeen *P. g. affinis* subjects were exposed to song recordings from both subspecies, with 6 occurring in the Artillery Impact Area (AIA) and 11 occurring within the

Rainier Training Areas. Most *P. g. affinis* subjects selected were color-banded, which ensured that the same individual male was observed responding to both playback treatments. Effort was made to stagger trials between sites throughout the season, but due to access restrictions in the AIA, trials at this site occurred opportunistically. The minimum length of time between treatments was one day, and the maximum length between treatments was 13 days.

Trials for *P. g. confinis* were conducted on Wenas, Quilomene, and Whiskey Dick wildlife areas from May 24th through July 3rd, 2020. Sixteen *P. g. confinis* subjects were exposed to playback treatments but two individuals were not relocated for the second treatment. Eight *P. g. confinis* subjects were selected at Wenas wildlife area, seven at Whiskey Dick wildlife area, and one at Quilomene wildlife area. None of the *P. g. confinis* subjects were color-banded and it was assumed that subjects who responded to playback with territorial aggression were males. In all of the *P. g. confinis* playback trials, the length of time between playback treatments was one day. *P. g. confinis* trials were staggered between sites and spread out between May and July.

Each subject was exposed to two song recordings: one from their own subspecies and one from a foreign subspecies, with the order both randomized and equally weighted among subjects. Subjects were never exposed to stimuli sourced from the same site as the subject, which limited the chance that a subject would be exposed to song of a bird it was familiar with (Temeles, 1992). Trials were aborted if a conspecific male approached the speaker, or if a predator was observed within the trial area. Trials began at sunrise and continued until around noon. Subjects were most often located by ear, especially in the *P. g. confinis* trials, but effort was made to choose visually detected individuals as well. Subjects could not always be easily located upon return for second trial, in which case playbacks would begin after a thorough search of the area.

In the majority of these cases, the subject was hiding nearby and would appear shortly after the playback started.

Playback treatments were broadcast from a single UBL JFLIP 4 Bluetooth speakers which played wav files through an auxiliary cord sourced from an iPod (Apple, Inc.). Stimuli were broadcast at approximately 90 dB(A), calibrated using SPLnFTT Noise Meter version 7.0 (2020) cellphone application placed 1 meter from the speaker. The speaker was mounted on a scope stand and placed at a height of two meters, based on the median and mode perch height noted from vesper sparrows recorded in 2019 ($n = 45$). Each mounted speaker was placed next to a preferred perch within a subject's territory to maximize the likelihood of a territorial response. Non-bright flagging was placed at 10 meters from the speaker in each cardinal direction. The same speaker location was used during the second playback trial for each subject.

Each treatment began with brief, categorical observations during speaker set-up, followed by the six-minute playback, and then another six minutes of silent observation resulting in 12 minutes of total observation for each treatment (Liu et al., 2008). Pre-playback observations included noting whether the bird was singing, stationary, the bird's initial proximity to the speaker, and whether there were any conspecifics present. Response variables recorded were: 1) number of songs (total count), 2) number of flights (total count), 3) minimum distance to speaker (m), 4) time spent within 10 meters of the speaker (seconds), 5) whether the bird wing-waved (binary), and 6) whether the bird performed a "soft" song (binary). Subjects were generally observed from approximately 20-30 meters from the speaker. Minimum distance to the speaker was defined as the closest distance the bird came to speaker in flight, perched, or on the ground. Observers were blind to which subspecies song was being played, which cannot be reliably distinguished by ear. Observers dictated the descriptions of each subject's territorial response

before, during and after each playback trial onto an Olympus WS-852 digital voice recorder and were transcribed at a later date.

Analysis

Eight territorial response variables to playback measured for each subject across all study sites were reduced using principal component analysis (PCA; McGregor, 1992). A correlation matrix was produced to confirm that the data met the assumptions of the analysis. For the pooled dataset, the four variables, each collected in both treatment and post-treatment periods, were reduced to three principal components. Linear mixed effects models were then created for the three principal components using the parameters that were most likely to have influenced territorial responses. Model ranking using Akaike's Information Criterion corrected for small sample size was then conducted for each principal component (AIC_c; Phillips & Derryberry, 2017).

The global model included playback stimuli type (coded as 'conspecific' or 'heterospecific', based on the subspecies of the subject and the playback stimuli), subject subspecies (*P. g. confinis* or *P. g. affinis*), subject's initial distance to speaker (m), and Julian date as fixed effects. The interaction between stimuli and subspecies was also included as a fixed effect. Study site, observer, subject-ID, and stimuli-ID (the specific playback recording) were designated as random effects (Greig, Baldassarre, & Webster, 2015). Random effects were removed from the model if they did not account for any variance (Bates, Machler, Bolker, & Walker, 2015). All models included subject-ID as a random effect, with the only other random effect included being observer in the model with the third principal component axis as the dependent variable. Variance inflation factors and quantile-quantile residual plots were examined for each model to check for collinearity and residual normality.

The top models with $\Delta AIC_c < 2.0$ for each principal component were examined for parameters with strong influence. Model parameters with 95% confidence intervals that did not overlap zero were considered to have a strong influence on vesper sparrow response behavior (Reed et al., in press). All statistical analyses were conducted with R version 3.5.3 (R Core Team, 2020) using the “psych” (Revelle, 2020), “lme4” (Bates et al., 2015), “car” (Fox & Weisberg, 2019), and “MuMIn” (Barton, 2020) packages.

Chapter 4: Results & Discussion

Results

Principal component analysis of the data identified three components with eigenvalues higher than one (Table 1). PC1_{approach} was most heavily loaded with variables related to approach distance, with the treatment and post-treatment variables “minimum distance to speaker” and “number of seconds spent within 10 meters of the speaker” represented within this component. PC2_{fly} was most heavily loaded with treatment and post-treatment flight behavior, or “number of flights”. PC3_{song} was most heavily loaded with treatment and post-treatment vocal behavior or “number of songs”. The cumulative percent of variation in the data accounted for by these three principal components was 65.4%.

Table 1.

Loadings of the principal component’s axis 1, 2, and 3 scores. Based on the specific response variables with the highest loadings for each PC axis (shown in bold), PC1 was designated the ‘Approach Behavior’ axis, PC2 the ‘Flight Behavior’ axis, and PC3 the ‘Song Behavior’ axis. The cumulative proportion of variance explained by PC1 through PC3 was 65.4%.

Response Variables	Loadings		
	PC1 _{approach}	PC2 _{fly}	PC3 _{song}
No. songs during treatment			0.845
No. flights during treatment	0.244	0.757	
Distance during treatment (m)	-0.747	-0.206	
Time within 10m during treatment	0.788	0.172	0.128
No. songs post-treatment	0.215		0.751
No. flights post-treatment		0.828	
Distance post-treatment	-0.717	-0.231	
Time within 10m post-treatment	0.799	-0.254	0.193
Eigenvalue	2.441	1.457	1.334
Proportion of variance	0.305	0.182	0.167

Vesper sparrows approached within ten meters of the speaker in 90% of playback trials and approached within one meter of the speaker in 48% of trials. While the subjects in this study showed strong overall approach behavior ($PC1_{\text{approach}}$), none of the parameters included in the global model had a strong influence on $PC1_{\text{approach}}$ scores. When ranked by AIC_c (Table 2), the best-supported model explaining $PC1_{\text{approach}}$ included treatment as the only fixed effect, with ‘conspecific’ stimuli having a positive effect on $PC1_{\text{approach}}$ scores (i.e., shorter distances to the playback during and post-treatment, and more time spent within 10m). The null model was ranked second, with a similar weight as the top-model, and other top ranked models included combinations of treatment and subject’s initial distance as fixed effects. All of the fixed effects among the top-ranked ($\Delta AIC_c < 2.00$) $PC1_{\text{approach}}$ models had 95% confidence intervals that overlapped zero, including the treatment (Table 3). Among the raw response variables related to approach behavior (Table 4), both subspecies averaged closer distances and more time spent within 10 meters to conspecific stimuli, although this was less pronounced among *P. g. confinis*.

Vesper sparrows responded with increased flight behavior ($PC2_{\text{fly}}$) when exposed with conspecific playback stimuli. Among the two subspecies, *P. g. confinis* subjects responded with more flights overall than *P. g. affinis* subjects. The best-supported $PC2_{\text{fly}}$ model included treatment, subject subspecies, and Julian date, with all three parameters having a 95% CI that did not overlap zero (Table 3). The second-ranked model included treatment and subject subspecies only. Principal component scores for $PC2_{\text{fly}}$ were strongly influenced by both the treatment and which subspecies was the subject of the playback trial (Figure 7). Julian date also had a strong effect on flight behavior, with vesper sparrows responding with reduced flight behavior later in the breeding season.

Table 2.

Model selection results using Akaike's Information Criterion corrected for small sample size (AIC_c). Principal components related to vesper sparrow approach, flight, and song behavior written as $PC1_{\text{approach}}$, $PC2_{\text{fly}}$, and $PC3_{\text{song}}$. Models with a delta value less than 2.0 ($\Delta AIC_c \leq 2.00$) are shown, along with the null (intercept-only). K equals the number of model parameters, $\log(\mathcal{L})$ equals the maximized log-likelihood value, Δ equals delta (the change in AIC_c from the top model), and w_i equals the Akaike weight for each well-supported model. Bold indicates parameters with 95% CIs that do not overlap zero. The direction of influence for each parameter is indicated with positive/negative signs (+/-). Null (intercept-only) subscripts indicate the random effects included in all models for each principal component, where ID = Bird ID and Obs = observer. $n = 63$ trials.

Model	K	$\log(\mathcal{L})$	AIC_c	Δ	w_i
PC1_{approach}					
Treatment (+)	4	-81.30	171.29	0.00	0.35
Null _{ID}	3	-82.63	171.67	0.38	0.29
Treatment (+), Distance (-)	5	-80.56	172.18	0.89	0.22
Distance (-)	4	-82.21	173.10	1.81	0.14
PC2_{fly}					
Subspecies (+), Treatment (+), Julian date (-)	6	-77.94	169.38	0.00	0.71
Subspecies (+), Treatment (+)	5	-80.09	171.23	1.85	0.29
Null _{ID}	3	-86.18	178.78	9.40	-
PC3_{song}					
Subspecies (-), Julian date (-)	6	-77.28	168.06	0.00	0.72
Subspecies (-), Julian date (-), Distance (-)	7	-76.97	169.97	1.88	0.28
Null _{ID+Obs}	4	-83.95	176.58	8.52	-

Although the subspecific treatment did not have a strong influence on vesper sparrow song behavior ($PC3_{\text{song}}$), the subject's subspecies did have a strong effect. *P. g. affinis* subjects responded with more songs overall than *P. g. confinis* subjects. The best-supported $PC3_{\text{song}}$ model included subject subspecies and Julian date as fixed effects (Table 2). The second-ranked model included these parameters with the addition of subject's initial distance to speaker.

Table 3.

The influence of fixed effects from the top-ranked models for vesper sparrow approach, flight, and song behavior. Principal components explaining approach, flight, and song behavior denoted PC1_{approach}, PC2_{fly}, and PC3_{song}. Parameter levels for treatment stimuli (conspecific, heterospecific) and subspecies (*P. g. affinis*, *P. g. confinis*) shown in parentheses. Intercept and categorical level of reference condition (parentheses) included for each component. Strong effects with 95% CIs that do not overlap zero are indicated in bold.

Parameter (level)	$\beta \pm SE$	Lower CI	Upper CI
PC1_{approach}			
Intercept (<i>Heterospecific</i>)	-0.13 ± 0.17	-0.47	0.21
Treatment (Conspecific)	0.26 ± 0.16	-0.04	0.57
PC2_{fly}			
Intercept (Heterospecific, <i>P. g. affinis</i>)	2.35 ± 1.40	-0.38	5.08
Treatment (Conspecific)	0.44 ± 0.17	0.1	0.78
Subspecies (<i>P. g. confinis</i>)	0.68 ± 0.25	0.18	1.18
Julian date	-0.02 ± 0.01	-0.03	-0.001
PC3_{song}			
Intercept (<i>P. g. affinis</i>)	3.80 ± 1.25	1.34	6.27
Subspecies (<i>P. g. confinis</i>)	-0.73 ± 0.23	-1.20	-0.28
Julian date	-0.02 ± 0.01	-0.03	-0.005

Playback stimulus type did not have a strong effect on song behavior among either *P. g. affinis* or *P. g. confinis*, with the treatment fixed effect not included in any of the models with $\Delta AIC_c < 2.00$ (Table 2). Subject subspecies and Julian date were the only parameters in any of the top ranked models with 95% confidence intervals that did not overlap zero (Table 3). Similar to vesper sparrow flight behavior, Julian date had a strong influence on the response in song behavior, with reduced singing later in the season.

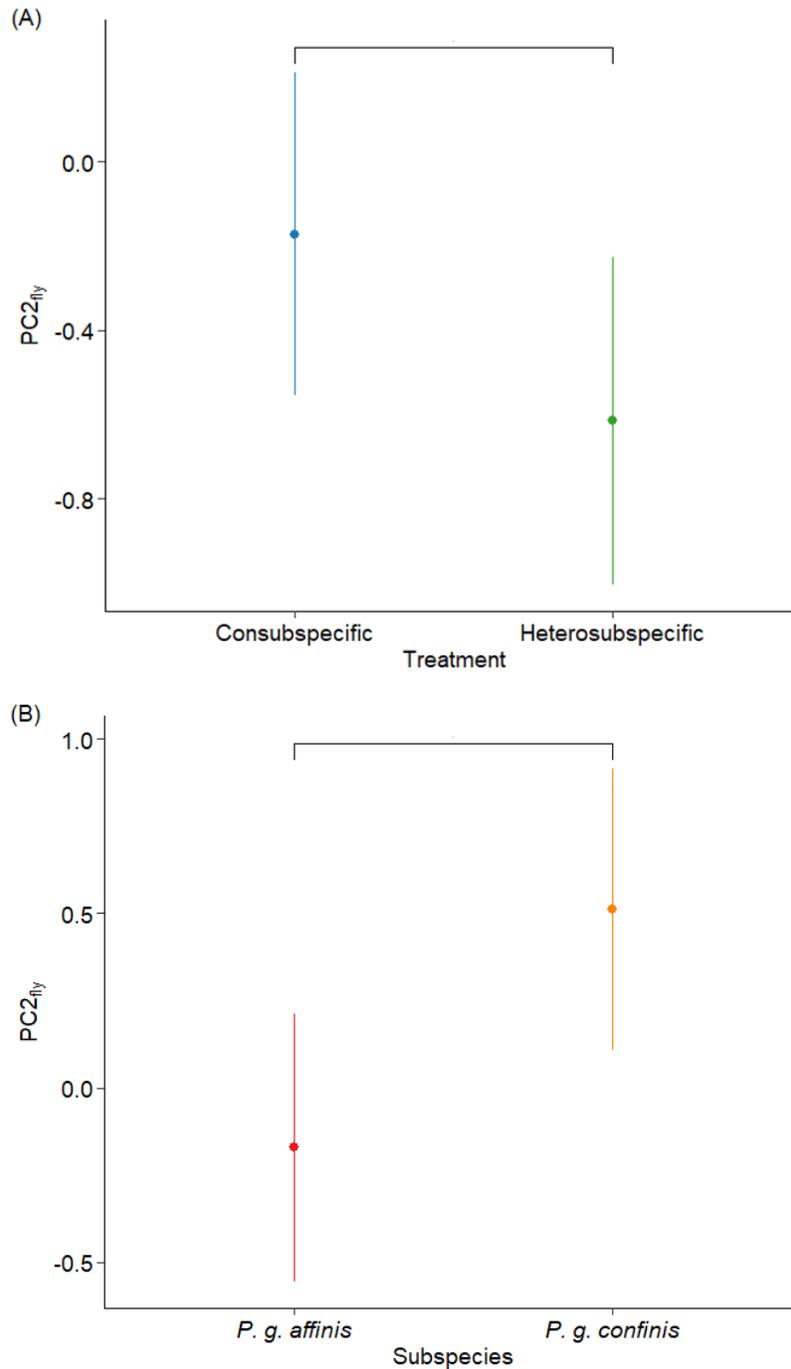


Figure 7. Plots of parameter effects on the second principal component explaining flight behavior (PC2_{fly}). Plot (A) shows mean PC2_{fly} values (with 95% CI) for playback trials separated by subspecific stimuli type, with ‘conspecific’ stimuli shown on the left, and ‘heterospecific’ stimuli on the right. Plot (B) shows mean PC2_{fly} values (with 95% CI) for playback trials separated by subject subspecies, with ‘*P. g. affinis*’ shown on left, and ‘*P. g. confinis*’ on the right.

P. g. affinis wing-waved during 29.4 % of trials when exposed to con-subspecific stimuli, versus 12.5% of trials when exposed to hetero-subspecific stimuli. *P. g. confinis* wing-waved during 26.7% of trials when exposed to con-subspecific stimuli, and during 26.7 % of trials when exposed to hetero-subspecific stimuli. *P. g. affinis* responded with soft-singing to 86.9 % of trials with con-subspecific stimuli versus 56.2 % of trials with hetero-subspecific stimuli. *P. g. confinis* responded with soft-singing to 86.7 % of trials with con-subspecific stimuli versus 66.7 % of trials with hetero-subspecific stimuli.

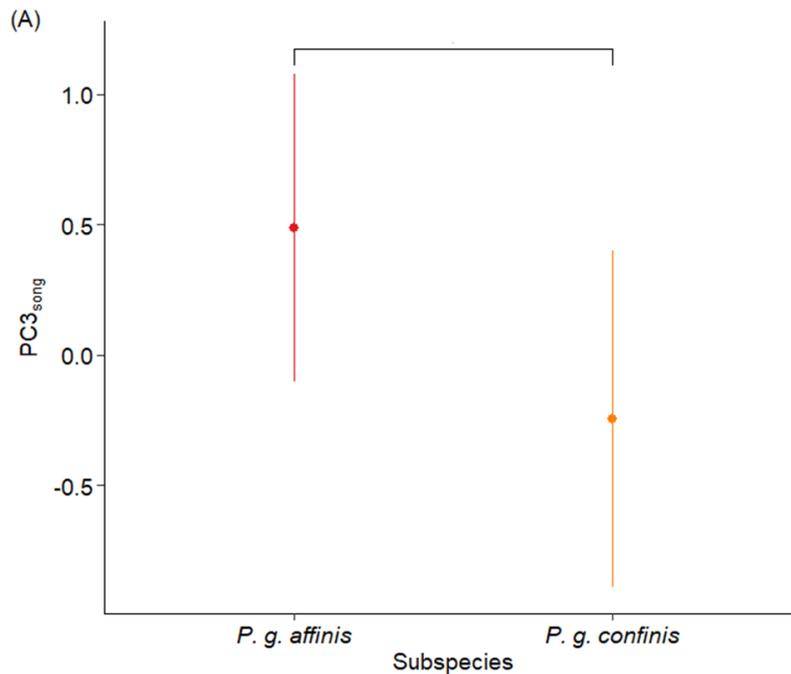


Figure 8. Plot of parameter effects on the third principal component explaining song behavior (PC3_{song}). Plot (A) shows mean PC3_{song} values (with 95% CI) for playback trials separated by subject subspecies, with '*P. g. affinis*' shown on left, and '*P. g. confinis*' on the right.

Table 4.

Means and standard deviations for each raw response variable collected during playback trials, separated by treatment stimuli type.

Response Variables	Raw response (mean \pm SD)	
	Consubspecific	Heterosubspecific
<i>P. g. affinis</i>		
No. songs during treatment	25.1 \pm 12.1	24.6 \pm 9.2
No. flights during treatment	7.8 \pm 5.7	5.8 \pm 5.3
Distance during treatment (m)	3.4 \pm 5.9	7.3 \pm 11.8
Time within 10m during treatment	177.1 \pm 106.2	154.2 \pm 128.6
No. songs post-treatment	29.4 \pm 12.0	25.2 \pm 10.0
No. flights post-treatment	2.8 \pm 2.9	2.0 \pm 2.8
Distance post-treatment	5.6 \pm 5.8	15.2 \pm 25.6
Time within 10m post-treatment	196.7 \pm 152.3	144.9 \pm 161.8
<i>P. g. confinis</i>		
No. songs during treatment	15.7 \pm 9.9	14.9 \pm 10.9
No. flights during treatment	11.8 \pm 6.8	9.1 \pm 5.5
Distance during treatment (m)	3.1 \pm 5.2	3.8 \pm 6.7
Time within 10m during treatment	168.1 \pm 86.8	163.3 \pm 85.4
No. songs post-treatment	20.3 \pm 11.0	20.1 \pm 12.8
No. flights post-treatment	4.2 \pm 3.1	3.1 \pm 1.7
Distance post-treatment	7.9 \pm 6.5	12.6 \pm 12.2
Time within 10m post-treatment	85.8 \pm 126.9	112.2 \pm 121.3

Discussion

Results from this experiment suggest the existence of song discrimination between the two subspecies of vesper sparrow, *P. g. affinis* and *P. g. confinis*. The strength of this response appeared to be moderate when compared to similar studies investigating passerine song discrimination at the subspecies level (Lipshutz et al., 2017; Liu et al., 2008). Based on these results, discriminatory response to subspecific stimuli among both subspecies was limited to flight behavior, with a lack of strong treatment effect among approach and song behavior. This study also identified several differences in territorial response behavior between the two subspecies, with *P. g. confinis* responding to playback with more flights, and *P. g. affinis* responding to playback with more songs.

Nearly all playback trials that were attempted garnered responses from subjects, with birds singing, approaching, and making short flights around the speaker. The vesper sparrows in this study would approach the speaker by flying or walking along areas of unvegetated bare ground. Vesper sparrows would most often sing from perches, but would also frequently sing from the ground, which contradicted some previous descriptions (Castrale, 1983). In a portion of the trials, subjects wing-waved or performed soft-singing. Although measures of latency were not analyzed, in some trials subjects would approach the speaker immediately after the first song was broadcast. The average distance of subjects prior to playback was 44.0 ± 21.6 meters. The broadcast of a song by the speaker would be immediately followed by a flight from some subjects, or by a song in others. Subjects would often fly from perch to perch within the playback area, usually making a close pass at the speaker in response to broadcast of a song. Many

subjects would remain near the speaker and continue singing after the six-minute playback treatment had ended.

Searcy, Anderson and Nowicki (2006) identified distance to playback speaker as the most reliable measure of territorial response to bird song playback when compared to other response behaviors. In this study, principal component analysis identified PC1_{approach} as accounting for the highest proportion of variance (30.5%) in the data and was heavily loaded with variables related to approach distance to playback speaker (Table 1). Of the response variables recorded during the playback trials, four were related to the subject's approach distance to the speaker as opposed to two for flight behavior and two for song behavior. When examining parameters of the best-supported PC1_{approach} models, none were shown to have a strong influence on approach behavior. While the influence of the treatment on approach behavior was not significant, review of raw response averages suggests a weak treatment effect (Table 4). Among response variables related to approach behavior, subjects averaged closer approach distances and more time spent within ten meters of the speaker when exposed to conspecific stimuli, although this pattern is mainly present in the *P. g. affinis* response variables.

Loadings for PC2_{fly} were greatest for “number of flights during treatment” and “number of flights post-treatment” (Table 1), which suggested that this component was related to flight behavior among subjects. Flight behavior was the only response type in which vesper sparrows showed strong discrimination between subspecific stimuli. Many of the flights during the playback trials were associated with close passes at the speaker, which could be interpreted as an attempt at physical confrontation with a perceived intruder. Therefore, subjects expended more energy towards physical confrontation with a perceived intruder when the subject detected an intruder of the same subspecies. Some researchers have used taxidermic mounts during playback

experiments and studied the territorial response of subjects when a visual target is presented (Greig et al., 2015; Searcy et al., 2006). Utilizing taxidermic mounts in future playback experiments among vesper sparrows might help determine whether flight behavior is in fact related to aggressive intent.

Vesper sparrow song behavior was not influenced by the treatment, but by the subject's subspecies and Julian date. *P. g. affinis* subjects responded to playback with significantly more songs than *P. g. confinis* subjects (Figure 8), reverse of the subject's subspecies effect on flight behavior. PC3_{song} was primarily loaded with the “number of songs during treatment” and “number of songs post-treatment” variables (Table 1), which indicated that this component was representative of vesper sparrow song behavior. Julian date had a strong influence on vesper sparrow song behavior, with subjects responding to playback with less singing as the season progressed. Near the end of the sampling period, vesper sparrows in Eastern Washington had become noticeably less vocal, which was likely due to breeding phenology, and possibly changes in weather (it was becoming hotter and drier).

Local versus non-local effects were controlled for in this experiment by only exposing subjects to stimuli sourced from a different study area. Each subject would hear a song of their own subspecies, but never from the specific population it was a part of. However, the *P. g. affinis* study areas were in closer proximity than the *P. g. confinis* study areas, and therefore there is a possibility of a mild local effect among the *P. g. affinis* trials. The *P. g. confinis* trials had a limited sampling period compared to the *P. g. affinis* trials. Visits to the Eastern Washington study sites only occurred on weekends, while on JBLM trials occurred throughout the week. For this reason, all *P. g. confinis* subjects received both playback treatments separated by only 24 hours. Some researchers have recommended a minimum of 48 hours between playback

treatments in their studies, but due to time and access constraints subjects were visited on subsequent days.

Differences in flight and song behavior between *P. g. affinis* and *P. g. confinis* could be attributed to either biological or ecological factors. While both vesper sparrow subspecies are morphologically similar, their habitats and some aspects of their life histories are distinct. In the Quilomene and Wenas study areas, vesper sparrows were among the most common passerine species. On JBLM vesper sparrows are not abundant, although territories tend to be clustered within suitable habitat. In Washington, *P. g. confinis* generally migrate to their breeding sites a few weeks earlier than *P. g. affinis*, and as a result, finish their breeding season earlier as well (Jones and Cornely, 2002). *P. g. confinis* breeding sites also differ in climate, with the study areas in the Columbia Basin being much drier than the *P. g. affinis* study areas on JBLM. Qualitatively, the Columbia Basin study areas appeared more abundant in perches and could be described as shrublands whereas the sites in the Puget Lowlands are more accurately characterized as ‘prairies’, as they are dominated by grasses and forbs with low numbers scattered conifers and small shrubs providing perches. The abundance of perches among *P. g. confinis* study areas could have possibly contributed to the increased flight behavior among that subspecies. More perches might allow subjects to change location more frequently as they searched for the perceived intruder, while less perches could force the subjects to remain on the limited perches within their territory.

Approach behavior, often considered a reliable measure territorial response, was not strongly influenced by the subspecific treatment. However, flight behavior was strongly influenced by the treatment, which could be interpreted as energy invested towards attempts at aggression. The treatment also appeared to influence the performance of soft songs and wing

waves among subjects, though this was less pronounced among *P. g. confinis*. Searcy, Anderson and Nowicki (2006) found that along with distance to playback, soft singing provided another reliable measure of aggressive intent. Regrettably, the binary variables that noted instances of soft-singing and wing-waving were not included in the main analysis of this study.

Overall, the results of this experiment support Jones and Cornely's (2020) description of vesper sparrow subspecies taxonomy as "moderately distinct". Both subspecies showed some degree of discrimination between subspecific song stimuli, although this was mainly limited to flight behavior. *P. g. confinis* responded to playback with more flights than *P. g. affinis* overall. Differences in singing behavior were also significant between the two subspecies, with *P. g. affinis* responding to playback with more singing than *P. g. confinis*. It is unclear whether the differences between the subspecies are biological, or due to temporal and environmental conditions during the limited sampling period. Limitations in time and site access undoubtedly had influence on the results of this study, but overall, there appears to be a moderate trend of subspecific discrimination.

References

- Abs, M. (1963). Essential Components of European Nightjar Song. *Proc. Int. Ornithol. Congr.*, 13(1), 202–205. <https://doi.org/10.1093/auk/94.3.615>
- Akçay, Ç., Tom, M. E., Holmes, D., Campbell, S. E., & Beecher, M. D. (2011). Sing Softly and Carry a Big Stick: Signals of Aggressive Intent in the Song Sparrow. *Animal Behaviour*, 82(2), 377–382. <https://doi.org/10.1016/j.anbehav.2011.05.016>
- Alström, P., & Olsson, U. (1999). The Golden-Spectacled Warbler: a Complex of Sibling Species, Including a Previously Undescribed Species. *Ibis*, 141, 545–568. <https://doi.org/10.1111/j.1474-919x.1999.tb07363.x>
- Alström, P., Rasmussen, P. C., Olsson, U., & Sundberg, P. (2008). Species Delimitation Based on Multiple Criteria: The Spotted Bush Warbler *Bradypterus thoracicus* Complex (Aves: Megaluridae). *Zoological Journal of the Linnean Society*, 154, 291–307. <https://doi.org/10.1111/j.1096-3642.2008.00418.x>
- Altman, B. (2011). Historical and Current Distribution and Populations of Bird Species in Prairie-Oak Habitats in the Pacific Northwest. *Northwest Science*, 85(2), 194–222. <https://doi.org/10.3955/046.085.0210>
- Altman, B. (2017). Conservation Assessment for Oregon Vesper Sparrow (*Pooecetes gramineus affinis*). Retrieved from <https://cascadiaprairieoak.org/documents/conservation-assessment-for-oregon-vesper-sparrow-pooecetes-gramineus-affinis>
- Altman, B., Stinson, D., & Hayes, G. (2020). Status Report for the Oregon Vesper Sparrow. (February), 31 + iii pp.

- American Bird Conservancy. (2016). Petition to List Oregon Vesper Sparrow (*Pooecetes gramineus affinis*) as Endangered or Threatened. Retrieved from <https://abcbirds.org/wp-content/uploads/2016/.../Oregon-Vesper-Sparrow-Petition.pdf>
- American Ornithologists' Union. (1957). Checklist of North American Birds (5th Editio). Baltimore: American Ornithologists' Union.
- Baker, M. C., & Cunningham, M. A. (1985). The Biology of Bird-Song Dialects. Behavioral and Brain Sciences, 8(1), 85–133. <https://doi.org/10.1017/S0140525X00019932>
- Ballentine, B., Hyman, J., & Nowicki, S. (2004). Vocal Performance Influences Female Response to Male Bird Song: An Experimental Test. Behavioral Ecology, 15(1), 163–168. <https://doi.org/10.1093/beheco/arg090>
- Baptista, L. F., & Gaunt, S. L. L. (1994). Advances in Studies of Avian Sound Communication. The Condor, 96(3), 817–830.
- Baptista, L. F., & Petrinovich, L. (1986). Song Development in the White-crowned Sparrow: Social Factors and Sex Differences. Animal Behaviour, 34(5), 1359-1371.
- Barker, F. K., Burns, K. J., Klicka, J., Lanyon, S. M., & Lovette, I. J. (2015). New Insights into New World Biogeography: An Integrated View from the Phylogeny of Blackbirds, Cardinals, Sparrows, Tanagers, Warblers, and Allies. The Auk, 132(2), 333–348. <https://doi.org/10.1642/auk-14-110.1>
- Barton, K. (2020). MuMIn: Multi-Model Inference. Retrieved from <https://cran.r-project.org/package=MuMIn>

- Bates, D., Machler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1–48.
<https://doi.org/10.18637/jss.v067.i01>
- Beauchesne, S. M. (2002). Coastal Vesper Sparrow Stewardship Account For the Garry Oak Ecosystems of Southwestern British Columbia. Retrieved from
http://goert.ca/documents/SA_pooegram.pdf
- Behle, W. H. (1978). Avian Biogeography of the Great Basin and Intermountain Region. *Great Basin Naturalist Memoirs*, 2, 55–80.
- Berger, A. J. (1968). Eastern Vesper Sparrow. In O. L. Austin Jr. (Ed.), *Life Histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies* (pp. 868–882).
- Best, L. B. (1972). First-Year Effects of Sagebrush Control on Two Sparrows. *The Journal of Wildlife Management*, 36(2), 534–544.
- Best, L. B., & Rodenhouse, N. L. (1984). Territory Preference of Vesper Sparrows in Cropland. *The Wilson Bulletin*, 96(1), 72–82.
- Borror, D. J. (1961). Songs of Finches (Fringillidae) of Eastern North America. *The Ohio Journal of Science*, 61, 161–174.
- Boyd, R. (1999). Introduction. In R. Boyd (Ed.), *Indians, Fire, and the Land in the Pacific Northwest* (pp. 1–30). Corvallis, Oregon: Oregon State University Press.
- Brennan, L. A., & Kuvlesky Jr., W. P. . (2005). North American Grassland Birds : An Unfolding Conservation Crisis? *Journal of Wildlife Management*, 69(1), 1–13.

- Brooks, W., & Wimberger, A. P. (2018). The Role of Song in Reproductive Isolation in a New Secondary Contact Zone of White-crowned Sparrows (*Zonotrichia leucophrys*). University of Puget Sound. Retrieved from:
https://soundideas.pugetsound.edu/summer_research/304
- Burroughs, J. (1905). The Ways of Nature. Retrieved from
<https://cdm16021.contentdm.oclc.org/digital/collection/p16021coll3/id/115>
- Camp, M., & Best, L. B. (1993). Bird Abundance and Species Richness in Roadsides Adjacent to Iowa Rowcrop Fields. *Wildlife Society Bulletin*, 21(3), 315–325.
- Castrale, J. S. (1983). Selection of Song Perches by Sagebrush-Grassland Birds. *The Wilson Bulletin*, 95(4), 647–655.
- Center for Conservation Bioacoustics. (2019). Raven Pro: Interactive Sound Analysis Software (Version 1.6.1). Retrieved from <http://ravensoundsoftware.com/>
- Chappell, C B, & Crawford, R. C. (1997). Native Vegetation of the South Puget Sound Prairie Landscape. *Ecology and Conservation of the South Puget Sound Prairie Vegetation*, 107–124. Retrieved from [http://w.southsoundprairies.org/tech/Native Veg of S Puget Sound Prairies.pdf](http://w.southsoundprairies.org/tech/Native_Veg_of_S_Puget_Sound_Prairies.pdf)
- Chappell, C. B., Gee, M. S., Stephens, B., Crawford, R., & Farone, S. (2001). Distribution and Decline of Native Grasslands and Oak Woodlands in the Puget Lowlands and Willamette Valley Ecoregions, Washington. In S. H. Reichard, P. W. Dunwiddie, J. G. Gamon, A. R. Kruckeberg, & D. L. Salstrom (Eds.), *Conservation of Washington's Native Plants and Ecosystems* (pp. 124–139).

- Collins, S. (2004). Vocal Fighting and Flirting: The Functions of Birdsong. In P. Marler & H. Slabbekoorn (Eds.), *Nature's Music: The Science of Birdsong* (pp. 39–78).
- Curnutt, J. L., Pimm, S. L., Maurer, B. A., Curnutt, J. L., Pimm, S. L., & Maurer, B. A. (1996). Population Variability of Sparrows in Space and Time. *Oikos*, 76(1), 131–144.
- Dechant, J. A., Dinkins, M. F., Johnson, D. H., Igl, L. D., Goldade, C. M., & Euliss, B. R. (2002). Effects of Management Practices on Grassland Birds: Vesper Sparrow. Northern Prairie Wildlife Research Center, Jamestown ND, pp 1–25.
- Demko, A. D., Sosa-López, J. R., & Mennill, D. J. (2019). Subspecies Discrimination on the Basis of Acoustic Signals: A Playback Experiment in a Neotropical Songbird. *Animal Behaviour*, 157, 77–85. <https://doi.org/10.1016/j.anbehav.2019.08.021>
- Dennehy, C., Alverson, E. R., Anderson, H. E., Clements, D. R., Gilbert, R., & Kaye, T. N. (2011). Management Strategies for Invasive Plants in Pacific Northwest Prairies, Savannas, and Oak Woodlands. *Northwest Science*, 85(2), 329–351. <https://doi.org/10.3955/046.085.0219>
- Derryberry, E. P. (2011). Male Response to Historical and Geographical Variation in Bird Song. *Biology Letters*, 7(1), 57–59. <https://doi.org/10.1098/rsbl.2010.0519>
- Derryberry, E. P., Seddon, N., Derryberry, G. E., Claramunt, S., Seeholzer, G. F., Brumfield, R. T., & Tobias, J. A. (2018). Ecological drivers of song evolution in birds: Disentangling the effects of habitat and morphology. *Ecology and Evolution*, 8(3), 1890–1905. <https://doi.org/10.1002/ece3.3760>

- Deur, D., & Turner, N. J. (Eds.). (2005). *Keeping it Living: Traditions of Plant Use and Cultivation on the Northwest Coast of North America*. Seattle, WA: University of Washington Press.
- Dilger, W. C. (1956). Hostile Behavior and Reproductive Isolating Mechanisms in the Avian Genera *Catharus* and *Hylocichla*. *The Auk*, 73(3), 313–353.
<https://doi.org/10.1525/auk.2008.61008>
- eBird. (2019). Vesper Sparrow (*Pooecetes gramineus*) - Species Map - eBird. Retrieved October 23, 2019, from <https://www.ebird.org>
- Erickson, R. A. (2008). Oregon Vesper Sparrow (*Pooecetes gramineus affinis*). In W. D. Shuford & T. Gardali (Eds.), *Studies of Western Birds* (Vol. 1, pp. 377–381).
- Falls, J. B. (1992). Playback: A Historical Perspective. *Playback and Studies of Animal Communication*, 11–33. https://doi.org/10.1007/978-1-4757-6203-7_2
- Finzel, J. E. (1964). Avian Populations of Four Herbaceous Communities in Southeastern Wyoming. *The Condor*, 66(6), 496–510. <https://doi.org/10.2307/1365226>
- Foster, J. R., & Shaff, S. E. (2003). Forest Colonization of Puget Lowland Grasslands. *Northwest Science*, 77, 283–296.
- Fox, J. & Weisberg, S. (2019). *An {R} Companion to Applied Regression, Third Edition*. Thousand Oaks, CA.
- Freeman, B. G., & Montgomery, G. A. (2017). Using Song Playback Experiments to Measure Species Recognition Between Geographically Isolated Populations: A Comparison with Acoustic Trait Analyses. *The Auk*, 134(4), 857–870. <https://doi.org/10.1642/auk-17-63.1>

- Greig, E. I., Baldassarre, D. T., & Webster, M. S. (2015). Differential Rates of Phenotypic Introgression are Associated with Male Behavioral Responses to Multiple Signals. *Evolution*, 69(10), 2602–2612. <https://doi.org/10.1111/evo.12756>
- Groves, C. R., Kutner, L. S., Storms, D. M., Murray, M. P., Scott, J. M., Schafale, M., ... Pressey, R. L. (2000). Owing Up to Our Responsibilities: Who Owns Lands Important for Biodiversity? In B. A. Stein, L. S. Kutner, & J. S. Adams (Eds.), *Precious Heritage: The Status of Biodiversity in the United States* (pp. 275–300). New York, New York: Oxford University Press.
- Haig, S. M., & Elia, J. D. (2010). Avian Subspecies and the U.S. Endangered Species Act. *Ornithological Monographs*, 67(67), 24–34. <https://doi.org/10.1525/om.2010.67.1.24.24>
- Harrison, K. G. (1974). Aspects of Habitat Selection in Grassland Birds. Master's Thesis, Western Michigan University. Retrieved from https://scholarworks.wmich.edu/cgi/viewcontent.cgi?article=3555&context=masters_theses
- Harrison, K. G. (1977). Perch Height Selection of Grassland Birds. *The Wilson Bulletin*, 89(3), 486–487.
- Hiebert, S. M., Stoddard, P. K., & Arcese, P. (1989). Repertoire Size, Territory Acquisition and Reproductive Success in the Song Sparrow. *Animal Behaviour*, 37, 266–273. [https://doi.org/10.1016/0003-3472\(89\)90115-2](https://doi.org/10.1016/0003-3472(89)90115-2)
- Hill, G. E. (1990). Female House Finches Prefer Colourful Males: Sexual Selection for a Condition-Dependent Trait. *Animal Behaviour*, Vol. 40, pp. 563–572. <https://doi.org/10.1136/vr.143.6.169>

- Hill, K., Kronland, B., & Martin, A. (2017). Fire Effects Monitoring Joint Base Lewis-McChord Annual Report. Retrieved from <https://cascadiaprairieoak.org/documents/fire-effects-monitoring-joint-base-lewis-mcchord-annual-report>
- Hinde, R. A. (1956). The Biological Significance of the Territories of Birds. *Ibis*, 98(3), 340–369. <https://doi.org/10.1111/j.1474-919X.1956.tb01419.x>
- Hinde, R. A. (1958). Alternative Motor Patterns in Chaffinch Song. *Animal Behaviour*, 6(3–4), 211–218. [https://doi.org/10.1016/0003-3472\(58\)90053-8](https://doi.org/10.1016/0003-3472(58)90053-8)
- Hing, J. S. (2014). Examining Vesper Sparrow (*Pooecetes gramineus*) Songs on the National Bison Range in Relation to Inter-individual Distances. Retrieved from https://underc.nd.edu/assets/174532/fullsize/hing_final_paper.pdf
- Illes, A. E., Hall, M. L., & Vehrencamp, S. L. (2006). Vocal Performance Influences Male Receiver Response in the Banded Wren. *Proceedings of the Royal Society B: Biological Sciences*, 273(1596), 1907–1912. <https://doi.org/10.1098/rspb.2006.3535>
- Jewett, S. G., Taylor, W. P., Shaw, W. T., & Aldrich, J. W. (1953). *The Birds of Washington State*. Seattle, WA: University of Washington Press.
- Johannessen, C. L., Davenport, W. A., Millet, A., & McWilliams, S. (1971). The Vegetation of the Willamette Valley. *Annals of the Association of American Geographers*, 61(2), 286–302. <https://doi.org/10.1111/j.1467-8306.1971.tb00783.x>
- Johnson, A. B., & Dickerman, R. W. (2006). Distribution of the Mountain Vesper Sparrow (*Pooecetes gramineus altus*) Phillips 1964. *NMOS Bulletin*, 34(1–2), 11.

- Jones, S. L., & Cornely, J. E. (2002). Vesper Sparrow (*Pooecetes gramineus*) (A. Poole & F. Gill, Eds.). <https://doi.org/10.2173/bna.624>
- Karin, B. R., Cicero, C., Koo, M. S., & Bowie, R. C. K. (2018). The Role of History and Ecology as Drivers of Song Divergence in Bell's and Sagebrush Sparrows (*Artemisiospiza*, Aves: Passerellidae). *Biological Journal of the Linnean Society*, 125(2), 421–440. <https://doi.org/10.1093/BIOLINNEAN/BLY090>
- Kenyon, H. L., Alcaide, M., Toews, D. P. L., & Irwin, D. E. (2017). Cultural Isolation is Greater than Genetic Isolation Across an Avian Hybrid Zone. *Journal of Evolutionary Biology*, 30(1), 81–95. <https://doi.org/10.1111/jeb.12989>
- King, J. R. (1968a). Oregon Vesper Sparrow. In O. L. Austin Jr. (Ed.), *Histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies*. (pp. 884–886).
- King, J. R. (1968b). Western Vesper Sparrow. In O. L. Austin Jr. (Ed.), *Histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies*. (pp. 882–884).
- Kolesnikova, Y., Liu, M., Kang, Z., & Opaev, A. (2019). Song Does Not Function as a Signal of Direct Aggression in Two Leaf-Warbler Species. *Ornithological Science*, 18(1), 17. <https://doi.org/10.2326/osj.18.17>
- Kronland, B., Hill, K., & Martin, A. (2018). *Prairie Habitat Enhancement Joint Base Lewis-McChord 2017 Annual Report*.

- Kroodsma, D. E. (1972). Variations in Songs of Vesper Sparrows in Oregon. *The Wilson Bulletin*, 84(2), 173–178.
- Kroodsma, D. E. (1986). Design of Song Playback Experiments. *The Auk*, 103(3), 640–642.
- Kroodsma, D. E. (1989). Suggested Experimental Designs for Song Playbacks. *Animal Behaviour*, 37(PART 4), 600–609. [https://doi.org/10.1016/0003-3472\(89\)90039-0](https://doi.org/10.1016/0003-3472(89)90039-0)
- Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S., & Liu, W. C. (2001). Pseudoreplication in Playback Experiments, Revisited a Decade Later. *Animal Behaviour*, 61(5), 1029–1033. <https://doi.org/10.1006/anbe.2000.1676>
- Kroodsma, D. E., & Konishi, M. (1991). A Suboscine Brd (Eastern Phoebe, *Sayornis phoebe*) Develops Normal Song without Auditory Feedback. *Animal Behaviour*, 42(3), 477–487. [https://doi.org/10.1016/S0003-3472\(05\)80047-8](https://doi.org/10.1016/S0003-3472(05)80047-8)
- Krosby, M., & Rohwer, S. (2010). Ongoing Movement of the Hermit Warbler X Townsend's Warbler Hybrid Zone. *PLoS ONE*, 5(11). <https://doi.org/10.1371/journal.pone.0014164>
- Lipshutz, S. E., Overcast, I. A., Hickerson, M. J., Brumfield, R. T., & Derryberry, E. P. (2017). Behavioural Response to Song and Genetic Divergence in Two Subspecies of White-crowned Sparrows (*Zonotrichia leucophrys*). *Molecular Ecology*, 26(11), 3011–3027. <https://doi.org/10.1111/mec.14002>
- Liu, I. A., Lohr, B., Olsen, B., & Greenburg, R. (2008). Macrogeographic Vocal Variation in Subspecies of Swamp Sparrow. *The Condor*, 110(1), 102–109. <https://doi.org/10.1525/cond.2008.110.1.102>

- Luther, D., & Magnotti, J. (2014). Can Animals Detect Differences in Vocalizations Adjusted for Anthropogenic Noise? *Animal Behaviour*, 92, 111–116.
<https://doi.org/10.1016/j.anbehav.2014.03.033>
- Marler, P. (2004). Bird Calls: Their Potential for Behavioral Neurobiology. *Annals of the New York Academy of Sciences*, 1016, 31–44. <https://doi.org/10.1196/annals.1298.034>
- Marler, P., & Tamura, M. (1964). Culturally Transmitted Patterns of Vocal Behavior in Sparrows. *Science*, 146(3650), 1483–1486.
<https://doi.org/10.1126/science.146.3650.1483>
- Mason, N. A., Burns, K. J., Tobias, J. A., Claramunt, S., Seddon, N., & Derryberry, E. P. (2017). Song Evolution, Speciation, and Vocal Learning in Passerine Birds. *Evolution*, 71(3), 786–796. <https://doi.org/10.1111/evo.13159>
- Matessi, G., Dabelsteen, T., & Pilastro, A. (2001). Subspecies Song Discrimination in a Mediterranean Population of the Reed Bunting *Emberiza schoeniclus intermedia*. *Italian Journal of Zoology*, 68(4), 311–314. <https://doi.org/10.1080/11250000109356424>
- McGregor, P. K. (2000). Playback Experiments : Design and Analysis. *Acta Ethologica*, 3, 3–8.
<https://doi.org/10.1007/s102110000023>
- McGregor, P. K. (1992). Quantifying Responses to Playback: One, Many, or Composite Multivariate Measures? *Playback and Studies of Animal Communication*, 79–96.
https://doi.org/10.1007/978-1-4757-6203-7_6

- Moseley, D. L., Lahti, D. C., & Podos, J. (2013). Responses to Song Playback Vary with the Vocal Performance of both Signal Senders and Receivers. *Proceedings of the Royal Society B: Biological Sciences*, 280(1768). <https://doi.org/10.1098/rspb.2013.1401>
- Moseley, D. L., Phillips, J. N., Derryberry, E. P., & Luther, D. A. (2019). Evidence for Differing Trajectories of Songs in Urban and Rural Populations. *Behavioral Ecology*, 1–9. <https://doi.org/10.1093/beheco/arz142>
- Moseley, D. L., & Podos, J. (2014). Vocal Performance in Songbirds: Territorial Defense and the Development of Male Song and Female Mating Preferences. *Organismic and Evolutionary Biology*, Doctor of, 95.
- Nelson, D. A. (1998). Geographic Variation in Song of Gambel's White-Crowned Sparrow. *Behaviour*, 135(3), 321–342.
- Nelson, D. A. (2000). A Preference for Own-Subspecies' Song Guides Vocal Learning in a Song Bird. *Proceedings of the National Academy of Sciences of the United States of America*, 97(24), 13348–13353. <https://doi.org/10.1073/pnas.240457797>
- Nelson, K. J., & Martin, K. (1999). Thermal Aspects of Nest-Site Location for Vesper Sparrows and Horned Larks in British Columbia. *Studies in Avian Biology*, (19), 137–143.
- Norton, H. (1979). The Association Between Anthropogenic Prairies and Important Food Plants in Western Washington. *Northwest Anthropological Research Notes*, 13(2), 175–200.
- Nowicki, S., Searcy, W. A., & Peters, S. (2002). Quality of Song Learning Affects Female Response to Male Bird Song. *Proceedings of the Royal Society B: Biological Sciences*, 269(1503), 1949–1954. <https://doi.org/10.1098/rspb.2002.2124>

- Owens, R. A., & Myres, M. T. (1973). Effects of Agriculture Upon Populations of Native Passerine Birds of an Alberta Fescue Grassland. *Canadian Journal of Zoology*, 51(7), 697–713. <https://doi.org/10.1139/z73-104>
- Parker, K. A., Anderson, M. J., Jenkins, P. F., & Brunton, D. H. (2012). The Effects of Translocation-Induced Isolation and Fragmentation on the Cultural Evolution of Bird Song. *Ecology Letters*, 15(8), 778–785. <https://doi.org/10.1111/j.1461-0248.2012.01797.x>
- Parker, T. H., Greig, E. I., Nakagawa, S., Parra, M., & Dalisio, A. C. (2018). Subspecies Status and Methods Explain Strength of Response to Local Versus Foreign Song by Oscine Birds in Meta-Analysis. *Animal Behaviour*, 142, 1–17. <https://doi.org/10.1016/j.anbehav.2018.05.023>
- Pegan, T. M., Rumelt, R. B., Dzielski, S. A., Ferraro, M. M., Flesher, L. E., Young, N., ... Freeman, B. G. (2015). Asymmetric Response of Costa Rican White-breasted Woodwrens (*Henicorhina leucosticta*) to Vocalizations from Allopatric Populations. *PLoS ONE*, 10(12), 1–16. <https://doi.org/10.1371/journal.pone.0144949>
- Petrinovich, L., & Patterson, T. L. (1981). The Responses of White-crowned Sparrows to Songs of Different Dialects and Subspecies. *Zeitschrift Für Tierpsychologie*, 57(1), 1–14. <https://doi.org/10.1111/j.1439-0310.1981.tb01309.x>
- Phillips, A. R. (1964). Notas Sistematicas Sobre Aves Mexicanas, III. *Revista de La Sociedad Mexicana de Historia Natural*, 25, 217–242.

- Phillips, J. N., & Derryberry, E. P. (2017). Vocal Performance is a Salient Signal for Male–Male Competition in White-Crowned Sparrows. *The Auk*, 134(3), 564–574.
<https://doi.org/10.1642/auk-17-2.1>
- Podos, J., & Warren, P. S. (2007). The Evolution of Geographic Variation in Birdsong. *Advances in the Study of Behavior*, 37(07), 403–458. [https://doi.org/10.1016/S0065-3454\(07\)37009-5](https://doi.org/10.1016/S0065-3454(07)37009-5)
- Potvin, D. A., Crawford, P. W., MacDougall-Shackleton, S. A., & MacDougall-Shackleton, E. A. (2015). Song Repertoire Size, not Territory Location, Predicts Reproductive Success and Territory Tenure in a Migratory Songbird. *Canadian Journal of Zoology*, 93(8), 627–633. <https://doi.org/10.1139/cjz-2015-0039>
- Pulliam, H. R., & Mills, G. S. (1977). The Use of Space by Wintering Sparrows. 58(6), 1393–1399.
- Pyle, P. (1997). *Identification Guide to North American Birds*. Bolinas, California: Slate Creek Press.
- R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. Retrieved from <https://www.r-project.org/>
- Randler, C., Förschler, M. I., Gonzalez, J., Aliabadian, M., Bairlein, F., & Wink, M. (2012). Phylogeography, Pre-Zygotic Isolation and Taxonomic Status in the Endemic Cyprus Wheatear *Oenanthe cypriaca*. *Journal of Ornithology*, 153(2), 303–312.
<https://doi.org/10.1007/s10336-011-0744-8>

- Reed, V. A., Toth, C. A., Wardle, R. N., Gomes, D. G. E., Barber, J. R., & Francis, C. D. (in press). Natural Noise Affects Conspecific Signal Detection and Territorial Defense Behaviors in Songbirds. *Behavioral Ecology*.
- Revelle, W. (2020). psych: Procedures for Psychological, Psychometric, and Personality Research. Evanston, Illinois: Northwestern University.
- Rising, J. D. (1996). A Guide to the Identification and Natural History of The Sparrows of the United States and Canada. San Diego, California: Academic Press.
- Ritchison, G. (1981). Variation in the Songs of Vesper Sparrows *Pooecetes gramineus*. *The American Midland Naturalist*, 106(2), 392–398.
- Rodenhouse, N. L., & Best, L. B. (1983). Breeding Ecology of Vesper Sparrows in Corn and Soybean Fields. *The American Midland Naturalist*, 110(2), 265–275.
- Roger, R. E. (2000). The Status and Microhabitat Selection of Four Grassland Bird Species in Western Washington. The Evergreen State College.
- Rosenberg, K. V, Rosenberg, K. V, Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., ... Marra, P. P. (2019). Decline of the North American Avifauna. *Science*, 1313(September), 1–10. <https://doi.org/10.1126/science.aaw1313>
- Sauer, J. R., Hines, J. E., Fallon, J. E., Pardieck, K. L., Ziolkowski jr., D. J., & Link, W. A. (2014). The North American Breeding Bird Survey, Results and Analysis 1966 - 2012. Version 02.19.2014.

- Schaid, T. A., Uresk, D. W., Tucker, W. L., & Linder, R. L. (1983). Effects of Surface Mining on the Vesper Sparrow in the Northern Great Plains. *Journal of Range Management*, 36(4), 500. <https://doi.org/10.2307/3897953>
- Searcy, W. A., Anderson, R. C., & Nowicki, S. (2006). Bird Song as a Signal of Aggressive Intent. *Behavioral Ecology and Sociobiology*, 60(2), 234–241. <https://doi.org/10.1007/s00265-006-0161-9>
- Searcy, W. A., & Beecher, M. D. (2009). Song as an Aggressive Signal in Songbirds. *Animal Behaviour*, 78(6), 1281–1292. <https://doi.org/10.1016/j.anbehav.2009.08.011>
- Searcy, W. A., Nowicki, S., & Hughes, M. (1997). The Response of Male and Female Song Sparrows to Geographic Variation in Song. *The Condor*, 99(3), 651–657. <https://doi.org/10.2307/1370477>
- Seneviratne, S. S., Davidson, P., Martin, K., & Irwin, D. E. (2016). Low Levels of Hybridization Across Two Contact Zones Among Three Species of Woodpeckers (*Sphyrapicus* Sapsuckers). *Journal of Avian Biology*, 47(6), 887–898. <https://doi.org/10.1111/jav.00946>
- Short, L. L. (1969). Taxonomic Aspects of Avian Hybridization. *The Auk*, 8(1), 84–105.
- Sibley, D. A. (2003). *The Sibley Field Guide to Birds of Western North America*. New York: Alfred A. Knopf, Inc.
- Slabbekoorn, H., & Smith, T. B. (2002). Bird Song, Ecology and Speciation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357(1420), 493–503. <https://doi.org/10.1098/rstb.2001.1056>

- Slater, P. J. B. (1986). The Cultural Transmission of Bird Song. *Trends in Ecology and Evolution*, 1(4), 94–97. [https://doi.org/10.1016/0169-5347\(86\)90032-7](https://doi.org/10.1016/0169-5347(86)90032-7)
- Smith, J. M. (1965). The Evolution of Alarm Calls. *The American Naturalist*, 99(904), 59–63.
- Sosa-López, J. R., Martínez Gómez, J. E., & Mennill, D. J. (2016). Divergence in Mating Signals Correlates with Genetic Distance and Behavioral Responses to Playback. *Journal of Evolutionary Biology*, 29(2), 306–318. <https://doi.org/10.1111/jeb.12782>
- Stein, B. A., Kutner, L. S., Hammerson, G. A., Master, L. L., & Morse, L. E. (2000). State of the States: Geographic Patterns of Diversity, Rarity and Endemism. In B. A. Stein, L. S. Kutner, & J. S. Adams (Eds.), *Precious Heritage: The Status of Biodiversity in the United States* (pp. 119–157). New York, New York: Oxford University Press.
- Stokes, A. W., & Williams, H. W. (1971). Courtship Feeding in Gallinaceous Birds. *The Auk*, 88(3), 543–559.
- Suckley, G., & Cooper, J. G. (1860). *The Natural History of Washington Territory and Oregon. Final Reports on the Survey of the Northern Pacific Railroad Route*. Retrieved from <https://www.biodiversitylibrary.org/item/184210#page/9/mode/1up>
- Swenson, N. G., & Howard, D. J. (2005). Clustering of Contact Zones, Hybrid Zones, and Phylogeographic Breaks in North America. *American Naturalist*, 166(5), 581–591. <https://doi.org/10.1086/491688>
- Temeles, E. J. (1992). The Role of Neighbors in Territorial Systems: When are they “Dear Enemies”? *Animal Behaviour*, 47, 339–350.

- Thorpe, W. H. (1958). The Learning of Song Patterns by Birds, With Especial Reference to the Song of the Chaffinch *Fringilla coelebs*. *Ibis*, 100, 535–570.
- Toews, D. P. L. (2017). From Song Dialects to Speciation in White-crowned Sparrows. *Molecular Ecology*, 26(11), 2842–2844. <https://doi.org/10.1111/mec.14104>
- Tveten, R. K., & Fonda, R. W. (1999). Fire Effects on Prairies and Oak Woodlands on Fort Lewis, Washington. *Northwest Science*, 73(3), 145–158.
- United States Army Corps of Engineers Portland District. (2014). Biological Assessment for the Continued Operations and Maintenance Dredging Program for the Columbia River Federal Navigation Channel. Retrieved from <https://cdm16021.contentdm.oclc.org/digital/collection/p16021coll3/id/115>
- Vickery, P. D., & Herkert, J. R. (2001). Recent Advances in Grassland Bird Research: Where Do We Go from Here? *The Auk*, 118(1), 11–15. <https://doi.org/10.2307/4089754>
- Vickery, P. D., Hunter, M. L., & Melvin, S. M. (1994). Effects of Habitat Area on the Distribution of Grassland Birds in Maine. *Conservation Biology*, 8(4), 1087–1097. <https://doi.org/10.1046/j.1523-1739.1994.08041087.x>
- Vickery, P. D., Hunter, M. L., & Wells, J. V. (1999). Effects of Fire and Herbicide Treatment on Habitat Selection in Grassland Birds in Southern Maine. *Studies in Avian Biology*, (19), 149–159.
- Weeden, J. S., & Falls, J. B. (1959). Differential Responses of Male Ovenbirds to Recorded Songs of Neighboring and More Distant Individuals. *The Auk*, 76(3), 343–351.

- Wells, J. V., & Vickery, P. D. (1994). Extended Flight-Songs of Vesper Sparrows. *The Wilson Bulletin*, 106(4), 696–702.
- White, R. (1980). *Land Use, Environment, and Social Change: The Shaping of Island County, WA*. Seattle and London: University of Washington Press.
- Wiens, J. A. (1969). An Approach to the Study of Ecological Relationships among Grassland Birds. *Ornithological Monographs*, (8), 1–93.
- Wilde, C. (2014). Evaluating The Endangered Species Act : Trends in Mega-Petitions , Judicial Review , and Budget Constraints Reveal a Costly Dilemma. *Villanova Environmental Law Journal*, 25(1), 307–350.
- Wilkins, M. R., Seddon, N., & Safran, R. J. (2013). Evolutionary Divergence in Acoustic Signals: Causes and Consequences. *Trends in Ecology and Evolution*, 28(3), 156–166.
<https://doi.org/10.1016/j.tree.2012.10.002>
- Wray, T., Strait, K. A., Whitmore, R. C., & Sparrow, F. (1982). Reproductive Success of Grassland Sparrows on a Reclaimed Surface Mine in West Virginia. *The Auk*, 99, 157–164.
- Ydenberg, R. C., Giraldeau, L. A., & Falls, J. B. (1988). Neighbours, Strangers, and the Asymmetric War of Attrition. *Animal Behaviour*, 36(2), 343–347.
[https://doi.org/10.1016/S0003-3472\(88\)80004-6](https://doi.org/10.1016/S0003-3472(88)80004-6)
- Zink, R. M. (1996). Comparative Phylogeography in North American Birds. *Evolution*, 50(1), 308. <https://doi.org/10.2307/2410802>

Zink, R. M., & Barrowclough, G. F. (2008). Mitochondrial DNA Under Siege in Avian Phylogeography. *Molecular Ecology*, 17(9), 2107–2121. <https://doi.org/10.1111/j.1365-294X.2008.03737.x>