

Female bird song rates do not covary with population density in a North American species

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Abstract

Bird song can vary across space and time or within different social environments. These variations in bird song have historically been considered from the perspective of males, particularly in North American temperate regions. In this study, we explored possible changes in singing behavior by females of a North American species, the canyon wren (*Catherpes mexicanus*). Male and female canyon wrens sing sex-specific songs to defend resources. Females rarely sing spontaneously but sing readily when challenged with playback. We sought to determine whether the rarity of spontaneous female song seen in previous studies stems from low population density. In areas with higher population density, female canyon wrens should encounter neighbors and competitors for resources more often, potentially driving up song rates. We examined female song rates both within a single population and compared between two populations, hypothesizing that females with closer neighbors would (1) sing more often without playback and (2) sing with more aggressive features in their songs and behave more aggressively in response to playback. We estimated population density on the ground using nearest-neighbor distances and verified these with eBird abundance models. We did not find that population density predicted rates of spontaneous song. Most song characters and playback response behaviors also did not vary with local canyon wren abundance. Females from our denser population sang with significantly lower pitch, but we attribute these differences mostly to geographic variation. Although population density is known to drive patterns and rates of male song behavior, it may be less important in determining female song behavior.

KEYWORDS

avian population density, *Catherpes mexicanus*, female bird song, nearest-neighbor distances, playback

1 | INTRODUCTION

Bird song has been best studied in north temperate-zone male songbirds (Odom & Benedict, 2018; Riebel et al., 2005). Singing female birds are globally distributed and possess a dynamic array of vocal capabilities, but these traits are particularly common in Australasian

and tropical lineages and are often reduced in north temperate zones (Riebel et al., 2019). In temperate regions of the world, female birds sing less than males, despite female song being an ancestral and widespread trait among songbirds (Odom et al., 2014). Observed patterns suggest that ecology and life history can drive female song use (Price et al., 2009; Slater & Mann, 2004); evolutionary losses of

female song are associated with the gains of migration and possibly with a general divergence in sex roles in temperate areas (Logue & Hall, 2014; Mitchell et al., 2019; Slater & Mann, 2004). Thus, environmental and life-history factors influence female song production at the species level. However, open questions remain about how local population level factors might drive rates of female song, particularly in species and regions where female song is relatively rare.

Social settings and interactions are known to impact avian song behavior (Kelly et al., 2018; Rose et al., 2020), and one factor that deserves more study is population density. As song is often used in resource defense, the presence of many close neighbors could drive up the rate of interactions and resultant singing rates if resources are not in abundance. Population density has been shown to shape male song form (Narango & Rodewald, 2016), song elaboration (Byers, 2015), signal honesty (Penteriani, 2003), and variation (Irwin, 2000) in songbirds. For example, male orange-crowned warblers (*Oreothypis celata*) in more densely populated California were more aggressive than those from less densely populated Alaska (Yoon et al., 2012). Whether population density similarly affects rates of female song is unknown. There is anecdotal evidence from a single densely packed breeding population of song sparrows (*Melospiza melodia*) that female song rates were elevated (Arcese et al., 1988), but no studies have systematically tested the hypothesis that higher population density promotes singing by female birds. At a global scale, tropical locations house higher densities of birds than temperate-zone locations and house more species with females that sing more songs (Jetz et al., 2012), a pattern that would be predicted if density promotes female song use.

Female bird songs have been demonstrated to function in many ways, including in resource defense, mate attraction, mate retention, pair bonding, and promoting breeding synchrony (Hall, 2009; Langmore, 1998; Mikula et al., 2020; Slater & Mann, 2004). Female songs may be similar in structure to male song (Cooney & Cockburn, 1995; Krieg & Getty, 2016; Ritchison, 1986) or may differ in form from male song (Pérez-Villafañá et al., 1999; Spencer, 2012; Figure 1). Some of the best studied examples of avian female singers

include members of the *Troglodytidae* family (New World wrens). Neotropical wrens use female songs and duets frequently to defend resources and mates, and in several tropical species females sing as much as males do (Hick et al., 2016; Levin, 1996; Logue & Gammon, 2004; Osmun & Mennill, 2011). In temperate North America, house wrens (*Troglodytes aedon*), winter wrens (*Troglodytes hiemalis*), cactus wrens (*Camphylorhynchus brunneicapillus*), and canyon wrens (*Catherpes mexicanus*) all have female songs that are used less frequently than male song (Billerman et al., 2020; Odom & Benedict, 2018). Despite that, some have very well-described functions; house and canyon wren females use songs to defend territories against conspecifics, particularly other females (Hathcock & Benedict, 2018; Krieg & Burnett, 2017; Krieg & Getty, 2016). Canyon wren female songs are distinct in form from male songs, creating the possibility for conspicuous sex-specific signaling (Benedict et al., 2013; Figure 1). In one low-density population, canyon wren females rarely sang spontaneously but sang reliably and often to defend resources when hearing conspecific female song playback (Hathcock & Benedict, 2018).

Canyon wrens offer an excellent system in which to explore whether population density influences female song rates and behaviors. At both local and continental scales, canyon wrens show highly variable population densities, and therefore, some individuals may be encountering conspecifics more often than others (Jones & Dieni, 2020). Because females sing a distinctive song that functions in sex-specific resource defense, they provide a good test case for the hypothesis that higher rates of neighbor-neighbor interaction could promote female song (Hathcock & Benedict, 2018). In this study, we investigated whether high population density increased rates of female song at a local scale within a single population, and we compared female song between two populations separated by approximately 1000 km. We conducted observational watches and song playback experiments at these two sites with varying population densities of canyon wrens. We predicted that females in the high-density population and with closer neighbors would spontaneously sing more often than females with more distant neighbors. We further predicted that females with closer neighbors would sing

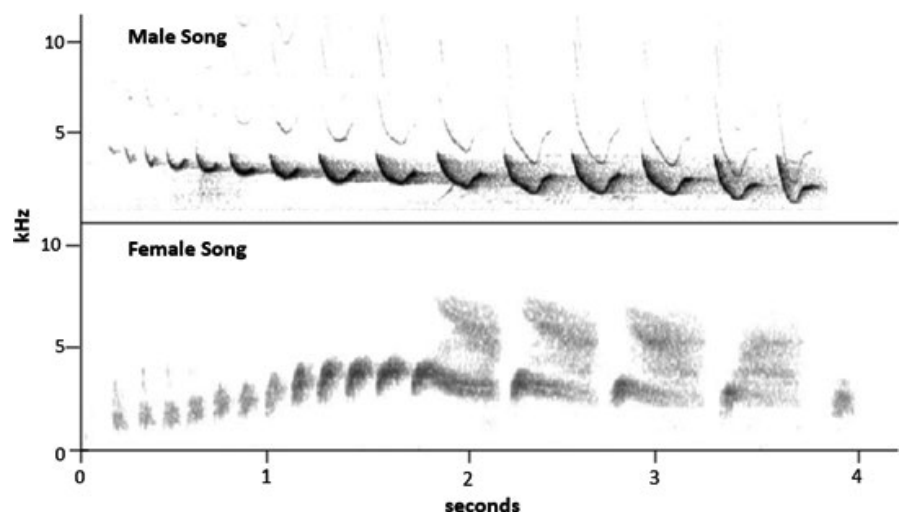


FIGURE 1 Male canyon wren song (top) versus female canyon wren song (bottom). Male songs typically include more pure tones, while female songs are composed primarily of buzzy broadband syllables

more often when exposed to playback and would have more aggressive characteristics in their songs. Measured song characteristics included acoustic entropy and song frequencies because higher entropy and lower acoustic frequencies are often associated with animal vocal aggression; both are known to signal aggression in male canyon wrens (Benedict et al., 2012; Morton, 1977; Ordóñez-Gómez et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Field sites

Research was conducted from May through July of 2018 in Larimer, Boulder, and Jefferson counties in Colorado and from April to June of 2019 around the Southwest Research Station in the Chiricahua Mountain region in Cochise County, Arizona. Colorado represented our low-density and Arizona our high-density population. Our within-population study was conducted in Arizona. In both areas, canyon wrens are habitat specialists found in and around vertical cliffs (Jones & Dieni, 2020; Rose, 2013). They are year-round residents that hold permanent territories, but males typically only sing to defend those territories in the spring and summer (Jones & Dieni, 2020). We used prior studies (Hathcock & Benedict, 2018; Warning et al., 2015), eBird reports, and recommendations by local scientists and birders to find territorial birds, as point count surveys would not be possible due to the inaccessible nature of most canyon wren habitat. We sought to find all territorial birds in each area and identified neighboring territories for each breeding pair by listening for vocalizations and searching suitable neighboring habitat. We included 12 pairs in Colorado and 24 in Arizona.

2.2 | Territory mapping and natural song observation

For each territorial pair of canyon wrens ($n = 36$), we conducted a two-hour focal watch, during which we observed unprompted, or spontaneous, rates of female song. During these watches, we also collected a minimum of 25 GIS location points to estimate a territory center for each pair. GIS location points included male and female singing perches and/or known nest locations. Because canyon wrens often occupy areas that are difficult to navigate, such as steep, rocky outcroppings, or slopes, we would sit or stand in an inconspicuous location and use a rangefinder and compass to estimate point locations. In this way, we could record territory points without disturbing bird behavior. If the birds moved out of sight, a researcher would follow to keep within sight of the bird while remaining inconspicuous. If the birds flew to an inaccessible area or were lost, the researcher would sit and wait within 10 m of the last singing perch until the birds returned. All 2-h observation watches were done after pairs had established territories. Breeding behaviors were recorded when possible. No additional territory points were taken after pairs were discovered to have fledglings,

as their territories can change dramatically after fledging (Warning et al., 2015).

GIS location points were uploaded to ArcGIS (www.arcgis.com) to create territory polygons using methods adapted from Yoon et al. (2012). We used minimum bounding geometry to create the smallest possible polygons from our point clusters and then created polygon centroid points to locate an average center for each territory. We measured distance to the nearest neighbor as the distance from centroid to centroid. This type of nearest-neighbor distance estimation is an established proxy for population density in similar studies (Fernández-Juricic et al., 2009; Penteriani, 2003; Yoon et al., 2012). We used centroid distance instead of edge distance measurements between polygons because our sampling was not comprehensive enough to produce robust estimates of the full territory size and shape (Jablonski et al., 2010; Streby et al., 2012). Full territory mapping was challenging due to the inaccessible nature of canyon wren habitat.

To further confirm population densities for each pair location in Colorado and Arizona, we used publicly available eBird abundance models representing the worldwide abundance of canyon wrens calculated from crowd-sourced data (Fink et al., 2020, <https://ebird.org/science/status-and-trends/canwre/abundance-map>). We extracted the average canyon wren abundance at each territory center point during the breeding season as predicted by the eBird model for 2018 (Fink et al., 2020) with a 2.96-km spatial resolution implemented in the EBIRDST package (v0.2.1) in R (v3.6.3). Breeding seasons were defined as April to July (weeks 14–30 of the year) in Arizona and May to August (weeks 18–34 of the year) in Colorado. We used these breeding season dates to capture the variation in the timing of breeding and the differential timing of playback experiments (see below) at each location.

2.3 | Interactive playback protocol

We assessed canyon wren female song features and singing behavior using interactive playback experiments. Playbacks in Colorado were conducted between May 15, 2018, and July 20, 2018. Playbacks in Arizona were conducted between April 15, 2019, and June 15, 2019. All playbacks were conducted during the breeding season prior to chicks fledging on each territory. Each female underwent one experimental playback trial. We used a SONY SRS-XB20 Bluetooth speaker and smartphone for playbacks, with sound pressure levels calibrated outside of the study area to 80 decibels at 1 m using an Extech SL510 sound pressure meter. Playback experiments were conducted between sunrise and 1000 h, Mountain Standard Time. We recorded trials with a Marantz PMD 661 solid-state digital recorder and a Sennheiser MKH 70 long shotgun microphone. To begin the protocol, we recorded the ambient environment for ten minutes to calibrate sound equipment and ensure that environmental conditions were not too severe for sound recording. A 5-min control trial of spotted towhee (*Pipilo maculatus*) song played first. This was followed by a 5-min experimental trial simulating territorial intrusion by

a female canyon wren. A single female song was played every 30 s until a female appeared. When the female sang in response to playback, we waited for 5 s after the end of her song and then responded with the recorded song. This continued for up to 5 min at which point we ended playback. While recording avian vocal responses, the experimenter also dictated behavioral responses into the microphone. We 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 using a range finder. We continued to record for ten minutes after playback ended to procure additional song samples from females. Our sample includes 12 playback experiments conducted in Colorado and 24 in Arizona, but four from Colorado were excluded from analysis due to lack of female response.

We used song recordings obtained from our previous experiments (Hathcock & Benedict, 2018) and from xeno-canto.org used with permission of the recordists (XC100999, XC102224, XC1022600) as playback stimuli. We constructed eight different playback tracks, each using a single song from one of eight different individuals. We rotated through these eight individual tracks between playback trials. All stimuli were recorded in Colorado and were the same song type (Benedict et al., 2013). We presented stimuli to different test subjects in a fixed order, using one track per experiment, but due to technical difficulties, one track was repeated in ten playbacks out of 24 in Arizona.

We predominantly used territory location to identify pairs and vocalizations to identify sex, but also 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 (Warning et al., 2015). In Arizona, most birds could be identified using territory boundaries and by listening for neighboring individuals singing at the same time or during counter-singing events. If birds were close enough to have overlapping territories, they were color-banded. All bird banding followed standard mist-netting protocols from the Institute of Bird Populations (DeSante et al., 2009). We color-banded males first, capturing them in mist nets using male song playback at least one day before female playback trials. We applied one USGS metal band and three plastic color bands to each bird. If males could not be caught within 20 min of playback while target netting, we tried again another day or left them unbanded and distinguished pair males from females via vocalizations. To ensure that females did not hear female playback until the experiments, we refrained from banding them until after playback trials. Due to the large territory sizes of these birds and their natural history as socially monogamous, it is unlikely that other females would enter a pair's territory to respond to playback. We banded females following our playback experiments following the same protocol as males. Research was performed under USGS banding permit #23741, Colorado state permit 18TRb2041, Arizona scientific collection permit D20259653, and University of Northern Colorado IACUC Protocol 1606C.

2.4 | Playback response and song form metrics

We analyzed the recordings of each playback experiment using Raven Pro 1.5 (K. Lisa Yang Center for Conservation Bioacoustics, 2014). We used these recordings to confirm each female's latency to approach the speaker in seconds and latency to sing from the start of playback in seconds, and to count the number of songs sung by each female during the trial. We also quantified the song duration and number of syllables for every recorded female song. To further examine song form, we measured the following for all syllables within female songs (e.g., for the 16 distinct syllables illustrated in the female song spectrogram in Figure 1): average entropy, bandwidth 90%, frequency 5%, frequency 95%, peak frequency, and duration of syllables. Average entropy can be conceptualized as the average acoustic disorder in the sound, or as the calculation of an entropy, or energy value for each segment in time, which is then averaged. The bandwidth 90% is the range of frequencies that contains 90% of the sound energy of the song. The frequencies at 5% and 95% are of the high and low frequencies that define the 90% bandwidth (K. Lisa Yang Center for Conservation Bioacoustics, 2014). Only recordings in which songs were not obscured by wind or other sounds were used in syllable parameter analyses. This gave us a sample of 10,825 syllables. Songs that could still be heard and seen on Raven 1.5 were used to determine the total number of songs in response to playback, and song length data, but excluded from syllable measurements.

To make a more robust comparison between female song form in Arizona and Colorado, we supplemented our dataset with song recordings from 12 females made in Colorado in 2015 and 2016 (Hathcock & Benedict, 2018). These data were included in the syllable measurement comparison between states, giving us a sample of 15,445 syllables in that analysis. These songs were not included in analyses of behavioral data (closest approach, latency to sing, number of songs), as those responses were based on our specific playback protocol.

2.5 | Statistical analysis

We used JMP[®], version 13 (SAS Institute Inc., 2021), and R 3.6.3 (R Core Team, 2020) to conduct statistical analyses. For our large-scale geographic comparison, nearest-neighbor distances, breeding season abundances, and individual playback behavioral responses (latency to sing, number of songs, mean song duration, and closest approach) were compared between Colorado and Arizona using nonparametric Wilcoxon rank-sum tests due to relatively small sample sizes. For our local-scale comparison, individual playback behavioral responses were regressed against nearest-neighbor distances for the 24 Arizona playback experiments. Prior to performing these regressions, we log-transformed nearest-neighbor distances for normality.

In our analyses of syllable form, we used principal components analysis to reduce the six measured variables to a smaller number

	Arizona	Colorado	Z	p
Latency to sing (sec)	89.6 ± 74.7	76.4 ± 88.8	-.96	.34
Total number of songs	19.0 ± 12.8	19.0 ± 15.4	-.13	.88
Song duration (sec)	3.7 ± 0.5	2.5 ± 1.9	-.86	.39
Closest approach (m)	5.5 ± 6.1	2.8 ± 4.8	-1.68	.09

Note: The table includes the mean and standard deviation for each population and results of Wilcoxon rank-sum tests comparing means.

TABLE 1 Four behavioral measures of female canyon wren response to female song playback in Arizona and Colorado

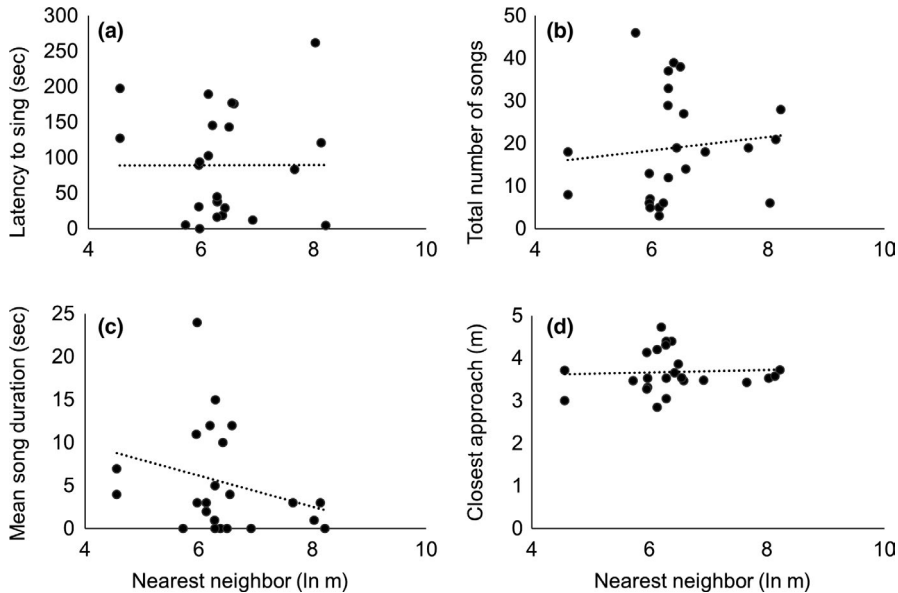


FIGURE 2 Three measures describing canyon wren female song behavior in response to conspecific female song playback (a), (b), (c) and one general measure of playback response (d) plotted against log-transformed nearest-neighbor distance for 24 experiments conducted in one population in Arizona. Dotted lines show the best fit linear regressions

of principal components for analysis. We used linear mixed models with state (Colorado or Arizona) as a fixed factor and individual bird identity as a random factor to test for differences in the principal components describing syllable form in Colorado versus Arizona. We ran this analysis twice, once using only the 36 birds tested in our playback experiments ($n = 10,825$ song syllables), and once using those birds plus the additional 12 from Colorado ($n = 15,445$ song syllables), to equalize sampling from the two regions. Finally, for a local-scale comparison, we regressed averaged individual song principal components against nearest-neighbor distances for the Arizona playback experiments.

3 | RESULTS

The mean nearest-neighbor distance for pairs in Arizona was 926 ± 22 (SE) meters, an order of magnitude smaller than the mean nearest-neighbor distance for pairs in Colorado of 9900 ± 5303 (SE) meters ($Z_{35} = 2.84$, $p = .004$) (Appendix Table A1). It was frequently possible to hear multiple males counter-singing at Arizona field sites, while we never heard males counter-singing at any Colorado sites. eBird abundance models show that the mean relative abundance of canyon wrens in Arizona is 0.35 birds/survey and that state contains about 12% of the total North American population. Colorado has a .02 mean relative abundance and only 2% of the North American

population (Fink et al., 2020). At our sampled locations, the canyon wren breeding season mean abundance was 1.74 ± 0.90 (SE) in Arizona and 0.56 ± 0.07 (SE) in Colorado; these abundances are significantly different ($Z_{35} = 2.84$, $p < .001$) (Appendix Table A1). The Colorado average abundances are lower than the range-wide average (0.75), while the Arizona averages approach the range-wide maximum (1.9) (Fink et al., 2020).

3.1 | Natural song rates and banding

We conducted a total of 48 h of focal observation in Arizona and 24 h of observation in Colorado (2 h per pair). In 2018, 18 canyon wrens were banded in Colorado, 11 of which were nestlings. In 2019, 15 were banded in Arizona, five of which were nestlings. One bird from each pair was color-banded to distinguish sex-specific behaviors. Females in Arizona and Colorado never sang during these observation periods. As a result, we never observed natural territory defense confrontations. Outside of these focal observations, we heard two females in Colorado sing spontaneously—once each before playback experiments began. Another female in Colorado was heard to sing spontaneously 12 times on the day after the playback experiment. In Arizona, two individuals were observed to sing outside of the observation windows once each after delivering food to nestlings.

3.2 | Behavioral responses to playback

Male and female canyon wrens never responded vocally or behaviorally to spotted towhee playback. During canyon wren female song playbacks, behavioral and vocal reactions from both males and females were reliable and obvious. Males often approached the speaker and called in rapid succession, but rarely sang male songs until a female responded with female songs or calls. Females typically approached the speaker and sang following playback, often continuing to sing for up to an hour after playback had ended. Pairs often approached the speaker together.

Female canyon wren behavioral responses to female song playback were similar in high-density Arizona and low-density Colorado (Table 1). We found no significant differences between the populations in latency to sing, total number of songs, song duration, or closest approach (Table 1).

As a within-population test of the effects of density on song behavior, we regressed song behavioral responses on log-transformed nearest-neighbor distances between territory polygon centroids in Arizona. Responses were variable, but this variation did not correlate with nearest-neighbor distance (Figure 2). Goodness-of-fit tests on linear regressions were not significant for latency to sing ($F_{1,22} = .00$, $p = .99$), total number of songs ($F_{1,22} = .27$, $p = .61$), song duration ($F_{1,22} = .06$, $p = .80$), or closest approach ($F_{1,22} = 1.71$, $p = .21$).

3.3 | Song spectral parameters

Principal components analysis condensed our six song measurements (syllable duration, bandwidth 90%, frequency 5%, frequency 95%, peak frequency, and entropy) into two principal components (PC1 and PC2) with eigenvalues above 1. Eigenvectors for principal components one and two are shown in Table 2. PC1 loaded most heavily on syllable frequency parameters, while PC2 loaded most heavily on bandwidth and entropy.

TABLE 2 Eigenvectors for two principal components describing female song form for the 36 females recorded during playback experiments

	PC1	PC2
Syllable duration	0.3 (0.3)	0.1 (0.1)
Bandwidth 90%	0.3 (0.3)	0.6 (0.6)
Frequency 5%	0.4 (0.4)	-0.5 (-0.5)
Frequency 95%	0.5 (0.6)	-0.02 (-0.01)
Peak frequency	0.5 (0.5)	-0.4 (-0.4)
Entropy	0.4 (0.3)	0.5 (0.5)
PC eigenvalue	3.3 (3.2)	1.6 (1.6)
Explained variance	54.5% (53.2%)	26.3% (27.3%)

Note: Bolded values are heavily weighted in the relevant principal components. Values in parentheses represent the results of a parallel analysis done on the same birds plus 12 others from Colorado to equalize sampling in each state.

When 24 females were included from each location, linear mixed models indicated a significant difference in PC1 between the Colorado and Arizona populations ($t = -2.73$, $p = .009$). PC2 did not vary significantly by population ($t = .10$, $p = .92$). Models with 24 females from Arizona and only 12 from Colorado showed similar results (PC1: $t = -3.92$, $p < .001$, PC2: $t = -.27$, $p = .79$). The consistent difference in PC1 is driven by lower syllable frequencies in Arizona, when compared with Colorado (Table 3).

Our local test for the effects of population density indicated that female song spectral parameters did not covary with nearest-neighbor distances in Arizona (Figure 3). Goodness-of-fit tests on linear regressions were not significant for PC1 ($F_{1,22} = .19$, $p = .67$) or PC2 ($F_{1,22} = .00$, $p = .99$).

4 | DISCUSSION

Both nearest-neighbor distance measures and eBird abundance modeling confirmed that Arizona was significantly more densely populated with canyon wrens than Colorado. Nearest-neighbor analysis showed that individuals had ten times shorter distances between territories in Arizona versus Colorado. This supports what we already know about individuals in Colorado; even when appropriate habitat is present, they rarely have close neighbors (Warning & Benedict, 2015; Warning et al., 2015). Arizona, in contrast, contains many canyon wrens with individuals typically having multiple female neighbors close enough that they would frequently hear each other when they sing (Fink et al., 2020). Despite that, we did not find evidence to support our hypothesis that close neighbors would drive up rates of female song. During focal observations, females in both Arizona and Colorado sang no songs during a collective 72 observation hours. Females were occasionally heard to sing spontaneously outside of these dedicated observation periods in both locales, but only very rarely. Our observations are consistent with previous studies indicating that female canyon wrens use song very infrequently during the breeding season (Benedict et al., 2013; Hathcock & Benedict, 2018). Here, we expand on previous findings by demonstrating this result in areas with both high and low population density and among individuals with closer or more distant neighbors. One existing study hints that population density might increase rates of spontaneous female song in a North American species with rare female song (Arcese et al., 1988), but that same trend is not present in our study. Male song rates increase with neighbor density in some species (Yoon et al., 2012), but not in others (Fernández-Juricic et al., 2009) making it premature to draw universal conclusions about the general effects of close neighbors on rates of spontaneous bird song.

Our playback experiments were designed to provoke song from territorial female canyon wrens to measure their resultant song behavior and song form. Females in both populations responded to female song playback by approaching the simulated intruder and singing, but population density and nearest-neighbor distance did not predict behavioral intensity during response. At the population scale, we found no difference in song rate, song duration,

and approach behavior between Colorado and Arizona. Within the Arizona population, nearest-neighbor distance did not correlate with the level of female aggressive response to female song playback. Thus, we cannot conclude that female song is a more salient aggressive signal to female canyon wrens in densely populated areas. We did have four territories in Colorado where we did not get a playback response, but it is important to note that we never confirmed the presence of a female canyon wren at each of those sites on the day of playback, making the lack of response difficult to interpret. Interestingly, responses were generally similar in the two populations, despite all playback stimuli coming from Colorado. This suggests that across the species' range, female songs are universally salient signals. Future work could test for differential response to local and foreign female songs. We were unable to do so in this study because we could not obtain enough high-quality recordings of female canyon wren songs in Arizona prior to playback experiments.

Female birds of other species, such as African black coucals (*Centropus grillii*), use song to assess and dispel rival females (Geberzahn et al., 2010). Among New Zealand bellbird (*Anthornis melanura*) females are highly aggressive to neighbors, indicating an important role for female song in mediating territory disputes (Brunton et al., 2008). In superb fairy-wrens (*Malurus cyaneus*), female song is important for territory defense and rates of female song in response to playback predict reproductive success (Cain et al., 2015; Cooney & Cockburn, 1995). Combined, these results from other species provide a basis for the hypothesis that close neighbors promote female song. Our data, however, fail to support that hypothesis in

canyon wrens. This may be due to several factors potentially relating to non-migratory status, social monogamy, or habitat. Canyon wrens appear to be socially monogamous year-round; they have been observed to forage together during winter months in pairs and maintain these pair bonds in the breeding season (Jones & Dieni, 2020; Kroodsmas, 1977; Tramontano, 1964). Because canyon wrens are sedentary and generally occupy the same habitat area year-round (Jones & Dieni, 2020), there may not be a need for females to continually defend territory from established neighbors. This differs from other species with female song, such as superb fairy-wrens, which commune into flocks during non-breeding seasons and sing to re-establish breeding territories (Cooney & Cockburn, 1995). Similarly, song sparrows and African black coucals may encounter many other individuals from whom they will need to defend annual resources (Arcese et al., 1988; Geberzahn et al., 2010). Canyon wrens, in contrast, have large territories for their body size and the linear nature of cliff habitats makes them unlikely to have more than two direct neighbors (Jones & Dieni, 2020; Warning & Benedict, 2015). This particular habitat occupancy pattern might help to generate levels of female aggression that are consistent in the face of any same sex competitor, no matter how frequently (as in Arizona) or infrequently (as in Colorado) that competitor is encountered.

Female canyon wrens in Arizona sing with lower song frequencies than do females in Colorado. This difference could be an honest signal of aggression that results from the higher abundance of canyon wrens in Arizona, or it may be a non-functional geographic difference that results from genetic or cultural drift (Lynch, 1996). If the difference is functional, low-frequency songs might indicate higher aggression in Arizona, as they do in males and females of other species (Benedict et al., 2012; Geberzahn et al., 2010; Krieg & Burnett, 2017). Future playback experiments using song stimuli with different frequencies could test for this type of aggressive functionality. Our other outcomes suggest, however, that the population differences in song frequencies likely represent non-functional geographic variation. If population density were the main driver of this effect, we predicted that we would see both lower frequencies and higher entropy in Arizona and when birds had closer neighbors. We did not observe any difference between populations in the song form variable that represented entropy (Benedict et al., 2012; Morton, 1977; Ordóñez-Gómez et al., 2015). Further, we did not find evidence that

TABLE 3 Six measures of female canyon wren syllable form in Arizona and Colorado

	Arizona	Colorado
Syllable duration (sec)	0.2 ± 0.2	0.2 ± 0.1
Bandwidth 90% (Hz)	1060.7 ± 417.4	1222.6 ± 682.6
Frequency 5% (Hz)	2373.3 ± 713.2	2701.5 ± 805.0
Frequency 95% (Hz)	3434.1 ± 796.4	3924.1 ± 1003.0
Peak frequency (Hz)	2939.7 ± 790.8	3259.5 ± 821.0
Entropy	3.2 ± 0.3	3.3 ± 0.4

Note: The table includes the mean and standard deviation for each population.

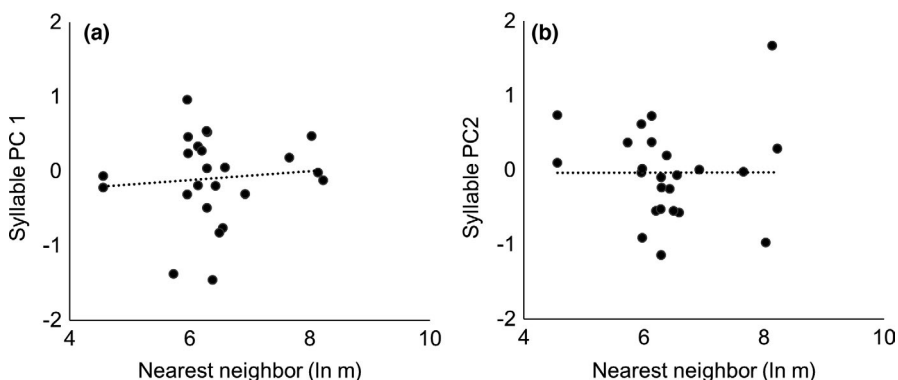


FIGURE 3 Two measures describing female syllable form plotted against nearest-neighbor distance (log-transformed) for 24 playback experiments conducted on canyon wrens in one population in Arizona. PC1 (a) primarily describes dominant frequencies, while PC2 (b) primarily describes bandwidth and entropy. Dotted lines show the best fit linear regressions

the presence of nearer neighbors within the Arizona population covaried with either entropy or song frequencies.

Results of this study confirmed that female canyon wrens sing infrequently and that population density varies substantially across the species' range. Different populations exhibited minor differences in female song form, but the use of female song varied little among individuals with differently spaced neighbors and between two distantly located study populations. Wider work on female song indicates that its presence often depends on a species' life-history traits and geographic distribution. Phylogeny, year-round territoriality, and sedentary lifestyles are all known evolutionary drivers of female song (Benedict, 2008; Logue & Hall, 2014; Odom et al., 2014; Tobias et al., 2016). Canyon wrens are non-migratory, territorial, and embedded in a family with frequent female song (Billerman et al., 2020; Mann et al., 2009). These species-level characteristics may explain why they have retained female song in their northern temperate-zone distribution. Unlike many wrens, however, they show low rates of female song (Mann et al., 2009). Canyon wren females used songs to defend resources during aggressive encounters but not as spontaneous broadcast signals during our study. The breeding females that we studied had already established territories and were engaged in the costly activities of nesting and raising young (Haftorn & Reinertsen, 1985; Mainwaring & Hartley, 2013; Monaghan & Nager, 1997). Perhaps, the selection pressure to maximize breeding activities outweighs any advantage of investing in spontaneous song (Gil & Gahr, 2002). In at least one species, the superb fairy-wren, females sing spontaneously mostly when they are newly establishing a territory, and spontaneous song drops off with tenure duration (Cooney & Cockburn, 1995). Female canyon wrens could follow a similar pattern, which would suggest they undergo low rates of territory turnover. Seasonal timing might also play a role in female song rates. Our focal birds were pre-fledging when we challenged them with playback. Fledgling birds wandering about a territory may increase the number of territorial encounters between pairs of birds, increasing song rates. It is also possible that female canyon wren songs are maintained due to functionality outside of the breeding season, particularly if territory boundaries are most contested in the winter when food resources are lowest. Colorado females have been heard to sing relatively frequently following the breeding season (LB, pers. obs.), a pattern very different from that of males who ramp up singing in March, prior to the breeding season (Rose, 2013). Future studies could investigate patterns and functions of female song throughout the year to track temporal variation in song use and neighbor-neighbor aggression. Monitoring actual encounter rates rather than using population density as a proxy and investigating the effects of newly establishing a territory may also prove fruitful avenues of research for explaining differences in the rates of spontaneous song.

Bird song has long been a model system in animal communication research, and studies of female song have much to contribute to our understanding of signal evolution (Odom & Benedict, 2018; Price, 2015). Here, we conclude that female song rates and use patterns can be a species-wide trait and do not show regional or local variation in response to population density. Whether similar patterns exist in other species remains to be investigated, but current

evidence does not strongly indicate that population and neighbor density drive rates of female song.

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DATA AVAILABILITY STATEMENT

In accordance with the "DFG Guidelines on the Handling of Research Data," data are available on FigShare.com. Audio recordings are available from the authors upon request.

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APPENDIX

TABLE A1 Descriptive metrics for canyon wren territories sampled in this study

Bird ID	State	Nearest-neighbor distance (m)	Latitude	Longitude	eBird model abundance
1	Colorado	386.55	40.564000	-105.177995	0.74887383
2	Colorado	386.55	40.566936	-105.186184	0.74887383
3	Colorado	1550.00	40.481352	-105.224214	0.89628786
4	Colorado	3119.98	40.478401	-105.136743	0.49841055
5	Colorado	14506.90	40.704073	-105.237896	0.61190307
6	Colorado	3003.69	40.587641	-105.162592	0.2620362
7	Colorado	20221.78	40.249285	-105.222198	0.69018835
8	Colorado	64802.68	39.666007	-105.204603	0.03104324
9	Colorado	1440.00	40.509710	-105.162379	0.54351807
10	Colorado	1440.00	40.496637	-105.160877	0.54351807
11	Colorado	1550.00	40.468801	-105.216509	0.89628786
12	Colorado	6400.00	40.426477	-105.165434	0.55171001
13	Arizona	724.68	32.020182	-109.336384	1.79974842
14	Arizona	2122.41	32.001102	-109.338165	2.1099689
15	Arizona	589.42	31.891463	-109.166170	2.14422774
16	Arizona	392.86	31.908498	-109.188094	2.14422774
17	Arizona	537.53	31.891955	-109.176620	2.14422774
18	Arizona	3712.41	31.941615	-109.193859	2.14422774
19	Arizona	3071.31	32.008114	-109.385273	2.11468625
20	Arizona	537.53	31.889305	-109.171863	2.14422774
21	Arizona	700.13	32.004095	-109.315449	1.60380602
22	Arizona	618.36	31.897532	-109.176559	2.14422774
23	Arizona	1012.00	31.908570	-109.177395	1.94846392
24	Arizona	386.16	32.020770	-109.348180	1.01654899
25	Arizona	459.97	31.998331	-109.311443	1.60380602
26	Arizona	459.97	32.001695	-109.308595	1.60380602
27	Arizona	661.56	32.026026	-109.339815	1.79974842
28	Arizona	493.03	32.027283	-109.352426	1.79974842
29	Arizona	538.88	32.026502	-109.346796	1.79974842
30	Arizona	95.42	32.028398	-109.357479	1.01654899
31	Arizona	95.42	32.029253	-109.357362	1.01654899
32	Arizona	306.12	32.025638	-109.357557	1.01654899
33	Arizona	533.92	32.020917	-109.356446	1.01654899
34	Arizona	386.16	32.018361	-109.351131	2.1099689
35	Arizona	392.86	31.905536	-109.190373	2.14422774
36	Arizona	3415.71	31.913731	-109.141219	1.36954308