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DOES POPULATION DENSITY AFFECT THE SINGING BEHAVIOR OF FEMALE CANYON WRENS (CATHERPES MEXICANUS)?

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DOES POPULATION DENSITY AFFECT THE SINGING
BEHAVIOR OF FEMALE CANYON WRENS
(*CATHERPES MEXICANUS*)?

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree
of Master of Science

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School of Biological Sciences
Biology Department

May 2020

This Thesis by: Lorraine Eileen Dargis

Entitled: *Does population density affect the singing behavior of female canyon wrens (Catherpes mexicanus)?*

has been approved as meeting the requirement for the Degree of Master of Science in College of Natural and Health Sciences in School of Biological Sciences

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ABSTRACT

Dargis, Lorraine Eileen. *Does population density affect the singing behavior of female canyon wrens (Catherpes mexicanus)?* Unpublished Master of Science thesis, University of Northern Colorado, 2020.

Bird song has historically been considered from the perspective of temperate males despite females in many bird species being prolific singers. In this study, I investigated one species with female song, the canyon wren (*Catherpes mexicanus*). Canyon wrens do not duet like many other species with female song or other wrens. Instead, males and females sing sex-specific songs. The resource defense function of male canyon wren song is well-described, and males sing often during the breeding season. Females have only been observed to sing sporadically during the breeding season but sing reliably and often when exposed to playback of other females. Therefore, I hypothesized that females in higher breeding density areas would sing more and be more aggressive than those in lower breeding density areas, and females with closer distances between neighbors would sing more and be more aggressive than those with farther neighbors. I conducted this study over the course of two field seasons in two regions: southeastern Arizona (high density) and northcentral Colorado (low density). I spot-mapped breeding pairs in both areas, observed unprompted levels of song from females, and conducted playback experiments on females. I measured several behavioral parameters and song spectral parameters. I found that individuals in Arizona had

significantly lower 95% frequencies in their songs, but did not find any other significant

relationships between behavioral or spectral parameters and nearest neighbor distance,

suggesting that other variables such as age, body size, breeding status, time of year, or

genetic drift may better explain the variation in female songs between populations in

Arizona vs. Colorado.

ACKNOWLEDGMENTS

two years who has told me that canyon wrens sing their favorite bird song. I hope this

study gives you another bird song to love.

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CHAPTER I

BACKGROUND AND LITERATURE REVIEW

Introduction

Bird song has historically been discussed from the perspective of temperate

males, in which males are the primarily singers and females are primarily listeners and

choosers of preferred traits (Catchpole and Slater 2003). While this is true, it does not

reflect the complete picture or the complexity of bird song globally. Recent research has

shown that female song is likely more widespread than recently thought, as well as an

ancestral trait of songbirds (Odom et al., 2014). By historically disregarding female song

and behavior as arbitrary or functionless, we have also disregarded many opportunities to

further our knowledge of the origins and dynamics of complex behaviors, neurobiology,

language, sexual selection, natural selection, and more (Odom and Benedict 2018, Price

2015, van de Pitte 1998). This study aims to investigate the complexities of one unique

system, canyon wrens (*Catherpes mexicanus*), to further our knowledge in bird song,

behavioral ecology, and evolutionary biology. Canyon wrens are members of the family

Troglodytidae and have a north-temperate geographic distribution across parts of Canada,

the United States of America, and Mexico.

Both male and female birds can be charismatic singers, and in a few species

females can even out-sing males during territorial intrusions, such as in neotropical

stripe-headed sparrows (*Peucaea ruficauda*). Stripe-headed sparrow females sang more

than males and tended to lead duets and sing competitively against other females (Illes and Yunes-Jimenez, 2009). Duetting is one of the most common contexts of female song, with duets occurring in forty percent of bird families worldwide (Hall, 2009). Duets can vary in form, ranging from briefly overlapping songs to highly coordinated vocalizations in which both males and females carefully time their songs to fit their partners'. There are many hypothesized functions of duets but preserving year-round territories and partners has been considered one of the largest selection pressures promoting the behavior (Hall, 2009, Dahlin and Benedict, 2014).

Despite the widespread presence of duetting species in tropical habitats, not all singing females are involved in duets. Like stripe-headed sparrows, female superb fairywrens (*Malurus cyaneus*) are vigorous solo-singers and often sing to defend a territory against intruders (Cooney and Cockburn 1995). Additionally, Western Australian magpie (*Gymnorhina tibicen dorsalis*) females sing more often than males and have a song significantly higher in frequency than males (Dutour and Ridley, 2020) Among the species with female song, wrens in the family *Troglodytidae* are particularly prolific in tropical as well as temperate habitats. New World tropical wrens are known to duet, such as in rufous and white wrens (*Thryophilus rufalbus*), banded wrens (*Thryopilus pleurostictus*), and plain wrens (*Cantorchilus zeledoni*). Temperate female wrens are also known to sing, although this trait is not as widespread phylogenetically. Female house wrens are fervent singers and often use song to defend territory against male and female intruders (Krieg and Getty 2016). Winter wrens (*Troglodytes hiemalis*) and cactus wrens (*Campylorhynchus brunneicapillus*) have also been observed to have

female song, but this has not been investigated in the literature (Odom and Benedict 2018).

Canyon wrens (*Catherpes mexicanus*) remain one of the most understudied and interesting singers in the family *Troglodytidae*. *Catherpes mexicanus* females sing a song different in structure and sound than males (fig. 1), setting them apart from most other temperate wrens with female song.

Figure 1: Spectrogram of canyon wren female song (top) and male song (bottom).
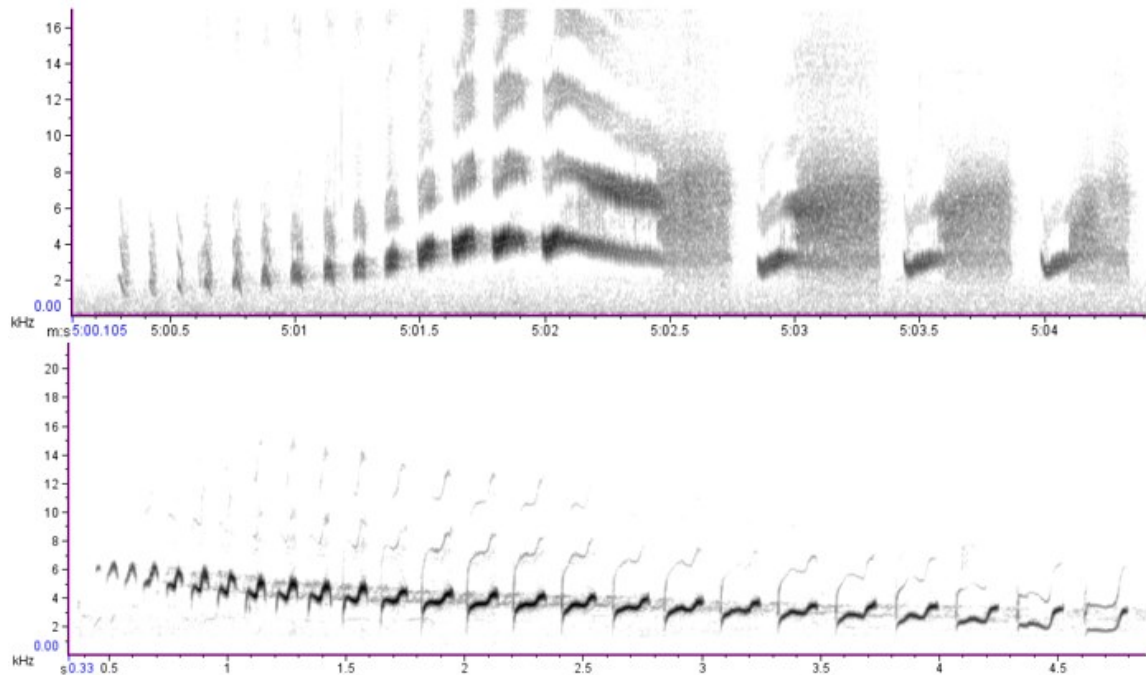
The function of this song has been studied recently, though many details about its form and function remain unclear. Female canyon wrens have been confirmed to sing but not to duet, as previously hypothesized (Spencer 2012, Hathcock and Benedict 2018). Researchers have concluded that certain life-history traits, such as being non-migratory, sexually monomorphic, and/or long-term monogamous, contribute to duetting behaviors and could perhaps serve as promoters of female solo-song (Benedict 2008; Logue and

Hall, 2014, Tobias et al., 2016). Canyon wrens fit this life-history profile, and while life history traits may be an important part of explaining the behaviors of these birds, life history is not the only relevant factor to consider. Singing behavior can also be influenced heavily by environmental factors such as geographical variation, habitat quality, or population density. Orange-crowned warblers (*Oreothypis celata*) in more densely populated California showed higher amount of territorial aggression than those in less densely populated Alaska; this hints that population density, rather than life history traits, can explain geographical variation in aggressive responses like song (Yoon et al., 2012).

Background and Literature Review

Why Should Female Birds Sing?

Male birds are known to sing to defend territories and attract mates (Catchpole and Slater, 2003). The advantages of male singing behavior, as they are known in temperate environments, are well documented to relate to natural and sexual selection. A frequently asked question on female song is "if males are fulfilling these responsibilities, why should females sing?" There are many current theories that attempt to answer this question. Existing investigations into species with female song have found that life history traits matter. Species with females who sing are often sexually monomorphic, and non-migratory (Benedict, 2008, Logue and Hall, 2014, Tobias et al., 2016). They maintain territories and pair-bonds year-round, typically in tropical areas (Benedict, 2008, Slater and Mann, 2004, Price, 2009). Some potential benefits of female singing are linked to these attributes. As sexually monomorphic individuals, it may be helpful to have a method of sex identification (Trail, 1990). Non-migratory birds are freed from the energetic cost of hefty migrations and therefore may have more energy to defend a

territory and continue to sing outside of the breeding season (Holberton et al., 2005).

Furthermore, a sedentary lifestyle may translate to heightened selection for year-round

singing and territory defense, particularly during a season when resources may be low,

such as winter or dry seasons (Wingfield and Monk, 1992). This may also contribute to

continued pair-bonds from year to year, as having a mate with whom to share half of the

defensive load would be advantageous (Langmore, 1998). Similarly, it is hypothesized

that in tropical areas females may be more likely to sing in order to create a consistent

breeding synchrony in aseasonal environments, as well as general sex role convergence

in these long-term, reliable pair bonds (Slater and Mann, 2004).

When considering function, females may be using song in a similar fashion to

males and may be under similarly described selection pressures. Though studies are slim,

there is evidence to show that females do experience male mate choice discrimination;

alpine accentor (*Prunella collaris*) female song elicited approaches from males, but not

from females, suggesting that females sing to get the attention of males (Langmore et al.,

1996). Polygynandrous females in this species sing to attract males and advertise

reproductive strengths (such as age); it is also suggested females use their song to signal

to multiple males within their groups, optimizing parental care for their offspring, which

may be sired by several males (Langmore et al. 1996). Superb fairy-wrens (*Malurus

cyaneus*) are cooperative breeders with female song; females who sang more often in

response to playbacks had greater reproductive success (Cain et al., 2015). Streak-backed

Oriole females (*Icterus pustulatus*) are solo-singers who have been observed to sing more

than males during the breeding season, presumably to defend resources from conspecifics

(Price et al., 2008).

The topic of male mate choice has been better studied regarding plumage than song. Female plumage ornamentation has sometimes been disregarded as a by-product of male ornamentation, but Amundsen (2000) found support for independent evolution of female ornamentation from male ornamentation. Sexual selection has often been described as a one-way street, in which one sex is selected upon while another is not, but simultaneous selection should be considered. Amundsen suggests natural and sexual selection are dynamic, variable, and simultaneous; our research should reflect this, and within the context of female ornamentation, including song, this resonates. There is evidence to show that males do value quality traits as well as ornaments. Male zebra finches chose experimentally fecund females over control females, suggesting males take reproductive quality into mate choices (Jones et al. 2001). Furthermore, there is evidence to suggest that males can be especially choosy towards females in polygynous systems or systems lacking in male parental care (Edward and Chapman, 2011). Female song in superb fairy-wrens has been suspected to be a multipurpose trait that can assist in identifying individuals, and most likely competition between females (Cain and Langmore, 2015). Overall, not only are females singing, but they are singing in a range of different circumstances, reflecting differing selection pressures relating to life history, environmental factors, sexual and natural selection.

**Females Song in Duets: Mate Attraction,
Retention, and Territoriality**

Female roles within duets offer many of the best described examples of female song. Duets have been defined as coordinated vocalizations between two individuals (Hall, 2009). They can be "overlapping" in time, in which males and females sing the same or different songs that are partially or fully simultaneous. Duets can also be

antiphonal, or a "call and response" song, starting with one vocalization from one individual, and ending with a vocalization from another, often alternating back and forth (Hall, 2009). Both types of duets require high levels of coordination in time and space, and can be difficult to execute, but have many advantages (Fortune et al., 2011). Duets can create and strengthen pair bonds and prevent mate-usurpation through the breeding season, as well as create a strong collaborative display in defense of territory (Hall 2009, Dahlin and Benedict, 2014). The benefits of retaining pair bonds, especially throughout harsh seasons such as wintering or dry seasons, can result in increased selection pressure for song in both sexes. Baldassarre et al. (2016) found that within red-backed fairy-wrens' duets, males that responded faster to duet initiations were cuckolded less in this highly promiscuous species. Amazonian warbling antbirds (*Hypocnemis cantator*) responded more aggressively to sex-specific calls than pair duets in their territory, suggesting cuckoldry may be a larger threat to the pair-bonds than territory resources (Seddon and Tobias 2006). Additionally, female antbirds were shown to adjust vocalizations in relation to the perceived threat and duetted more with males in order to repel opposing females (Seddon and Tobias 2006).

In terms of territorial defense, white-bellied antbird (*Myrmeciza longipes)* males and females respond aggressively to the songs of both sexes. Fedy and Stutchbury (2005) found that both males and females responded aggressively to territorial intrusions during the breeding season. Purple-crowned fairy-wrens also duet during the breeding and nonbreeding seasons to protect scarce resources (Hall and Peters, 2008). In slate-colored boubous (*Laniarius funebris*), males and females can sing several different song types together for multiple purposes, such as mating or territory defense (Sonnenschein and

Reyer, 1983). Interestingly, there are some species that express both duets and solo songs, such as in Australian magpie-larks (*Grallina cyanoleuca*) in which solo and duet songs are used in different contexts between males and females; both sexes respond to same-sex conspecific song strongly, signifying solo songs can deter same-sex rivals from the territory. Additionally in this species, duets were suspected of primarily serving a cooperative territorial defense strategy (Mulder et al., 2003). California towhees (*Pipilo crissalis*) use duets to interact with their own mates as well as extra-pair individuals and duets serve multiple different purposes in many different contexts (Benedict 2010). In conclusion, duets are incredibly diverse and dynamic. They can contain specific messages for specific receivers in a certain context, or multiple messages for multiple receivers. Females can play active roles both within these duets, and as solo singers.

Female Solo Singers

Although many females sing in the form of duets, many also sing separately from males. This is most common in the tropics but happens in temperate areas as well, albeit less frequently. Often female songs will be of the same repertoire as males, such as in Northern Cardinals (*Cardinalis cardinalis*) (Ritchison, 1986), whose females use differing song types during the breeding season to encourage males to bring food (Halkin, 1997). Northern cardinals can also learn songs from either sex (Yamaguchi, 2001). Female superb fairywrens (*Malurus cyaneus*) also sing the same song types as males. Many studies have concluded that this song's main function is territory defense, and birds can distinguish neighbor females from strangers through song, so individuals may use these to recognize known or unknown conspecifics (Cooney and Cockburn, 1995). There are other species, such as canyon wrens (*Catherpes mexicanus*), in which the male and

female song are different in form and are used in sex-specific interactions (Spencer, 2012, Hathcock and Benedict, 2018). Similarly, female red-winged blackbirds (*Agelaius pboeniceus*) have two song types, one for maintaining pair bonds with males in this polygynous species, and one for dispelling female conspecifics (Beletsky 1983).

In addition to the species in which female song has an understood function, there are increasing numbers of newly observed female singers who may sing opportunistically in North American temperate zones. This many occur when a bird is under extreme stress, or it may be typical, but the behavior is simply being observed for the first time. Many of these are in the family Parulidae, or New World wood-warblers (Najar and Benedict 2015). Two cerulean warbler females (*Steophaga cerulea*) were observed singing in southern Indiana in 2017 (MacDonald et al., 2019). The song structure did not resemble male song, and the function is unclear, but anecdotal observations suggest it is to express communication between males and females (MacDonald et al. 2019). Female yellow warblers (*Dendroica petechia*) have been observed singing during transect observations, though the function of this song remains unclear. Prothonotary warblers (*Protonotaria citrea*) have also been shown to sing during the mate acquisition period of the breeding season (Matthews et al., 2017). With more research, we may decode the mysterious songs of a wide taxonomic range of solo singing females.

Female Song in Tropical and Temperate
***Troglodytidae* Wren**s

Wrens in the family *Troglodytidae* are notoriously aggressive and well-studied birds, with some being recognizable backyard visitors, and others tropical understory dwellers. Female tropical and temperate wrens vary considerably in their life history characters and behavior despite being in the same family (Brewer, 2010). Certain species

have been observed to be long -term socially monogamous birds, others have been recognized as polygynous. Some duet, some sing solo, and some do a combination of both behaviors (Mann et al., 2009). Their aggressive behavior towards conspecifics and heterospecifics as well as the presence of female song within this family has made it a focus of many studies (Kattan, 2016, Pribil and Picman, 1991).

Female song in tropical wrens. Most tropical wren species duet (Mann et al., 2009). Although our understanding of many of these is somewhat lacking, there are a handful of species that have been studied extensively. Rufous and white wrens (*Thyrophilus rufalbus*) are well-known duetters. They rely most heavily on song to communicate between sexes as well as between conspecific pairs (Hick et al., 2016). They are known to duet more during fertile periods in both male and female physiology, suggesting that this behavior is linked to mate-guarding and paternity-guarding (Kahn et al., 2018). Conversely, duetting in bay wrens (*Thryothorus nigricapillus*) does not appear to be related to mate guarding or territorial defense (Levin, 1996). Additionally, the results of Levin's (1996) study suggested that females' and males' songs served different purposes. Female song rates were suspected to be sex-specific signals for other females, and male singing rates increased in the presence of females for unpaired males, suggesting a mate-attraction function. Duet function within established pairs remained unclear (Levin, 1996).

Another tropical duetter, the plain wren (*Thryothorus modestus zeledoni)* has a tightly coordinated antiphonal song, initiated by the female. This duet requires rapid response and synchronization by the male (Mann et al., 2009). These wrens perform several different duet types, and both males and females will insert several inter-phrase

calls when their duets are not answered (Rivera-Cáceres, 2015). Due to the complexity of their timing, coordination, and effort, these duets are suspected to have high mutual mate-retention value to pairs (Rivera-Cáceres, 2015). Black-belled wren (*Pheugopedius fasciatoventris*) duetting behavior is also well-studied. Females and males respond to one another using similar song types year after year, suggesting that they match distinctive song types with mates (Logue, 2006). There is also evidence to suggest that individuals can distinguish between one another using song features (Logue, 2006). Black-bellied wrens' duets are suspected to be spatially correlated; Logue (2007) found that duets were more likely to happen when individuals were closer together and individuals remained closer together after duetting. These wrens can tell us more about how birds use song to distinguish individuals and potential mates, as well as how proximity to neighboring individuals, or areas of higher breeding density, can affect song.

Some non-duetting wrens are known to sing two different songs types, one sung by females and one sung by males. A Mexican endemic, the Sumichrast's wren (*Hylochilus sumicrasti*) has females that sing a song different from males in form and context (Pérez-Villafaña et al., 1999). This system has not been explored extensively, but work suggests that solo female songs are more common than previously though in this family of duetters (Pérez-Villafaña et al., 1999). Nava's wren (*Hylorchilus navai*) females have also been observed to sing a song separate from males outside of duets, but these vocalization are quite understudied, as is the natural history in general of this little-known genus (de Silva et al., 2004).

Female song in temperate wrens. There are several species of North American wrens that have been confirmed to have female song: Canyon wrens (*Catherpes*

mexicanus), house wrens (*Troglodytes aedon*), winter wrens (*Troglodytes troglodytes*), and cactus wrens (*Campylorhynchus brunneicapillus*) (Odom and Benedict, 2018). Observations from winter wrens and cactus wrens have not been recorded in primary literature but have been observed in citizen science accounts (Jones and Dieni, 1995, Jones et al., 2002). Female and male house wrens sing similar songs, with females singing slightly higher pitched elements that are not included in male's song (Spencer, 2012, Hathcock and Benedict, 2018) Females sing extensively towards conspecific females, and, use a high-pitched, low-amplitude call when encountering other females, which is quite similar in form and function to what researchers have observed in males (Krieg and Burnett, 2017). This proves to be useful for females; in one study, females who sang more often had larger offspring at certain points in development, as well as young that were more likely to fledge (Krieg and Getty 2020). Canyon wrens are also well-studied female solo singers in the *Troglodytidae* family. Canyon wrens are unique due to their differentiation in sex-specific song form. Males and females sing different songs (fig. 1) and are suspected to use them in different scenarios. As they are the focus of this thesis, I examine canyon wren song in more detail below.

Natural History and General Description
of Song in Canyon Wrens

Canyon wrens are a western and southwestern North American distributed species (Jones and Dieni, 1995). They are insectivorous cavity nesters, that occupy rocky outcroppings, typically sandstone (Jones and Dieni, 1995). Their territories are often large and widely spaced; this may be due to their natural history or due to availability of preferred canyon and cliff habitat (Warning and Benedict, 2015). They nest and forage in rocky crevices and occasionally in human made structures (Jones and Dieni, 1995,

Warning and Benedict, 2015). They have been found anecdotally to nest in houses, barns, garages, or in previously documented cases, abandoned cliff swallow nests (Warning and Benedict 2013). They are known to exist at low densities in Colorado's front range and are typically understudied due to the difficulty in navigating their steep, rocky habitat (Warning et al., 2015, Jones et al., 2002).

Canyon wren males have a loud, recognizable song that bounces easily off canyon walls and can be heard almost one hundred meters from their singing perch. Male song sound pressure levels may reach 99 decibels at 1 m, or roughly as loud as a helicopter (Braelei Hardt, unpublished data). Females also sing, but it their songs are far less frequent and not often recognized by human listeners (Jones and Dieni 1995). Male song repertoires and function are well described. Male canyon wrens tend to increase their song rates in the springtime when territories are being established, and will continue to sing throughout the breeding season, though somewhat less frequently (Jones and Dieni, 1995). Males sing around five song types, all constructed of descending notes, with the song ending in several broadband notes (Benedict et al., 2012). They generally sing one song type per singing bout and have small temporal breaks between bouts. Benedict et al. (2012) found that males share song types and their song repertoires overlapped by 94% with their neighbors. Some song types were found to be geographically restricted while some are used across the range of the species (Benedict et al., 2012).

Male canyon wren songs function in resource defense (Benedict et al. 2012). As a result of simulated intrusion by a male conspecific, males will increase song rates, and significantly lower the lowest song frequencies, as well as added harsher, wider broadband notes to the ends of their songs (Benedict et al., 2012). This is consistent with

literature suggesting that lower frequencies are associated with aggression and can indicate larger body size and therefore higher territorial threat (Bowling et al., 2017, Geberzahn et al., 2010).

There has been a significant increase in studies on this interesting species over the past ten years, however, studies of female canyon wrens are still sparse. Female canyon wrens have been observed to sing since 1964 (Tramontano, 1964) and female song was briefly described in 1995 by Jones and Dieni (Jones and Dieni, 1995). Female song has been described in multiple sources as a buzzier, less frequently occurring than male song, less pure in tone sound, and occurring year-round (Jones and Dieni, 1995, Tramontano, 1964, Brewer, 2010, fig 1). This is like what we see described in the Sumichrast's wren and the Nava's wren in Mexico; these species are theorized to be closely related to canyon wrens, but there is little genetic evidence to fully support this (Brewer, 2010). There are also comparisons drawn to the similarity in song of the males which have been suggested to indicate closer relationships, but this could also be an example of convergent evolution (Brewer, 2010). There is not much information on the form and function of female song in Sumichrast's or Nava's wren other than general descriptors (Pérez-Villafaña et al., 1999, de Silva et al., 2004).

The first in-depth observations of canyon wren female song in an experimental context come from Andrew Spencer in 2012. Spencer used one song file recorded by Nathan Pieplow in 2012 from a female in Pima County, Arizona, to conduct the first playback experiments on females in Moffat county and Rio Blanco county, Colorado (Spencer 2012). He observed a pair of canyon wrens responding aggressively to the female playback, and he recorded female song in response to the playback (Spencer

2012). He also played male song to pairs, in order to observe if both sexes responded aggressively as they had to the female song. In this encounter, he observed several instances of male and female song overlapping, leading him to hypothesize that males and females may duet when approached with female or male song. Spencer's (2012) study inspired previous University of Northern Colorado graduate student TJ Hathcock to conduct an experiment to detect whether canyon wrens regularly duet. Hathcock conducted playback experiments in the front range of Colorado in 2016 in which he exposed pairs of canyon wrens to overlapping male and female song, as well as female and male song separately (Spencer, 2012; Hathcock and Benedict 2018). Results indicated that females and males do not overlap songs more than expected by chance, but instead, sing separately and perhaps have sex-specific signals directed to members of their own sexes (Hathcock and Benedict 2018). Both males and females may use song to keep conspecifics off their territory, communicate in their pairs, defend resources, or use vocalizations for sex identification purposes (Hathcock and Benedict 2018).

Overall, the literature on canyon wren female song is brief, but informative. Female song outside of playback experiments is known to be rare (Benedict et al 2012 Hathcock and Benedict 2018). Although it is rare, it is suspected to have function; females and males do not duet, but females do respond aggressively and immediately to conspecific females in their territories (Hathcock and Benedict 2018). Males may also be indirect receivers in female song signaling; the selection pressures related to this are, however, unexplored. Realizing that females sing infrequently at least during the breeding season but sing immediately in the presence of playback was inspirational in the formation of my master's research question. I wondered: do females only sing when they

are close to other females? According to the playback results of Spencer (2012) and

Hathcock and Benedict (2018), this appeared to be true. Therefore, this led me to the

question: will females in areas of higher population density sing more often, or altogether

be more aggressive than females in areas of lower population density due to higher

competition for space and more frequent interactions with other females?

How Can Population Density
 Affect Behavior?

Changes in environmental variables can affect behavior in conjunction with life

history traits (Balbontín et al, 2009). For example, one important factor may be habitat

quality, which can serve as a metric in predicting behavioral responses; many species

increase territoriality or singing behavior in response to varying levels of habitat quality

(Cain and Langmore, 2015, Robinson and Terborgh, 1995, Foltz et al., 2015).

Geographical variation within a species' distribution has also shown to correlate with

behavioral differences in song (Krebs and Kroodsma 1980) and breeding behavior

(Rohwer and Purcell, 2019). Environmental variation has even been postulated as a

reason for birds' large brains (Sayol et al., 2016). Varying environmental pressures create

variable selection pressures on many avian behaviors.

My research is focused on the effects of a particular social environmental factor:

population density. Population density is defined as the number of individuals per unit

area, and has been measuring using various techniques, most involving GIS (Butler et al.,

1995, Wilkin et al., 2006). Population densities can be determined observationally with

point-count surveys, but these are often time consuming and difficult to carry out without

a large field crew or widely accessible habitat (Emlen, 1971). Many species in which the

effects of population density have been investigated experimentally have been cavity-

nesting species such as tree swallows (*Tachycineta bicolor*) and blue tits (*Parus caeruleus*) for which nest boxes can be installed in high-density and low-density configurations (Dunn et al., 1994, Charmantier and Perret, 2004). Wilkin et al., (2006) studied great tit (*Parus major*) breeding density by combining both approaches; they created Thiessen polygons around occupied nest boxes in order to approximate territory sizes and density. Other studies have simply referenced the Bird of North America species accounts (Noreau and Desrochers, 2018). Yoon et al., (2012) used a combination of field and GIS data to create breeding density measures; individual orange-crowned warblers were banded and Juanesobserved in the field and location points were taken in the mornings of individuals' singing perches (Yoon et al., 2012). Yoon et al., (2012) uploaded these points to ArcGIS and created minimum-convex polygons, and breeding density was calculated as the number of territories divided by the total area of each study plot.

Other researchers have used similar approaches, combining field data collection and GIS methods. Hoover et al., (2020) used a grid of 170 nest boxes on two 40-hectare study sites in southern Illinois, one site being high density and the second site being lower, or normal density. The low/normal density site had assigned nest boxes had approximately 65 boxes with 100 meters spacing between. The second/high density site had 65 boxes with approximately 35 to 50 meters spacing between. (Hoover et al., 2020). Distances between nests were measured using Trimble GPS units and GIS. This nest box approach is ideal, but not dissimilar from nearest neighbor distances. Because this study was conducted during nesting stages, individuals are spending most of their time at or nearby (< 200 m) the nest (Hoover et al., 2020). Hoover et al., (2020) calculated "local

density" as the number of warbler pairs breeding in nest boxes within a 200-meter radius of their nest. Other studies have created 25 by 25-meter plots in which they counted the total number of territories inside of those plots (Sofaer et al., 2014). These methods are appropriate given the natural history of the species involved (wood warblers). These species often occupy a given area of appropriate habitat (usually forested). The accessibility of these areas is relatively uniform. The habitat of canyon wrens can be incredibly variable, from human-made structures to remote outcroppings (Jones and Dieni, 1995). For this project, I approximated density with nearest neighbor distances as best as was possible given the natural history of these organisms. Overall, a combination of field methods, GIS methods, and a general calculation of proximity of individuals has been used to investigate breeding density, dependent on the natural history of each species.

The effects of population density on bird populations has been studied extensively. Population density affects factors such as body size, extra-pair paternity, breeding biology, and more (Juanes, 1986, Charmantier and Perret, 2004, Arcese and Smith, 1988). Body size has been shown to decrease in areas of higher population density, as resources are more limited in areas with more competition between individuals (Juanes 1986). Extra-pair paternity has been hypothesized to increase in areas of higher population density as a result of increased interaction with more diverse individuals. For example, blue tit nest boxes placed in a higher density configuration showed higher rates of extra-pair young (Charmantier and Perret, 2004). Population density may also affect reproductive output: song sparrow females (*Melospiza melodia*) in high density areas decreased the number of eggs laid per clutch by one quarter when

compared to areas of low-density (Arcese and Smith, 1988). It has been recently suggested that population density may be an important driver of life history traits, potentially including those that covary with female song and duetting (Wright et al., 2019). While these and other environmental factors may be constantly changing, we can conclude that population density can indeed cause behavioral changes in birds over evolutionary time.

Despite what we know about how population density can affect bird behavior, there is a deficit in our knowledge on how population densities affect song. Yoon et al., (2012) observed an increase in vocal aggression, particularly song, in response to playback in male orange-crowned warblers (*Leiothlypis celata*) in higher density California than lower density Alaska. In northern cardinals (*Cardinalis cardinalis*) breeding density was correlated with longer and faster songs in males (Narango and Rodewald, 2016). Furthermore, Eurasian eagle owls (*Bubo bubo*) in higher breeding density areas had more honest vocalization signals associated with habitat quality (Penteriani, 2003). In this way, male vocalizations may be representing a signal of male fitness in areas of higher breeding density (Penteriani, 2003).

There are a few studies in which increased population density has been suggested to increase overall song production, especially in females. Arcese et al. (1988) observed that female song sparrows do not sing often, but when they do, it is in areas of higher population density. It is hypothesized that this may be due to an increase in testosterone, as higher population densities can lead to increased aggression (Yoon et al., 2012). Additionally, it is worth stating that low population densities have been known to correlate with increased aggression among females, such as in brown-headed cowbirds

(*Molothrus ater*) in which females in lower densities areas were found to be more aggressive vocally to other females, indicating that aggression may encourage dispersal among individuals (Yokel 1989). Nevertheless, density has been correlated with changes in singing behavior, but this has not been extensively studied. Within canyon wrens, we have an opportunity to explore these relationships in-depth to uncover more about how their songs may vary across density gradients.

Summary

In this chapter, I have provided background on the current literature describing what we know about female singing in duetting species and female soloist species. Additionally, I have investigated how female song may vary between closely related species in tropical and temperate wrens. I have described what we currently know about how these species change general behaviors and singing behaviors in different social environments, and finally, how birds change their behaviors in contrasting areas of population density. In chapter two, I will present and describe my data on canyon wren female singing behavior, song characteristics, and breeding density. And finally in chapter three, I will discuss the final conclusions of this study, natural history remarks, and future directions. Bird song has largely been considered well-studied and described, but can we consider it these things when half of all birds (females) have not been closely investigated? Continuing to study canyon wrens can help explain why some females sing and others do not, how more female came to sing in the tropics, what information is being exchanged during male and female song, and how these differences may be acted upon by natural and sexual selection.

CHAPTER II

POPULATION DENSITY IS NOT A LIKELY DRIVER OF FEMALE CANYON
WREN (*CATHERPES MEXICANUS*) SINGING BEHAVIOR

Introduction

Bird song has historically been considered from the temperate male perspective,

despite females of many species playing an active role in singing as well. However,

recent studies have shown that females that sing are more globally widespread and

dynamic than previously thought, and that female song may be an ancestral trait among

songbirds (Odom et al., 2014). Many females that sing do so within duets, representing

about forty percent of bird families worldwide (Hall, 2009). Or, females can sing

independently, either with a song similar in structure to males' (Ritchison, 1986; Cooney

and Cockburn 1995; Krieg and Getty, 2016) or a song that is different in form (Spencer,

2012; Pérez-Villafaña et al., 1999, fig 1). Both duets and female solo songs have been

demonstrated to function in many ways, including resource defense, mate attraction and

retention, pair bonding, and promoting breeding synchrony (Langmore, 1998, Slater and

Mann, 2004).

Some of the best examples of avian female singers from both tropical and

temperate areas include members of the *Troglodytidae* family - wrens. Most tropical

wrens duet, including rufous-and-white wrens (*Thyrophilus rufalbus*) which use their

song for intra- and inter-specific communication (Hick et al., 2016). Bay wren (*Thryothorus nigricapillus*) songs have also been hypothesized to have multiple functions; females use song in order to reduce competition for mates, and males increase song rates in the presence of females when unpaired (Levin 1996). In temperate North America, House wrens (*Troglodytes aedon*), winter wrens (*Troglodytes hiemalis*), cactus wrens (*Camphylorhynchus brunneicapillus*) and canyon wrens (*Catherpes*

Figure 2: Spectrogram of canyon wren female song (top) and male song (bottom).
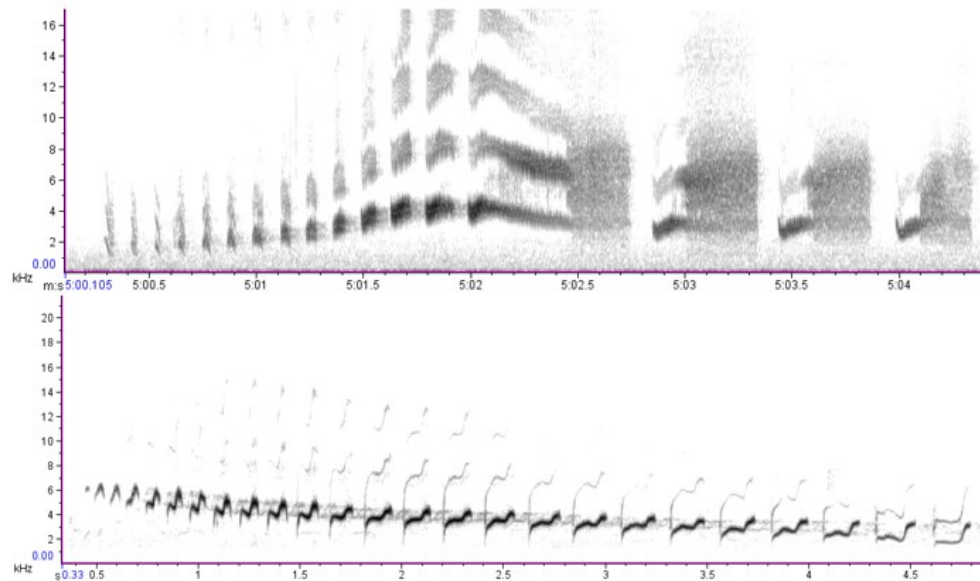
mexicanus) all have female songs. Some of these species' female songs have very well-described repertoires and functions; for example, house wren female songs are known to defend territory against conspecifics, particularly other females (Krieg and Getty 2016; Krieg and Burnett, 2017). Canyon wrens are one of the least studied wren species with female song, perhaps due to their difficult to navigate habitat which includes steep, rocky slopes. Canyon wren females sing a song completely different in structure and sound than males (fig. 2), which is uncommon among species with female song.

Canyon wren females sing infrequently during the breeding season but sing reliably and often when hearing female song playback (Hathcock and Benedict, 2018). They had been hypothesized by Spencer (2012) to duet, but this has not been supported with further research (Hathcock and Benedict, 2018). Life history characters, such as being non-migratory, sexually monomorphic, and/or long-term monogamous, have been associated with female song and duetting in many temperate species, and canyon wrens express many of these traits (Benedict, 2008; Jones and Dieni 1995). Life history may therefore partially explain the origins and long-term drivers of singing behavior in this species, but life history is not the only contributor to a plastic bird behavior such as song. Social and environmental factors such as urban noise (Hamao et al., 2011) habitat quality (Goretskaia et al., 2018), social desirability (Sung and Handford, 2020), and population density (Arcese et al., 1988) have also been known to affect the ways in which birds sing.

Population density can be defined as the number of individuals per unit area (Marques et al., 2013). Avian population density is commonly measured using a combination of field and lab analyses, often collecting territory data on known individuals from singing perches and transferring this data to ArcGIS to create digital maps and calculate distances between territories (Jablonski et al., 2010, Yoon et al., 2012). Density has been known to affect singing behavior in passerines, particularly in song elaboration, such as in the Parulidae family (Byers, 2015) and song variation, as in the greenish warbler (*Phylloscopus trochilodes*) (Irwin, 2000). Density has been shown to overshadow life history traits as influencing variables in orange-crowned warblers (*Oreothypis celata*). Between populations, male orange crowned warblers in more densely populated California areas out-sang those from less densely populated Alaska

(Yoon et al., 2012). Among females, work has shown that female song sparrows rarely sing, but when they do, it is in years or areas of higher population density (Arcese et al., 1988).

Research Questions and Hypotheses

Results of previous studies lead me to explore whether population density will influence how often and how aggressively female canyon wrens sing. Given that females sing when hearing female playback, can I infer that they sing more often in environments in which they more frequently encounter females?

Q1   Do females in higher density areas sing more often without playback than females in less densely populated areas?

H1   Females in high density areas will sing more often without playback than females in less densely populated areas.

Tests and predictions of Q1. I conducted two-hour behavioral observations upon pair discovery to observe whether females sing outside of playbacks.

- I predicted that females in a high-density population will sing more often than females in a low-density population within these observation periods.
- I predicted that females with closer neighbors will sing more often than females with farther neighbors.

Q2   Do females in more densely populated areas response more aggressively to playbacks than females in less densely populated areas?

H2   Females in high-density areas will sing more often when exposed to playback and will have more aggressive characteristics in their songs.

Tests and predictions of Q2. I conducted playback experiments, recorded acoustic responses by females, and analyzed data to measure song spectral qualities and compare populations.

- I predicted that females in more densely populated areas will have longer songs, longer wide broadband syllables, lower peak frequencies, and higher entropies,
- I predicted that females in more densely populated areas will have shorter times between songs, will approach more quickly, and will approach closer when challenged with playback.
- I predicted that females with closer neighbors will also have longer songs, longer wide broadband syllables, lower peak frequencies, higher entropies, shorter times between songs, will approach more quickly and will approach closer when challenged with playback.

Materials and Methods

Field Sites

This study was conducted over two years: from May through July of 2018 in Larimer, Boulder, and Jefferson counties in Colorado, and from April to June of 2019 at the Southwest Research Station in the Chiricahua Mountain region in Cochise county, Arizona. The total study area ranged from 40.7º N, -105.2º W to about 31.9 º N and 109.2º W. Colorado represents our low-density site, as it is documented that canyon wrens exist at low population densities there (Warning et al., 2015, Fink et al., 2020). I chose Colorado field sites based on user-reported canyon wren location information from eBird and information from previous research in our laboratory (Hathcock and Benedict, 2018). The Southwest Research Station and Chiricahua Mountain region was chosen as our high-density site due to eBird sightings as well as recommendations by station scientists and birders. eBird data suggests that around 12% of the total population of canyon wrens resides in Arizona (Fink et al., 2020). We sought to find all birds in each area and searched to find neighboring territories after finding breeding pairs. The total number of breeding pairs found in Colorado was 12, and the total number from Arizona was 24.

Figure 1: Canyon wren territories in the 2018 Field season in the front range of northcentral Colorado. Each triangle represents an average territory center; different colors represent different individuals.
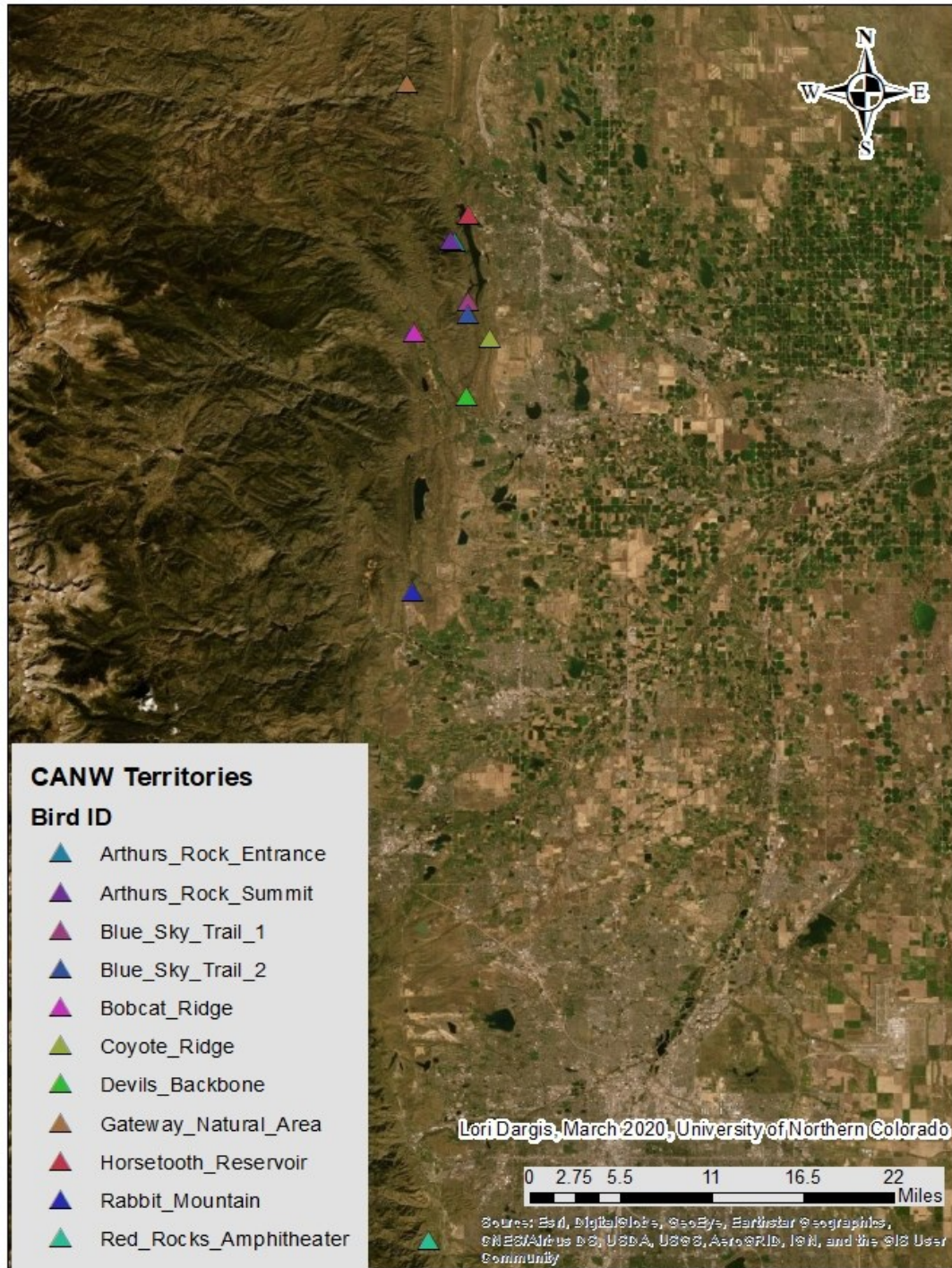
Figure 2: Canyon wren territories in the 2019 field season in southeastern Arizona at the Southwest Research Station in Portal, AZ. Each triangle represents an average territory center, different colors represent different individuals.
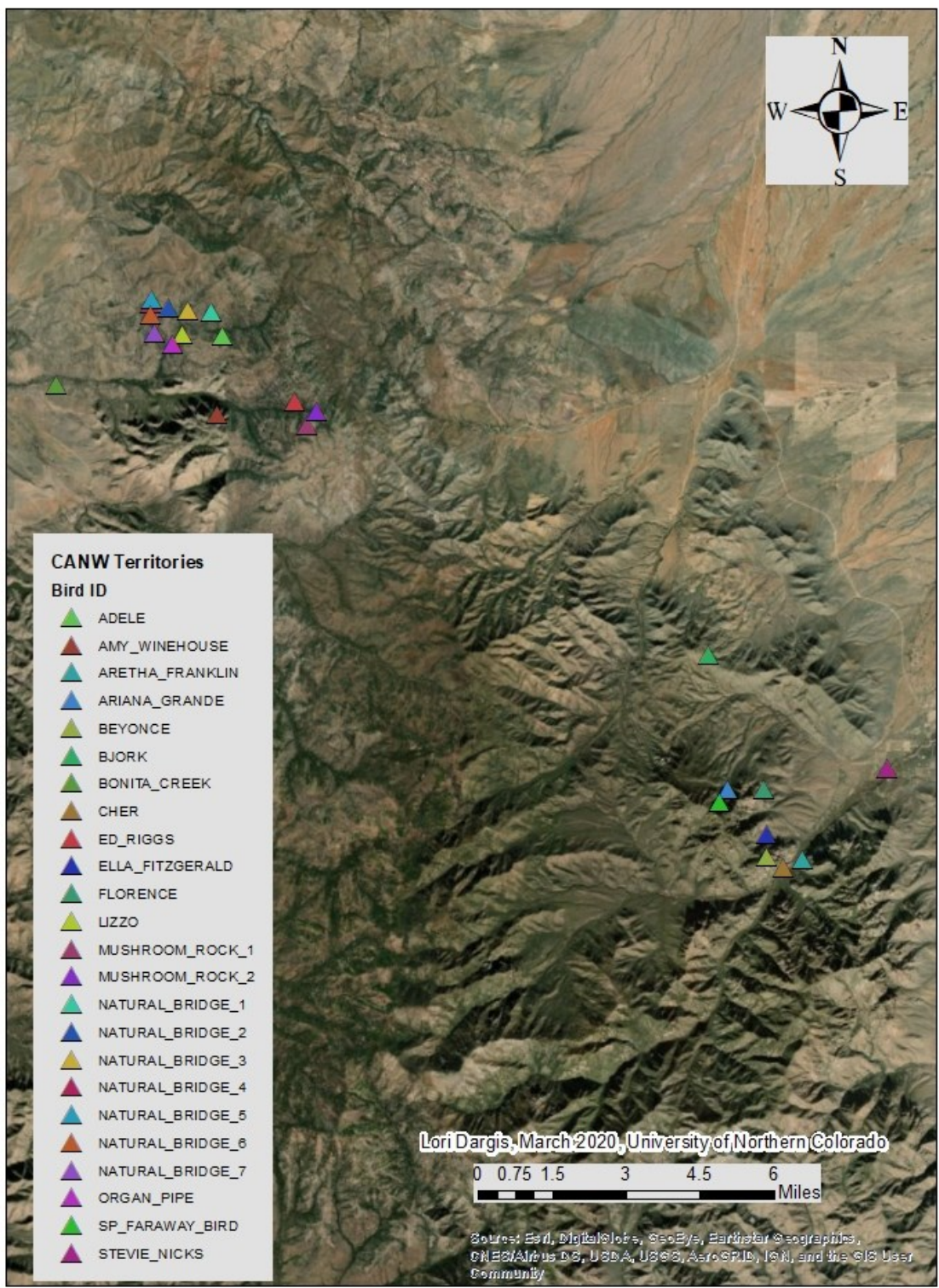
Territory Mapping and Natural
Song Observation

I or a field assistant located individual birds by hiking on trails at indicated

locations and found individuals primarily by sight and sound. After a pair of birds was

discovered, I began a two-hour observation period. I used this time to observe

unprompted, or natural, rates of female song. Additionally, I created territory maps that

included singing perches and/or known nest locations of pairs. I used a Trimble GPS unit,

a compass, and range finder to estimate distances from an observation location. Because

canyon wrens often occupy areas that are difficult to navigate such as steep, rocky

outcroppings or slopes, a researcher would sit or stand in an inconspicuous location and

use the range finder and compass to accurately enter points into the Trimble. In this way,

I could record territory points without disturbing bird behavior. If the bird moved out of

sight, a researcher would move from their initial location to keep within sight of the bird

while remaining inconspicuous. If the bird flew to an inaccessible area or was lost, the

researcher would sit and wait within 10 meters of the last singing perch and often the bird

returned. I collected a minimum of twenty-five territory points per pair of birds, which

were used to determine the center of the pairs' territory. All two-hour observations were

done after pairs had established territories. No additional territory points were taken after

pairs were discovered to have fledglings, as their territories can change dramatically after

fledgling (Warning et al., 2015). Points were uploaded to ArcGIS to create territory

polygons using methods adapted from Yoon et al. (2012).

Banding

In 2018 and 2019, I banded birds opportunistically, depending on the

accessibility of their habitat. Pairs in Colorado had such significant distances between

territories that it was possible to be certain of individual identity and sex by sight and sound, without color-bands. In Arizona, if I could not band individuals, I verified bird identity using their normal territory boundaries and if I could hear neighboring individuals singing at the same time or during counter-singing events. During both the 2018 and 2019 field seasons, I banded birds using the standard mist-netting protocols from the Institute of Bird Population handling manual (DeSante et al., 2009). I color banded males first in order to identify individuals by sex during following experimental trials if they did not sing. I captured males in mist nets at least one day before female playback trials using male song playback. I wanted to ensure that females did not hear female playback until the experiments, therefore I refrained from banding them until after playback trials. I applied one USGS silver band and three color-bands to each bird's legs to distinguish individuals during observations. If males could not be caught without severe stress induced (greater than 20 minutes of playback while target netting), I tried again another day, or I left them unbanded and distinguished pair males from females via vocalizations. I banded females following our playback experiments and banded according to same protocol as males. Our research was performed under federal BBL federal banding permit #23741 and University of Northern CO's IACUC Protocol 1606C

Interactive Playback Protocol

In addition to taking observational data, I assessed female singing behavior using interactive playback experiments. Playbacks in 2018 were conducted between May 15th, 2018 and July 20th, 2018. Playbacks in 2019 were conducted between April 15th, 2019 and June 15th, 2019. I recorded all trials with a Marantz PMD 661 solid-state digital recorder and a Sennheiser MKH 70 long shotgun microphone. I used a SONY SRS-XB20

Bluetooth speaker and smartphone for all playbacks, with sound pressure levels calibrated to 80 decibels at 1 meter using an Extech SL510 sound pressure meter outside of the study area. All playback experiments were conducted between sunrise and 1000 hours, Mountain Standard Time. To begin the protocol, I recorded the ambient environment for ten minutes to calibrate my sound equipment and ensure that environmental conditions were not too severe for sound recording (too windy, too much extraneous noise, etc.). A five-minute control trial of spotted towhee (*Pipilo maculatus*) song played first to ensure that later reactions from females were due to conspecific stimuli and not the speaker itself. This was followed by a five-minute experimental trial simulating territorial intrusion by a female canyon wren.

To create the most accurate acoustic simulation of an intruding female, I conducted an interactive playback consisting of a total of five minutes of active playback, with a 5-second long song clip playing every 30 seconds until a female appeared. When the female sang in response, I waited five seconds, and then responded to her song with one recorded song. This continued for five minutes. While recording avian auditory responses, I also dictated behavioral responses. I noted each female's latency to approach the speaker in seconds, latency to sing from the start of playback in seconds, and closest approach to the speaker in meters, estimated visually. Following the five minutes of interactive playback, I continued to record for ten minutes after playback ended to procure additional song samples from females. I performed 12 playback experiments in Colorado and 24 in Arizona.

I used song files obtained from our laboratory's previous experiments (Hathcock and Benedict 2018) and from xeno-canto used with permission of the recordists

(XC100999, XC 102224, XC 1022600). I used eight five-second long song files from eight different individuals, all from Colorado, and cycled through these during each different playback. All song files were the same song type and length. Due to technical difficulties in accessing all sound files, one of these sound files was repeated for 10 playbacks out of 24 for Arizona.

Song and Behavioral Analyses

I analyzed song files using Raven Pro 1.5 for the following song form data: song duration, amount of time between songs, and number of syllables. I measured the following for all syllables within songs: average entropy, bandwidth at 90%, frequency 5%, frequency 95%, and duration of syllables. Average entropy is defined as the average disorder in the song (Charif et al., 2010). The bandwidth 90% is the range of frequencies that contains 90% of the sound energy of the song. The frequency at 5% and 95% are two divisions of the sound selection in which the top 5% and the bottom 95% of the energy is represented (Charif et al., 2010). Because not all song recordings had equal quality due to wind, other birds singing, or other noise pollution, each song within song files was scored visually with a quality score from 1 to 5; 1 being completely obstructed by other acoustic interference, and 5 being completely unobstructed. Only recordings with scores above and including 3 were used in syllable parameter analyses (syllable duration, entropy, bandwidth 90%, frequency 5%, frequency 95%). Songs that could still be heard and seen on Raven 1.5 were used for syllable count, total number of songs in response to playback, time between songs, and song length data, but excluded from syllable selections measurements.

For syllable form analyses, my Colorado data set was supplemented by previous female song recordings made in Colorado in 2015 and 2016 (Hathcock and Benedict 2018). These data were included in Raven song selections, but not included in behavioral data observations (first approach, closest approach, latency to approach, latency to sing), as those responses were based on my specific playback protocol.

Population Density Estimates

I assessed population density using spot-mapped points and ArcMap Geographic Information Systems Software. Territory points were uploaded to create territory polygons for individuals. I used Minimum Bounding Geometry to create the smallest possible polygons from our point clusters. Then, I created centroid points of these polygons to create an average center of the territory. I measured distances to nearest neighbor by measuring distances from centroid to centroid (Yoon et al., 2012, Sofaer et al., 2014, Hoover et al., 2020). These were used instead of point-to-point distance measurements between polygons because some territories overlapped producing distance measurements of zero, and because our sampling was not comprehensive enough to produce robust estimates of the full territory size and shape due to the inaccessible nature of canyon wren habitat. Additionally, because the territory mapping data I collected is expected to underrepresent the territory area by spot-mapping individuals (Streby et al., 2012, Jablonski et al., 2010), I used eBird abundance maps to confirm our field data using worldwide abundance data of canyon wrens via crowd-sourced data (Fink et al., 2020). These tools report the mean relative abundance of populations in Colorado and Arizona. Mean relative abundance is the average estimated relative abundance within Colorado (269,201 km^2) or Arizona (295,066 km^2) year-round. They also reported the

percentage of seasonal North American population, which is calculated as the total of the estimated relative abundance within Arizona and Colorado divided by the sum of the estimated relative abundance across North America, year-round. These are calculated separately per state (Fink et al., 2020).

Statistics

I used JMP to conduct statistical analyses. Population density and playback responses were compared between Colorado and Arizona using non-parametric Wilcoxon rank-sum tests due to relatively small sample sizes. Nearest neighbor distance for Arizona birds was regressed against song parameters from Raven as well as the total number of songs in response to playback, latency to approach, closest approach, and latency to sing. To account for differential sampling of individuals, I used linear mixed models with individual bird as a random factor to compare syllable features in Colorado versus Arizona. Bonferroni corrections were applied to correct for multiple comparisons.

Results

The mean distance between individuals in Arizona was 926 meters and the mean distance between pairs in Colorado was 11 kilometers. In Colorado, we may have failed to locate intervening pairs as some land was private and unable to be accessed, but surveys conducted in Colorado were as comprehensive as possible. Observationally, at Arizona field sites it was possible to hear multiple males counter-singing at a field site, while it was not possible to hear males counter-singing at any Colorado sites. Density measurements showed that territory centroid points were significantly closer together in Arizona than in Colorado (fig. 5).

Figure 5: Nearest neighbor centroid distances in Colorado vs. Arizona (Wilcoxon rank sum test: Z = 2.86, Prob > Z = 0.042). Canyon wren territories in Arizona are far closer together between individuals than in Colorado.
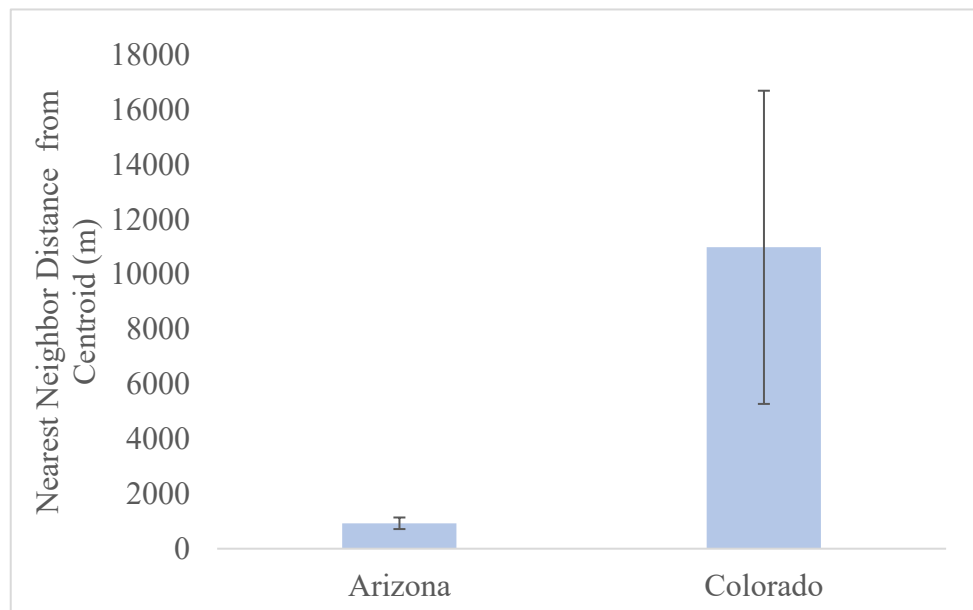
(Z = 2.86, Prob > Z = 0.042). Additionally, eBird abundance maps show that the mean relative abundance of Arizona canyon wrens is 0.35 and that state contains about 12% of the total North American population. Colorado contains about 0.02 mean relative abundance and only 2% of the North American population when considering eBird data from 2014 to 2018 (Fink et al., 2020).

Natural Song Analyses

We conducted a total of 48 hours of focal observation in Arizona and 24 hours of observation in Colorado (2 hours per pair, 24 pairs in Arizona, 12 pairs in Colorado). Females in neither Arizona nor Colorado sang during my two-hour observation windows. Outside of these windows, I observed two females in Colorado to sing spontaneously once immediately before playback experiments began. Another female in Colorado was

observed to sing spontaneously 12 times on the day after the playback experiment protocol. In Arizona, two individuals were observed to sing outside of the observation windows once each after delivering food to nestlings.

Behavioral Responses

In response to playback, female canyon wrens generally showed no difference in behavior between high density and low-density Colorado in terms of behavioral variables (Table 1). No differences were found between states for closest approach, latency to sing, latency to approach, song duration, time between songs, total number of syllables, or total number of songs, using Wilcoxon signed-rank tests (table 1).

Table 1: Wilcoxon rank-sum tests of behavioral parameter means measured between states, and standard error of the means. No significant relationships were found after Bonferroni corrections were applied.

Female Song Behavioral Reponses	Arizona	*SEM*	Colorado	*SEM*	Z	Prob >|Z|
Closest Approach (m)	5.46	1.25	2.83	1.38	-1.68	0.09
Latency to Sing (s)	89.59	15.24	76.44	25.62	-0.96	0.34
Latency to Approach (s)	65.96	12.01	31.59	8.65	-1.97	0.88
Song Duration (s)	3.68	0.10	2.52	0.54	-0.86	0.39
Time Between Songs (s)	5.65	4.86	15.90	3.87	-1.56	0.12
Total Number Syllables	15.47	0.71	11.29	2.54	-0.79	0.43
Total Number of Songs	19.04	2.62	19	4.46	-0.13	0.89

Nearest Neighbor and Behavioral Response Regressions

As a second test of the effects of density on song behavior, I regressed song behavioral responses on nearest neighbor distances between territory polygon centroids in

Arizona (fig. 5). There was a large amount of variation in responses, but this variation did

not correlate with nearest neighbor distance (fig. 6).

Figure 6: Regressions of behavioral parameters in response to female song
playback and nearest neighbor distances within Arizona. Each point represents
the average of an individual.
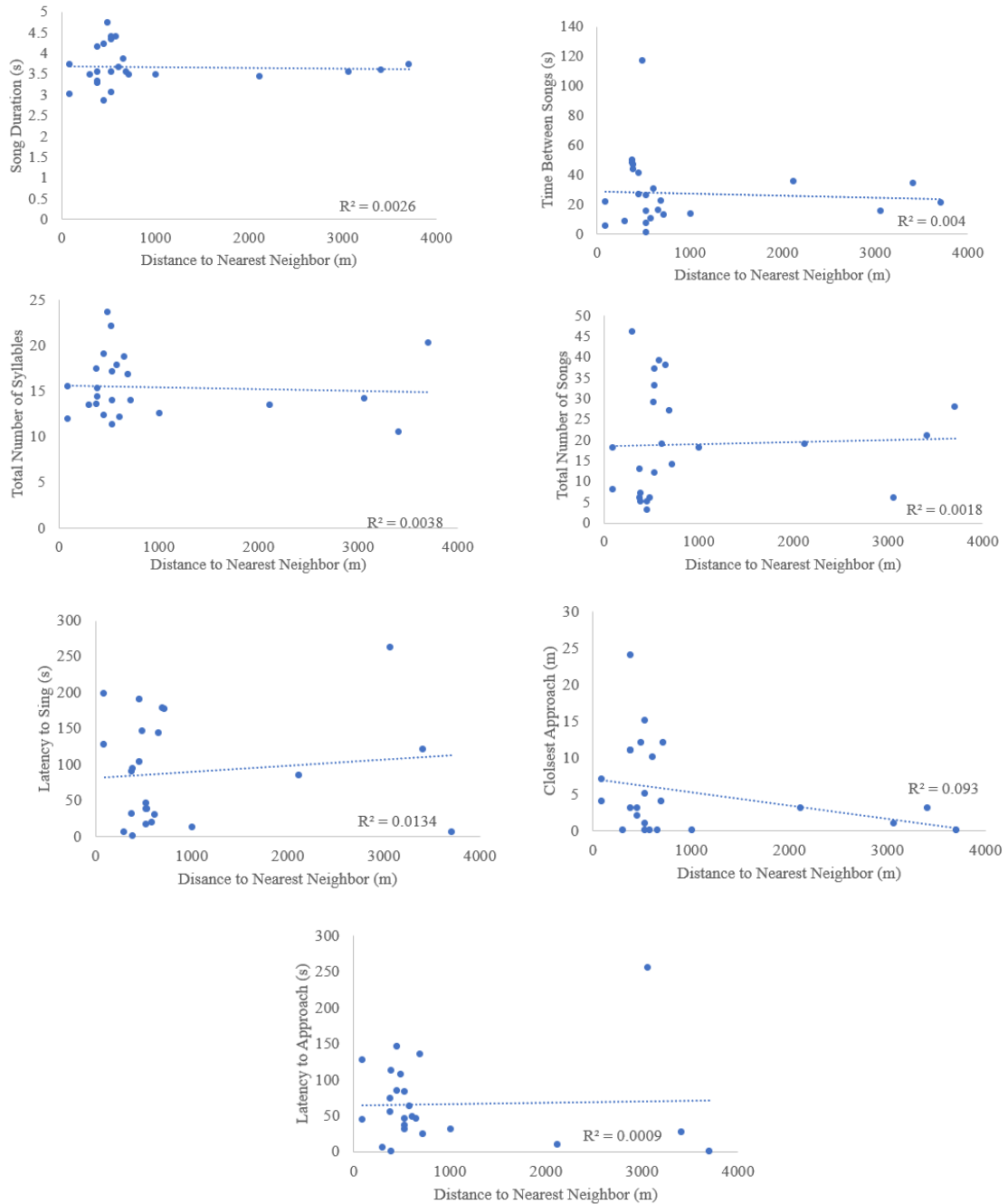
Song Spectral Parameters

I used Linear Mixed Models with individual as a random factor to compare these female song measurements between Colorado and Arizona: syllable duration, bandwidth 90%, syllable duration, frequency 5%, frequency 95%, peak frequency, and entropy. Means between high density Arizona and low-density Colorado did not vary significantly for syllable duration, bandwidth 90%, or entropy (table 2). Frequency 5%, frequency 95%, and peak frequency all varied significantly (table 2). However, Bonferroni correction for multiple tests sets a critical p-value of 0.008, and under that criterion only Frequency 95% remains significantly different.

Table 2: Mean female song spectral characters and standard error of the means analyzed with a Linear Mixed Model, Bonferroni corrections applied. One asterisk indicates significance without Bonferroni correction, two indicates significance after correction.

Female Song Parameters	Arizona	*SEM*	Colorado	*SEM*	Prob < |t|
Syllable Duration (s)	0.21	0.001	0.20	0.008	0.28
Bandwidth 90% (Hz)	1164.82	51.28	1225.98	60.21	0.11
Frequency 5% (Hz)	**2444.87**	72.88	**2680.44**	66.58	**0.0155***
Frequency 95% (Hz)	**3548.53**	84.40	**3906.47**	98.76	**0.0037****
Peak Frequency (Hz)	**3047.23**	64.89	**3246.19**	58.41	**0.0267***
Entropy (bits)	3.24	0.04	3.31	0.041	0.211

Nearest Neighbor Distances

As a second test of the effects of density on song form, I regressed song behavioral responses on nearest neighbor distances between territory polygon centroids in Arizona (fig. 5). No significant relationships were found between nearest neighbor distance and song form (fig. 7).

Figure 7: Regressions of spectral characters and nearest neighbor distances among individuals in Arizona. Each point represents an average of an individual.
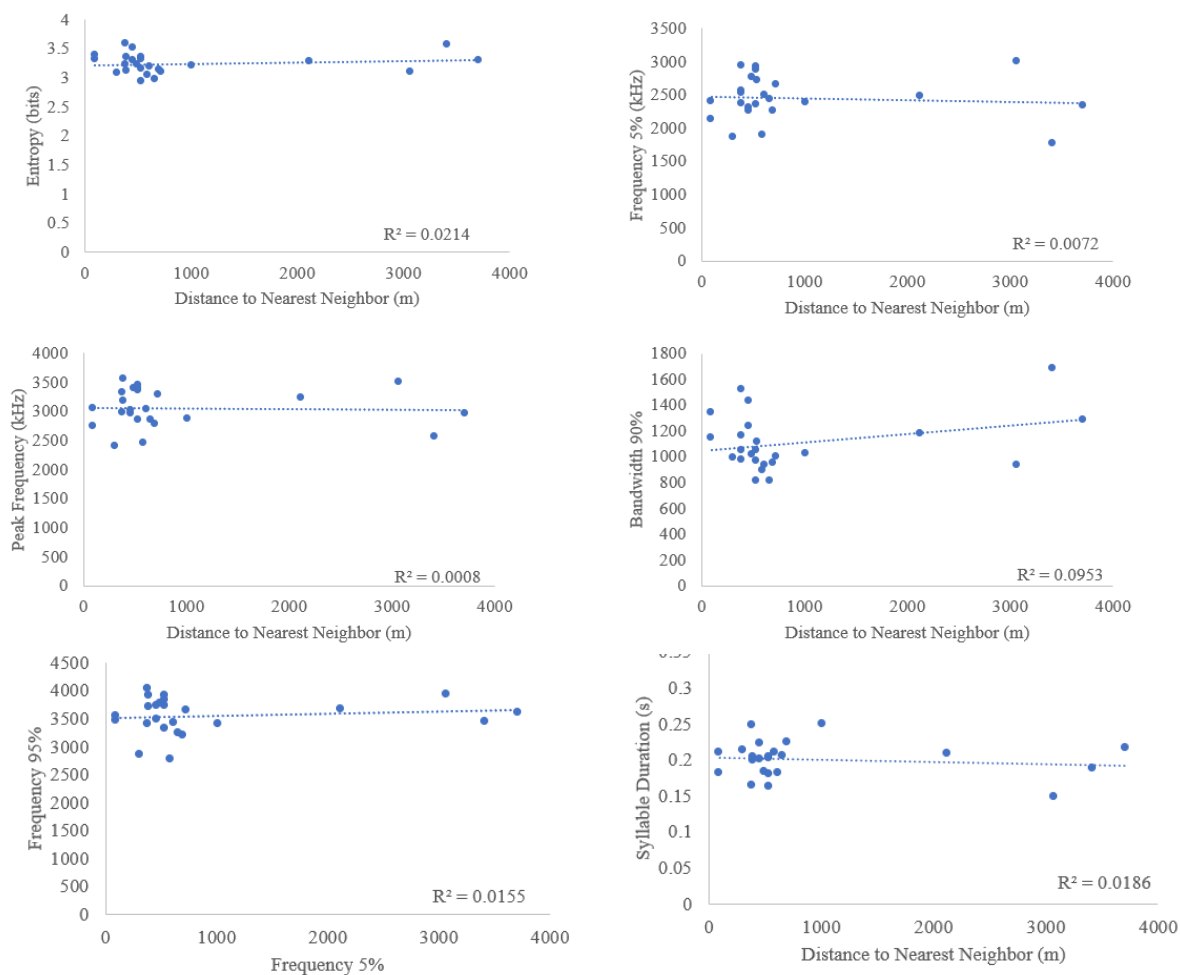
Discussion

**Population Density and Natural
Song Observations**

Arizona was significantly more densely populated than Colorado with canyon

wrens, including pairs of individuals far closer together than those of CO. Centroids of

territory polygons showed that individuals had ten-times shorter distance between

territories in Arizona versus Colorado. This supports what we already know about

individuals in Colorado (Warning et al., 2015). Arizona populations of canyon wrens do

not have literature describing their distribution in the state, however, according to their

distribution map the entire state is within canyon wren range while Colorado is only

partially within their range and approaches range limits. The eastern plains of Colorado

do not support canyon wren habitat, and this may contribute to lower overall densities of

wrens in that state (Jones and Dieni, 1995). This is further supported by eBird's canyon

wren data set, in which Arizona contains a larger number of canyon wrens as well as

higher mean relative abundance at 0.35 birds observed per km/hr, versus 0.02 in

Colorado (Fink et al., 2020).

Females in both Arizona and Colorado over a collective 72 observation hours did

not sing at all. They were occasionally heard to sing spontaneously at other times outside

of dedicated observation periods, but still not frequently. Overall, my data show that

female canyon wrens during the breeding season do not sing spontaneously very often.

This is true in areas with both high and low population density. Females during the

breeding season already have established territories and have begun nesting, laying eggs,

incubating eggs, and raising young which require significant energy investments

(Mainwaring and Hartley, 2013, Monaghan and Nager, 1997, Haftorn and Reinertsen,

1985). Perhaps the selection pressure to invest in these other breeding activities outweighs any advantage of investing in spontaneous song (Gil and Gahr, 2002).

The timing of my experiments might have driven the low number of spontaneous songs that I detected. There are some anecdotal observations that female and male canyon wrens sing in response to one another before the breeding season begins (pre-March) (Jones and Dieni, 1995) as a courtship display. Female birds of other species, such as African black coucals. use song to assess and dispel rival females before breeding begins, (Geberzhan et al., 2010). Perhaps canyon wren female song has no function within the breeding season but has function in the pre-breeding season. Females may need to identify their sex to potential males and may sing before breeding begins to achieve breeding synchrony and defend a territory, like tropical females (Slater and Mann, 2004). In this way, females could distinguish themselves from males vocally in this sexually monomorphic species, as well as advertise breeding readiness to males.

At the other end of the breeding season, females may sing through winter to dispel conspecifics from their territory in order to protect resources when they are scarce. It is hypothesized that year-round territoriality is one of the evolutionary drivers of female song (Benedict 2008; Logue and Hall, 2014, Tobias et al., 2016), but there are no studies observing canyon wrens during the non-breeding winter months: September through February. There is evidence to support that female song occurs often in non-migratory species due to the increased selection pressure for year-round territory maintenance (Benedict, 2008). There is also evidence that males do not sing in the winter, but ramp up singing in March, just prior to the breeding season, in Colorado (Rose, 2013). Therefore, perhaps males and females take turns singing during the non-

breeding and breeding seasons. This could be investigated by looking into sound archive recordings by time of year.

Behavioral and Spectral Song Parameters
and Nearest Neighbor Distances

I did not find any significant correlations between nearest neighbor distances and behavioral or spectral song parameters. Neighbors nearest to one another may be more familiar with each other, as described in the "dear enemy" hypothesis, in which animals respond less aggressively to neighbors than strangers (Temeles 1994). This has been observed in other territorial females such as New Zealand Bellbirds (*Anthornis melanura*) (Brunton et al., 2008). However, this relationship is not supported in wren species, including winter wrens and rufous-and-white wrens (Courvoisier et al., 2014; Battiston et al., 2015). A dear enemy effect would predict low rates of song in response to known neighbors and might explain the lack of spontaneous song in Arizona but does not explain reduced rates of song to simulated strangers. More research on neighbor verses stranger songs should be conducted to elucidate this relationship.

Song Parameters by State

We found that peak frequency, frequency 5%, and frequency 95% were significantly lower in our high-density study area than our low-density study area. This result might be a non-functional regional difference, or it could relate to signal function in contest situations. Low-frequency songs might indicate higher aggression in Arizona and fall in line with what we know about aggression in canyon wren males, as well as other females with song. Male canyon wrens significantly lowered the lowest frequencies in their songs after being challenged with playback (Benedict et al., 2012). Female African black coucals (*Centropus grillii*) lowered the frequency of their vocalizations

when challenged with playback when compared with unprompted song; larger females also responded with lower frequencies to playback (Geberzahn et al., 2009). This hints that female song may be an index signal for body size or motivation to fight. I was not able to band every female in this study due to inaccessibility of habitat; however it would be interesting to take stock of this variable in future studies and test whether larger birds sing lower frequency songs. If females are advertising breeding quality to males as well as fighting ability to conspecific females, it may be advantageous to have a vocal index signal matching your body size, as seen in studies on purple-crowned fairywrens (Hall et al., 2013). A similar phenomenon has been observed in female house wrens, who use a low-amplitude, high-frequency call immediately before a physical attack with another female (Krieg and Burnett, 2017). Further playback studies manipulating, or exaggerating song parameters must be performed to unearth more of the information embedded within female song.

There is literature to suggest that singing ability changes over a bird's lifetime, such as in male swamp sparrows (*Melospiza georgiana*) in which larger, older males sang more physically challenging songs (Ballentine, 2009). Female blue tits also prefer older males and use song characters and time of day to gauge male age (Poesel et al., 200). Therefore, females who sang with lower frequencies could also be older, more experienced females. It is possible that lifespans differ between Arizona (at the heart of the Canyon wren's range) and Colorado (at the edge of its range) and that this difference is reflected in song.

Finally, changes in the acoustic frequencies of female canyon wren song may differ between populations due to genetic or cultural drift (Lynch, 1996). Differences

between populations may arise due to normal mutations and cultural changes in song patterns arising from generation to generation via social learning, and this should be considered as a possibility (Lynch, 1996).

General Conclusions

Results of this study indicate that population density is not a strong driver of female song behavior, Overall, spontaneous female song may not be necessary in the breeding season, either due to a shift in energy investment towards breeding responsibilities or if females are already familiar with neighboring females and do not need to gauge their threat. Females singing in more densely populated Arizona may be displaying their breeding experience, fighting ability, body size, or age by singing songs with lower peak frequencies, but further follow-up would be needed to rule out other factors. Differences between populations may also be explained by genetic drift.

Bird song has been a model system to investigate many subjects within biology, but by disregarding female song we have lost many opportunities to further our knowledge of the origins and dynamics of complex behaviors, neurobiology, language, sexual selection, natural selection, and more (Odom and Benedict 2018, Price, 2015). By continuing to study the complexities of one unique system, canyon wrens, we can further our knowledge in bird song, behavioral ecology, and evolutionary biology.

CHAPTER III

BEHAVIORAL OBSERVATIONS, NATURAL HISTORY
REMARKS, AND FUTURE DIRECTIONS

Although I focused on female vocalizations for this project, I felt it was warranted

to make a note of other natural history observations I encountered in my studies of

canyon wrens. This includes behavioral responses from males. Furthermore, I will use

this space to suggest ideas for future projects based on the results of this Thesis. As there

has been with male song, there is a tremendous amount to explore in this unique species

with female song.

Behavioral Observations and Natural History Remarks

**Male Behavioral Reactions and
Vocalizations During Female
Song Playback Experiments**

While conducting field work, I normally found breeding pairs by listening for

male song, as males sing more often than females during the breeding season. After

discovery, I would observe these individuals for about two hours and if I did not observe

any females in the area, I would conduct a playback experiment, in hopes of eliciting a

response from a female who may have been incubating or foraging in another part of the

territory. I found that males made one of two responses when hearing a female song.

First, males responded aggressively. In this situation they sometimes gave a rapid

succession of calls often in a tight pattern initially (immediately after hearing

female song) and then quickly reducing the number of calls to evenly spaced ones

(fig 8).

Figure 8: Rapid succession calls, followed by more evenly spaced calls, done by males after hearing female song playback. Both sound files were taken in Arizona at the Chiricahua National Monument. The top is from Bonita Creek picnic area, and the bottom is from Natural Bridge pair 1. Y-axis is frequency in kilohertz, and x-axis is time in minutes: seconds.
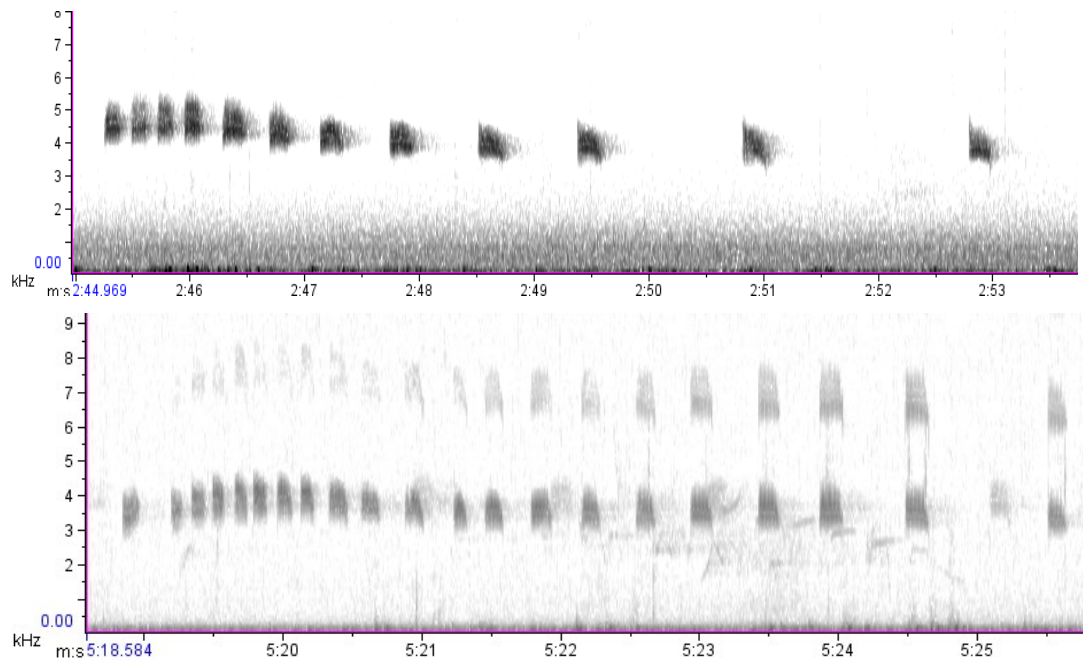
Additionally, some males would, after singing these rapid succession calls, also sing

another rapid succession of higher frequency calls between the typical rapid calls (fig. 9).

If the male responded in this manner, a female always revealed herself. I speculate that

this male vocalization may be a female-directed alarm call that alerts the paired female to

a female intruder in their territory. If males and females have a successful pair bond,

Figure 9: In response to female song playback, some males responded with rapid succession calls with higher frequency calls between. This sound file is from Arizona at the Chiricahua National Monument (Mushroom Rock Trail 1).
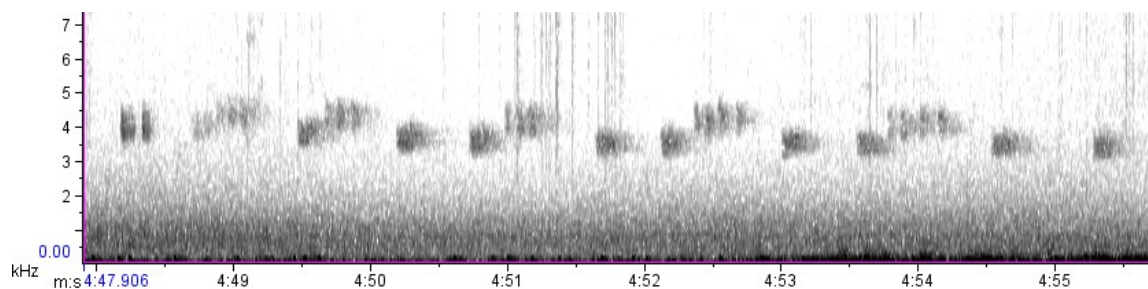
males may be attempting to call a female in to alert her to the territorial rival. It may be a display of certain mate-guarding behavior. Male magpie larks (*Grallina cyanoleuca*) will stay closer to female magpie larks if they are more fertile, as a form of mate-guarding, but do not duet together during her fertile period (Hall and Magrath, 2000). Perhaps female song works in a similar way; males and females do not duet together to defend territory; however, they display other behaviors that indicate they are paired/fertile/etc. Therefore, males may alarm-call to females to indicate that they are paired and values their mates; this supports the suspicion that canyon wrens are highly monogamous, like many other species with female song (Benedict, 2008).

During playback experiments of female song, males also responded aggressively with a vocalization I called a "chatter call" (fig. 10). The significance of this call is

Figure 10: Chatter call performed by males in response to seeing and hearing another pair of canyon wrens. This was recorded in Arizona at the Chiricahua National Monument along the Natural Bridge trail.
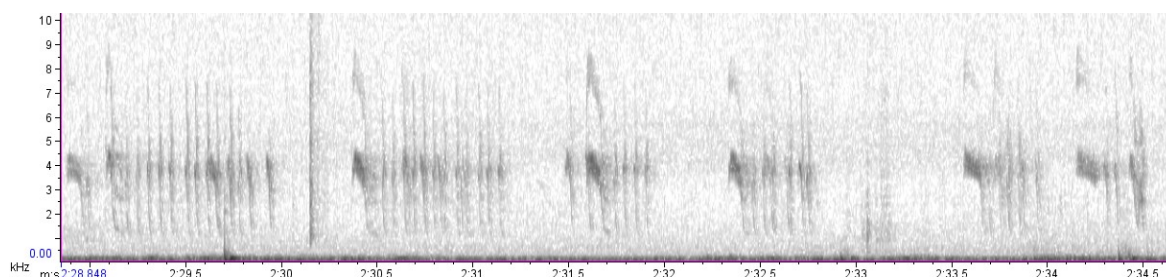
unknown, however, males only produced this in reaction to a female song. I only observed this call one time. It was in an area in which there were multiple breeding pairs within earshot, along the Natural Bridge Trail in the Chiricahua National Monument. I postulate that this call may be an extreme reaction to being within hearing distance of a male and female canyon wren. Normally, females would sing in reaction to the playback, while males stayed close (< 2 m) while occasionally leaving the immediate area to apparently search for an intruder and occasionally sing male song. This was the first time I observed a second pair of canyon wrens approach a pair I observed. Because this vocalization has not been observed in more commonly studied male-male interactions, is possible that males are using this call to identify that there is a pair instead of a single female in the area.

Secondly, males would occasionally sing male song in response to hearing female song. They would not do a rapid call sequence or the "chatter" call type or act aggressively. Instead, they would sing male song around their territory, disinterested in the speaker itself. Most males that sang stayed within 15 meters of the speaker. In these instances, a female never made an appearance in my observations (about 6 times). Therefore, I speculate that most of these males were unpaired males that did not have females in the area. Upon hearing female song, they attempted to court the simulated females, as opposed to being threated that they entered their territories. After further observation, I concluded that these males normally remained unpaired throughout the breeding season. Changing vocalizations based on paired or unpaired status has been observed in other wren

species, such as the tropical rufous and white wrens, in which males sing more songs with less diversity than paired males (Hennin et al., 2009).

The observed male reactions hint that female song may act as a sex-specific signal that results in a cascade of other sex-specific signals in males, or signals directed at other males. Sex-specific signaling is not unheard of, but is relatively uncommon in birds, albeit more common in waterfowl, parrots, rails, raptors, doves, auks and shearwaters (Volodin et al., 2015). Female and male canyon wrens are most likely responding directly to their own sexes with song, as hypothesized in previous studies (Hathcock and Benedict, 2018). Furthermore, as a male, call versus song vocalizations could be a way to display paired or unpaired status to females. If males hear a female in their territory as a paired male, they will work to preserve their territory and bond with established mates. Females can advertise their presence in their territory, advertise other characters (fighting ability via body size, age, status, etc.) via their song, and threaten other females from usurping resources in their territories. Male rapid succession/chatter calls, cooccurring with female song, could allow male and female canyon wrens to strengthen and maintain their pair bonds and territory boundaries throughout the year. Both males and female may be interested in female songs because females represent a threat to their territories. *Troglodytidae* as a family are known to be small but mighty aggressors to conspecifics and heterospecifics (Kattan, 2016, Picman and Belles-Isles, 1987). Other wren species, like house wrens and marsh wrens, have been known to commit conspecific ovicide (Krieg and Getty, 2020, Picman and Belles-Isles, 1987). Males are known to commit filial ovicide among conspecifics as well (Pribil and Pieman, 1992). Female song in house wrens has been linked to decreased conspecific ovicide (Krieg and Getty 2016).

Perhaps there is an incentive for both males and females (most likely a pair, not separately) to defend in their territories against invading females.

Future Directions

What Information Are Females Displaying with Song?

Females may be displaying information in their songs by lowering the peak frequencies. Is this potentially related to age? Age can be an indicator of breeding ability as in blue tits (*Cyanistes caeruleus*), in which females prefer older males (Poesel et al., 2006). In addition to displaying breeding ability, song can change over time and therefore could be an indicator of age generally as singing remains plastic through adulthood in some species (Nottebohm and Nottebohm, 1978, Kipper and Kiefer, 2010). Certain song characteristics can prove to be more challenging to perform than others and performing these can display an individuals' age (Ballentine, 2009). Perhaps lower frequencies display these things as well in canyon wrens. There has also been significant evidence to support that body size can lower frequencies in vocalizations across taxa (Ryan and Brenowitz, 1985), although this is not always the case and could therefore be a deceptive signal (Brumm, 2009, Patel et al., 2010). Body size's effect on individual's song frequencies could be further investigated across the latitudinal gradient of canyon wrens, as body size is generally larger at higher latitudes, and smaller at lower latitudes (Olson et al., 2009). This could be investigated across the range of canyon wrens, which are distributed from Mexico to Canada. Perhaps females closer to the tropics are larger than females further north, which does

subvert our current understanding of how body size relates to avian distribution (Olson et al., 2009), but may make sense for canyon wrens given their distribution

Female Song Propagation

The female song of canyon wrens contrasts with male song in sound quality and features. Male song is made up of clear toned whistled syllables, sometimes ending in longer, more broadband "harsher" end notes. Females' songs are entirely made of buzzier, harsher, more broadband syllables. The acoustic adaptation hypothesis suggests that songs with lower frequencies, narrower frequency ranges, and longer inter-element intervals should occur more frequently in densely vegetated compared with herbaceous habitats (Morton, 1975). There is some evidence to suggest that male songs are louder, about 100 decibels at 1 meter (Braelei Hardt, unpublished data), but we do not know how loudly females sing; it is unlikely that they sing as loudly as males due to these wider broadband, buzzier syllables in their songs, which are often lower in amplitude than whistled syllables. Therefore, we may speculate further on the function of this song based on the sound quality. Are males' clear toned songs signaling for longer distances to other males? Are females' buzzier, wide broadband songs, only singing at short distances when encountering other females on their territory who are a threat to resources and pair bonds? Or are males and females only singing within close range to one another during breeding season? Either way, male song may be displaying long-range information, and females may be displaying short-range information to conspecific females.

Female Song Spectral Characters

We know that male canyon wrens alter their songs in response to playback from rival males (Benedict et al., 2012). In response to male song, males lowered their lowest

song frequencies and added more wide broadband syllables to the ends of songs. Similar experiments could be conducted for females. Does adding more syllables to songs, or lowering peak frequencies, or adding more wide broadband notes to the ends of songs cause females to change their songs? This could be easily investigated following a similar protocol to Benedict et al., (2012); using Raven Pro 1.5 one could add additional harsh end notes or create longer songs with lower frequencies and observe if females change their songs to match these song types. This would indicate that certain song features would be associated with aggressive individuals.

Female Song: Time of Year
and Breeding Status

It is well known that males' song rates and/or characters change seasonally, in part due to hormonal changes (MacDonald and Islam, 2019, Chiver et al., 2014). There is also evidence to suggest that female singers can undergo similar seasonal changes as well, such in northern cardinals (*Cardinalis cardinalis*); females sang at higher rates at the beginning of the breeding season, and also sang more in newly established pairs versus pairs who had previously mated (Vondrasek, 2006). Female European starlings (*Sturnus vulgaris*) vary their singing amounts seasonally; females sing the most during December through mid-April (Pavlova et al., 2007). Females who occupied a nest box also sang more often than females with no nest box (Pavlova et al., 2007). There is little known about how female canyon wrens are singing outside of the breeding season. Perhaps although they are not singing within the breeding season, they have higher singing rates pre-breeding, as suggested by Jones and Dieni (1995), and

seen in prothonotary warblers (*Protonotaria citrea*) (Matthews et al., 2017). We also do not know if the breeding status of females affects song rates or characters, as I was not able to find all nests for birds over the course of the breeding season. Would females react differently to playback in different breeding stages (nest building/incubation/etc.) as in field sparrows (*Spizella pusilla*) (Zhang et al., 2016)? Would they sing more if unpaired? Many of these questions remain unanswered.

Male Preference for Female Song
Characters, Female Lifetime
Fitness and Extra-Pair
Paternity

Bird song has been historically regarded as one of the best examples of sexual selection (Catchpole 1987, Kroodsma and Byers, 1991, Macdougall-Shackleton, 1997). Temperate females have been found to prefer many characters of male songs (Drăgănoiu et al., 2002, Ballentine et al., 2004) which can display important pieces of information such as age, size, habitat quality, and breeding quality (Ballentine, 2009, Grava et al., 2012, Schmidt et al., 2013). However, very few of these variables have been investigated from the female perspective. Given that female canyon wrens are most likely using female song to dispel other females from their territory, it is likely that males are eavesdropping on these songs and gleaning pieces of information from females, as female black-capped chickadees to do males (*Poecile atricapilla*) (Mennill et al., 2002). Some female New Zealand bellbirds' (*Anthronis melanura*) reproductive success can be predicted by their rate of song and song structure; females with more syllable types and greater number of transitions between different syllable types had higher breeding success over three years (Brunton et al., 2016). Are male canyon wrens preferring females with certain song characters? Do females who have certain song features (lower

frequency, more syllables, etc.) have a higher lifetime fitness or seek more extra-pair copulations? There is also evidence to suggest that attractive song features can contribute to higher fitness rates in males in both within pair and extra-pair copulations (Forstmeier et al., 2002, Birkhead and Fletcher, 1995, Sheldon, 1994). Bird song biology is rich in literature on how female birds respond to male song, but there is much to learn about how males respond to female vocalizations.

Song Learning in Canyon Wren Females

Canyon wren males and females sing two different songs with different structures, and males and females have never been observed singing each other's songs. If female song is very rare outside of playback experiments, how are young female canyon wrens learning to sing? There are numerous studies investigating the role of song learning in males, but we know very little about the mechanisms for song learning in females (Riebel, 2003). There are only a few studies that investigate how female birds learn their songs. There can be dramatic differences between the way male and female birds learn songs; female cardinals (*Cardinalis cardinalis*) learn the same number of songs as males, but in less than one third of the time (Yamaguchi, 2001). White-crowned sparrow (*Zonotrichia leucophrys*) sons and daughters rarely learn songs from their fathers, instead learning them from neighbors (Baptista and Morton, 1988). Additionally, male and female rufous-and-white wrens (Thryophilus rufalbus) learn their songs after post-natal dispersal from their new breeding populations (Graham et al., 2018). Are female canyon wrens learning songs primarily from mothers or from neighbors? If from neighbors, is their song learning affected by population density? Or, is female

song innate? These questions can be answered via rearing experiments, or by collecting song data in the field from mothers and daughters over the course of several years. This may be difficult since males and females immediately display adult plumage after hatch-year plumage. However, this would be possible to investigate this with a color-banded population over the course of several years and/or genetic testing. There are significant medical applications of avian research for human language learning. If there are differences between males and females in terms of song learning, this may have applications for the audiology and biomedical fields, as well as evolutionary biology and ecology (Fujii et al., 2016, Jarvis, 2004).

Conclusions

We have an immense bias in our ornithological literature due to the focus on temperate deciduous birds by temperate deciduous biologists. Bird song is generally considered well-studied, but there is still a tremendous amount to be learned from female bird song generally, as well as in the specific system of canyon wrens. In recent years, there are many reported observations of female birds singing through eBird and xeno-canto.org as well as through primary literature (MacDonald et al., 2019, Matthews et al., 2017, Najar and Benedict, 2015, Taff et al., 2012). There are also many studies that note female song in certain species that have not been investigated in recent literature (Staicer, 1989, Gilbert and Carroll, 1999, Hobson and Sealy 1990). Canyon wrens are a unique system in which males and females sing differently structured songs, most likely used for different purposes. By continuing to study this system, we may be able to find out why some females sing in North America while others do not, why two sexes may have different songs, why some species duet when others do not, and how males and females

differ in their song and behavioral learning. Studying female song allows us to further

investigate evolutionary biology, behavioral ecology, conservation biology,

neurobiology, and more, if we only listen for it (Odom and Benedict, 2018).

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APPENDIX A

AVERAGES PER INDIVIDUAL OF SONG SPECTRAL CHARACTERS

Appendix A: Averages per individual for each spectral parameter measured in Raven Pro 1.5.
Data was collected in Arizona (AZ) and Colorado (CO).

Bird ID	State	Syllable Duration	BW 90%	Freq 5%	Freq 95%	Peak Freq	Entropy
Adele/Echo Canyon 2	AZ	0.21	999.67	2659.49	3659.17	3283.68	3.10
Amy Winehouse/Lower Rhyolite Trail	AZ	0.21	1176.54	2486.43	3662.97	3222.61	3.29
Aretha Franklin/Idlewilde	AZ	0.20	891.03	1890.95	2781.98	2452.90	3.05
Ariana Grande	AZ	0.18	977.80	2945.68	3923.49	3551.99	3.12
Beyonce	AZ	0.22	810.33	2915.87	3726.20	3355.27	2.94
Bjork	AZ	0.15	1284.62	2330.47	3615.10	2955.37	3.30
Bonita Creek	AZ	0.20	936.40	2997.79	3934.19	3508.45	3.10
Cher	AZ	0.22	968.83	2355.04	3323.86	2856.96	3.16
Ed Riggs	AZ	0.18	951.64	2260.18	3211.82	2773.21	3.14
Ella Fitzgerald	AZ	0.25	931.51	2491.86	3423.37	3039.81	3.19
Florence and the Machine	AZ	0.25	1025.09	2381.16	3406.25	2866.20	3.21
Lizzo/Echo Canyon 1	AZ	0.22	1521.55	2524.85	4046.39	3320.84	3.60
Mushroom Rock 1	AZ	0.20	1431.91	2306.25	3738.17	3006.91	3.52
Mushroom Rock 2	AZ	0.21	1231.43	2252.53	3483.95	2964.52	3.29
Natural Bridge 1	AZ	0.18	811.93	2424.62	3236.55	2853.53	2.97
Natural Bridge 2	AZ	0.16	1012.84	2765.07	3777.90	3389.51	3.23
Natural Bridge 3	AZ	0.21	1110.42	2717.19	3827.60	3391.15	3.36
Natural Bridge 4	AZ	0.18	1145.84	2406.99	3552.83	3049.10	3.31
Natural Bridge 5	AZ	0.21	1344.26	2128.36	3472.62	2734.57	3.38
Natural Bridge 6	AZ	0.20	988.64	1868.91	2857.55	2390.78	3.08
Natural Bridge 7	AZ	0.17	1046.32	2874.51	3920.83	3452.07	3.31
Organ Pipe	AZ	0.20	1048.61	2363.43	3412.05	2983.80	3.22
Silver Peak Faraway	AZ	0.19	1160.15	2557.29	3717.45	3167.97	3.36
Stevie Nicks	AZ	0.30	1680.42	1771.96	3452.39	2562.20	3.57
Arthur's Rock	CO	0.31	1716.28	3125.00	4841.29	3637.34	3.49
Arthur's Rock Summit	CO	0.21	1430.92	2439.85	3871.94	2992.24	3.48
Bobcat Ridge	CO	0.17	1618.87	2840.28	4459.15	3429.13	3.68
Coyote Ridge	CO	0.21	1038.40	2884.40	3922.79	3361.52	3.22

Gateway	CO	0.12	858.71	2817.08	3675.80	3339.88	2.98
Horsetooth Reservoir	CO	0.17	1724.34	3009.87	4734.21	3589.47	3.30
Rabbit Mountain	CO	0.16	1210.35	2407.55	3617.90	2948.11	3.42
Red Rocks	CO	0.24	1695.81	3059.81	4755.62	3669.07	3.66
TH003	CO	0.21	1648.96	2651.04	4300.00	3290.63	3.61
TH004	CO	0.23	1534.97	2701.08	4236.04	3183.66	3.43
TH005	CO	0.18	1317.19	2558.20	3875.39	3150.59	3.50
TH007	CO	0.19	1178.65	2331.69	3510.34	2967.27	3.26
TH009	CO	0.21	1069.59	2946.67	4016.26	3404.97	3.22
TH010	CO	0.21	1005.70	2490.47	3496.16	3061.09	3.14
TH011	CO	0.19	1175.75	2976.60	4152.35	3570.69	3.38
TH014	CO	0.23	1156.25	2464.75	3620.99	3180.30	3.30
TH016	CO	0.17	1190.05	2071.43	3261.48	2820.15	3.21
TH018	CO	0.17	1155.26	2533.56	3688.81	3161.19	3.26
TH019	CO	0.23	1105.12	2164.77	3269.89	2806.83	3.07
TH022	CO	0.20	755.57	2799.97	3555.54	3189.35	2.97
TH023	CO	0.16	1067.55	3151.06	4218.61	3589.54	3.34
TH025	CO	0.17	997.83	2126.38	3124.22	2734.13	3.21
TH027	CO	0.17	950.44	3125.54	4075.97	3680.49	3.16
TH028	CO	0.17	820.86	2653.63	3474.47	3151.00	3.11

APPENDIX B

AVERAGES PER INDIVIDUAL OF BEHAVIORAL PARAMETERS AND

DISTANCES TO NEAREST NEIGHBORS

Appendix B: Individual averages for all behavioral parameters measured and distances to nearest neighbors by Arizona (AZ) and Colorado (CO). Song duration (SD), time between songs (Time BW Songs), closest approach (CA), latency to approach (LtA), latency to sing (LtS), and nearest neighbor distances (NND) are shown as averages. Total number of songs (total # of songs) is shown as a whole number as it is the total number of songs sung by females and was counted.

Bird ID	State	SD (s)	Time BW Songs (s)	Avg Total Syllables (s)	CA (m)	LtS (s)	LtA (s)	Total # of Songs	NND (m)
Adele/Echo Canyon 2	AZ	3.47	12.76	13.93	12.00	176.07	23.27	14	724.68
Amy Winehouse/ Lower Rhyolite Trail	AZ	3.44	35.44	13.47	3.00	83.73	9.20	19	2122.41
Aretha Franklin/ Idlewilde	AZ	4.40	10.41	17.79	0.00	18.80	62.01	39	589.42
Ariana Grande	AZ	3.32	43.47	15.29	3.00	0.00	0.00	7	392.86
Beyonce	AZ	4.40	15.23	17.15	5.00	38.20	82.85	33	537.53
Bjork	AZ	3.73	21.17	20.21	0.00	4.89	0.00	28	3712.41
Bonita Creek	AZ	3.54	15.11	14.17	1.00	261.93	255.63	6	3071.31
Cher	AZ	3.05	7.46	11.30	0.00	16.60	35.70	37	537.53
Ed Riggs	AZ	3.54	22.25	16.85	4.00	177.27	135.20	27	700.13
Ella Fitzgerald	AZ	3.66	30.21	12.17	10.00	29.40	48.03	19	618.36
Florence and the Machine	AZ	3.49	13.38	12.50	0.00	12.40	31.10	18	1012.00
Lizzo/Echo Canyon 1	AZ	4.14	47.90	17.46	11.00	89.74	73.34	13	386.16
Mushroom Rock 1	AZ	4.21	26.40	19.00	3.00	189.80	146.20	5	459.97
Mushroom Rock 2	AZ	2.85	41.19	12.33	2.00	102.97	83.50	3	459.97
Natural Bridge 1	AZ	3.87	16.16	18.76	0.00	143.14	45.44	38	661.56
Natural Bridge 2	AZ	4.73	117.03	23.67	12.00	145.83	106.33	6	493.03
Natural Bridge 3	AZ	3.54	25.68	13.92	15.00	38.08	30.88	12	538.88

Name	State								
Natural Bridge 4	AZ	3.72	21.86	15.50	4.00	127.40	127.40	8	95.42
Natural Bridge 5	AZ	3.01	5.52	11.94	7.00	197.46	43.76	18	95.42
Natural Bridge 6	AZ	3.48	8.51	13.39	0.00	5.20	5.01	46	306.12
Natural Bridge 7	AZ	4.32	1.08	22.07	1.00	45.13	45.13	29	533.92
Organ Pipe	AZ	3.28	49.57	13.50	11.00	31.10	54.40	6	386.16
Silver Peak Faraway Bird	AZ	3.54	46.82	14.40	24.00	94.20	111.90	5	392.86
Stevie Nicks	AZ	3.59	34.09	10.52	3.00	120.88	26.68	21	3415.71
Arthur's Rock Entrance	CO	3.71	23.93	12.00	0.00	30.50	30.50	26	386.55
Arthur's Rock Summit	CO	3.97	26.18	16.58	5.00	238.82	38.42	24	386.55
Bobcat Ridge	CO	3.78	17.44	17.77	7.00	36.43	36.43	32	5647.36
Coyote Ridge	CO	3.68	20.62	15.88	7.00	77.00	77.00	35	3119.98
Gateway Natural Area	CO	3.37	41.03	18.24	15.00	81.76	81.76	19	14506.90
Horsetooth Reservoir	CO	4.36	25.66	20.83	0.00	231.97	27.77	18	3003.69
Rabbit Mountain	CO	3.88	13.90	21.72	0.00	168.28	65.28	41	20221.78
Red Rocks	CO	3.52	22.03	13.24	0.00	52.56	21.96	33	64802.68

UNIVERSITY OF NORTHERN COLORADO

IACUC Memorandum

To:	Dr. Lauryn Benedict
From:	Laura Martin, Director of Compliance and Operations
CC:	IACUC Files
Date:	5/3/18
Re:	IACUC Protocol 1606C-LB-Birds-18 Annual Renewal and Amendment Approval

The UNC IACUC has reviewed your annual renewal and amendment request for animal use protocol 1606C-LB-Birds-19.

The committee's review was based on the requirements of the Government Principles, the Public Health Policy, the USDA Animal Welfare Act and Regulations, and the Guide for the Care and Use of Laboratory Animals, as well as university policies and procedures related to the care and use of live vertebrate animals at the University of Northern Colorado.

Based on the review, the IACUC has determined that all review criteria have been adequately addressed. The PI/PD is approved to perform the experiments or procedures as described in the identified protocol for an additional year.