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Communications

Female dark-eyed juncos *Junco hyemalis thurberi* produce male-like song in a territorial context during the early breeding season

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Reports of female song, once considered a rarity, have recently increased across a variety of avian taxa. Females of many species can be induced to produce male-like song with exogenous testosterone, but observations of female song in free-living birds remain limited by incomplete sampling of females. Here, we report three independent observations of female dark-eyed juncos *Junco hyemalis* producing male-like song early in the breeding season (i.e. post-territory establishment, pre-nesting) in a recently established non-migratory, urban population. To elicit song, we presented 17 free-living junco pairs with a live, caged female conspecific. Three unique females responded to our trials by diving at the intruding female, chasing their (male) mate, fanning their tail feathers, and singing a trilled song similar in structure to male long-range (broadcast) song. We compared male and female songs quantitatively and found that the two sexes were statistically similar in many spectral and temporal characteristics, but female songs had significantly lower minimum and peak frequencies than males. This result is particularly surprising, as males in this urban population are known to sing at a significantly higher minimum frequency than males in a nearby montane population. Both the seasonal and social context in which these songs were observed suggest a potential function for female song in mate guarding and polygyny prevention, but more data are needed to test this hypothesis. Whether female song is common in all dark-eyed juncos during the early breeding season or if it is restricted to this particular urban and non-migratory population remains an important question for future research.

Introduction

Birdsong represents one of the most thoroughly studied systems for investigating signal evolution, and the evolutionary significance of male song in both territorial behavior and mate attraction are well established (Searcy and Nowicki 2005, Catchpole and Slater 2008). Female songbirds also produce songs in a variety of contexts, but the proximate and ultimate mechanisms underlying female song remain poorly understood



in most species (Langmore 1998, Riebel et al. 2005, Reichard and Welklin 2015, Hall and Langmore 2017). Recent work has shown that female song is substantially more common than previously thought, and that the ancestral songbird likely was a species in which both sexes sang (Price 2009, Odom et al. 2014). In light of this new information, studies that investigate the structure, function, and fitness correlates of female song are essential for determining why selection has acted against female song in certain species while favoring it in others (Hall and Langmore 2017).

The hypothesized functions for female song overlap considerably with those for male song and include defense of resources and mates, mate attraction, pair bond maintenance, and coordinating breeding activities (reviewed by Langmore 1998, Hall 2004). Comparative analyses indicate that female song is associated with a variety of life history and ecological traits such as a tropical breeding range, year-round territoriality, lack of migration, and monogamy (Slater and Mann 2004, Price 2009, Price et al. 2009, Logue and Hall 2014). Thus, females appear to sing more often in conditions involving long-term territoriality and high competition for mates and resources, which would favor songs that serve a function in aggression and defense. Temperate breeding species often lack many of these life history traits, and as a result, female song appears to be less conspicuous and restricted to life history stages that include elevated aggression such as the pre-nesting period of territory and pair bond establishment (Arcese et al. 1988, Baptista et al. 1993, Matthews et al. 2017). The pre-nesting life history stage also coincides with peak levels of circulating androgens in many temperate species (Wingfield et al. 1990, Ketterson et al. 2005), and elevated androgen levels can act as an important proximate signal underlying song production in both males and females (Dloniak and Deviche 2001, Langmore et al. 2002, Alward et al. 2017).

The dark-eyed junco *Junco hyemalis* is a temperate songbird in which female song has been previously reported as either absent (Nolan et al. 2002) or rare (Cardoso and Reichard 2016). One exception occurs in captive female juncos treated with exogenous testosterone, which were observed producing a trilled song that resembled male long-range song (Konishi 1964, EDK unpubl.). These data suggest that female juncos are capable of producing male-like song when certain physiological conditions are met, but whether this behavior is common in free-living females and how female song may differ from male song remains unknown.

Here, we tested whether female juncos sing in response to a simulated, live female intruder during the early breeding season in a recently established non-migratory, urban population. Previous research in other species has suggested that females respond particularly strongly to female intruders and may be more likely to sing during a same-sex challenge (Langmore 1998, Seddon and Tobias 2006, Krieg and Getty 2016). Consistent with those results, we documented three independent observations of free-living female juncos producing male-like song when presented with a female intruder.

Methods

We conducted our research with free-living dark-eyed juncos *Junco hyemalis thurberi* at the campus of the Univ. of California at San Diego (UCSD; 32°52'N, 117°14'W) from 12 to 20 February 2010 between the hours of 08:30 and 17:00. This junco population is sedentary with the first egg date typically occurring around 15 March (Yeh and Price 2004, Atwell et al. 2014). As a result, these data were collected during the pre-nesting, but post-territory establishment breeding stage as evidenced by observations during the sampling period of males defending territories and singing long-range (broadcast) songs and pairs foraging together rather than in large flocks. Intensive prior monitoring efforts, including longitudinal observations of marked (banded) individuals from 1999–2002 and 2006–2007, indicate that junco pairs in this population may remain bonded on or near their breeding territories year-round, with known male-female pairs observed foraging on breeding territories, in a behavioral pattern distinct from visiting wintering flocks (Yeh and Price 2004, Atwell et al. 2016).

During this study much of the population was unbanded, and as a result, we largely relied on plumage characteristics and behavior to differentiate between the sexes. At the time of this study, the primary observer and recordist (DGR) had previously morphologically sexed and observed hundreds of junco pairs responding to simulated or non-simulated territorial intruders of both sexes in five different junco subspecies. Collectively, this experience provided a strong foundation for confidently differentiating between the sexes by plumage and behavior, the latter of which is quite distinct in the courtship context observed here (see Results). With respect to plumage differences, female juncos of the Oregon *Junco* group (or 'Rassenkreis', Miller 1941), which includes the *J. h. thurberi* subspecies studied here, exhibit a light gray head that contrasts markedly with the dark black head of males and allows the sexes to be readily distinguished visually. We captured one of the three singing females and confirmed our visual identification of her sex using both morphological and molecular techniques (N. M. Gerlach pers. comm.). Seven of the 31 males observed or recorded in the study were previously banded on their territories during prior breeding seasons and sexed morphologically while in the hand.

We used a shotgun microphone (Audio-Technica model AT835b) paired with a Marantz digital recorder (model PMD661), and all recordings were stored in an uncompressed 'WAV' format for analysis (16 bits; 44.1 kHz). To locate territories and potential junco pairs, we relied on observations of spontaneously singing juncos, territorial responses to brief playbacks, and historical observations of territory locations and densities established from previous breeding seasons during which the population was extensively monitored (Yeh and Price 2004, Atwell et al. 2014). While canvassing the study site to locate territories, we also opportunistically recorded songs that were produced both spontaneously ($n=9$) and in response to playback ($n=6$). We then conducted 25 simulated courtship interactions (SCI; Reichard et al. 2017a) and

recorded all of the vocalizations produced by any juncos that responded.

Each SCI involved presenting free-living juncos with a live, caged female junco paired with a playback of a female precopulatory trill, a signal of female sexual receptivity. The playback consisted of three repetitions of the same precopulatory trill separated by 1.5 s of silence, and the entire bout of three trills was repeated every twenty seconds until a male junco approached the caged female. The same captive female and trill playback was used in all SCIs. The captive female was a member of the local population that was captured at the beginning of data collection, but the precopulatory trill was recorded from a female belonging to a different junco subspecies (*J. h. carolinensis*) endemic to the eastern United States. A previous study found that junco precopulatory trills recorded from multiple females all consisted of an identical note type with only slight differences among individuals in frequency bandwidth and trill length (Reichard et al. 2013), and qualitative observations from multiple populations, including the population studied here, suggest that these trills also vary little geographically (DGR unpubl.). In addition to recording vocalizations during the SCI, we also noted the presence or absence of courtship behavior (short-range song; Reichard et al. 2011, 2013), aggressive behavior (high frequency trills, dives and lunges at the cage; Balph 1977, Nolan et al. 2002), and behaviors that can occur in both contexts (tail spreads, erection of body feathers [ptiloerection]; Nolan et al. 2002).

Two independent observers (DEB, SEG) that were blind to the sex of the singer analyzed all songs using Raven Pro 1.4 (Cornell Lab of Ornithology, Ithaca, New York, USA). We generated spectrograms (512 FFT, 50% overlap, Hann Window) and chose one exemplar of each song type that was relatively free from overlap with background noise and other birdsong. Songs of sufficient quality for analysis were collected from three females and 21 males. Seven males produced multiple songs types, which resulted in a sample of 33 distinct male songs. We visually identified the start and end time and minimum and maximum frequency for each song by creating a bounded 'selection box' with the cursor. Once the temporal and frequency boundaries were established, we counted the number of syllables and divided by the song length to quantify trill rate. We also recorded the peak frequency, which is the frequency produced at the highest amplitude.

Because these songs were collected in an urban environment where noise is pervasive, we were unable to find an appropriate threshold value that would allow us to analyze all of our songs via the power spectra method recommended by some researchers (Zollinger et al. 2012, Ríos-Chelén et al. 2016; but see Cardoso and Atwell 2012). The 'by-eye-method' that we employed may result in a bias towards higher measures of frequency across all of our recordings (Ríos-Chelén et al. 2016), but that limitation should have minimal effects on our comparison of males and females as all samples were recorded in the same noisy environment. We averaged the acoustic data collected by both observers

to minimize the likelihood of individual biases in measurement technique affecting the results. Male and female acoustic characteristics were compared statistically using nonparametric Mann–Whitney U tests.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.3c827>> (Reichard et al. 2017b).

Results

We observed 17 pairs of juncos and 8 solo males responding to a SCI (n=25 total SCIs). We also observed and recorded an additional 6 males singing either spontaneously or in response to a brief playback while canvassing the study site. Females were not observed singing in any context other than in response to the SCIs. Males and females were visually distinguishable by differences in head coloration and their distinct behavioral responses during the SCI. Males frequently approached the caged female in a typical courtship posture with their body feathers erect (16/25, 64%) and tails spread (13/25, 52%) while singing predominantly short-range song (21/25, 84%), a soft song that functions in courtship (Reichard et al. 2011, 2013), and less frequently, long-range song (9/25, 36%). Females approached more aggressively as evidenced by dives and lunges at the caged female (8/17, 47%), tail spreads (an uncommon behavior for females; 4/17, 24%), the production of a high frequency trill call (7/17, 41%), and the absence of any short-range song (0/17). We also observed females behaving aggressively towards their presumed mate by frequently displacing and chasing the male from the vicinity of the SCI.

Three of the responding females performed the behaviors mentioned above (dives, tail spreads, high frequency trills) during the SCI, while also producing a quiet song with a trilled structure that was very similar to male long-range song (3/17, 18%; Fig. 1). Each female sang only a single song type and remained close to the caged female while singing. In one case, the female's presumed mate also sang a bout of long-range song after each female song for a brief time. Female songs had a significantly lower minimum frequency ($p=0.001$) and peak frequency ($p=0.03$) than male songs (Fig. 2); however, peak frequency would no longer be significant after a conservative Bonferroni correction ($\alpha=0.008$). We found no detectable differences between the sexes in maximum frequency ($p=0.59$; Fig. 2), frequency bandwidth ($p=0.22$), song length ($p=0.51$), or trill rate ($p=0.51$).

Discussion

Three independent female dark-eyed juncos produced a male-like song during the pre-nesting stage of the early breeding season in response to live, caged female conspecific. Previous experiments have shown that female song can be induced in juncos with exogenous testosterone (Konishi 1964), but to our

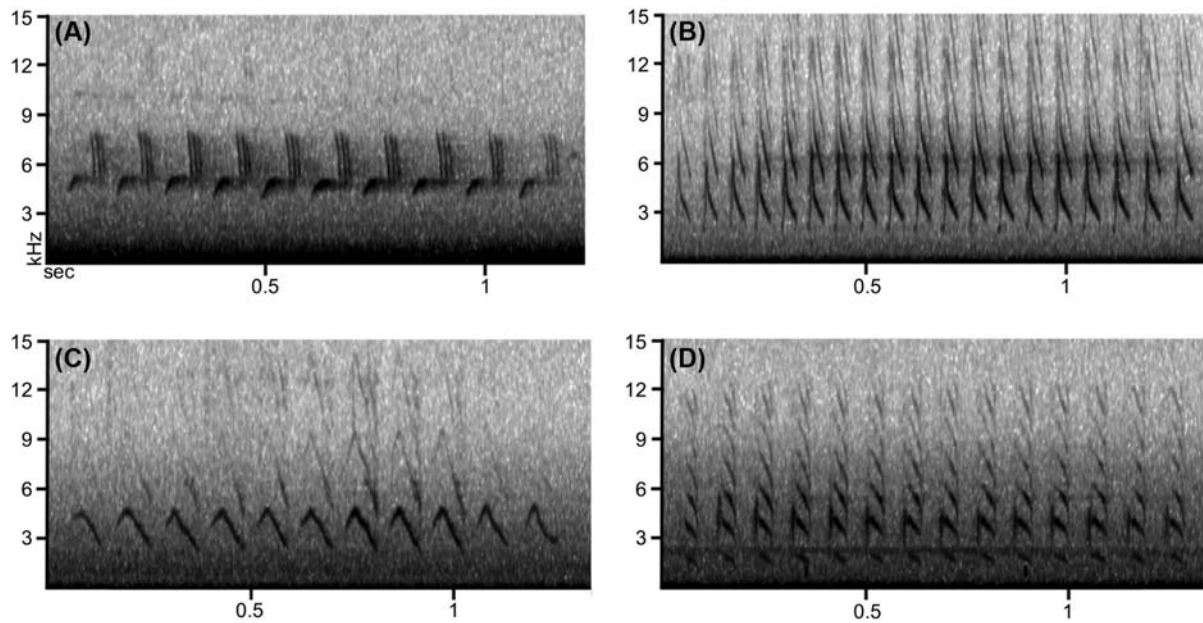


Figure 1. Sonograms of a representative male long-range song (A) and songs from three independent females (B–D) recorded in the presence of a live, caged female conspecific.

knowledge this is the first published account of songs produced by free-living females. The seasonal timing of these observations coincides with the highest levels of circulating testosterone in female juncos (Ketterson et al. 2005, Jawor et al. 2007), which suggests a potential role for testosterone in promoting female song. This link between high testosterone levels, pre-nesting behavior, and female song has also been identified in other temperate species where female song is thought to be relatively rare (Arcese et al. 1988, Hobson and Sealy 1990, Baptista et al. 1993, Matthews et al. 2017).

Early researchers hypothesized that female song lacked an adaptive function and was rather a maladaptive byproduct of abnormally high testosterone levels (Nice 1943, Langmore 1998). If accurate, female song should not be associated with a specific social context and be largely unpredictable across

time and space. Contrary to this prediction, we observed females singing only in response to a simulated intrusion from a rival female, supporting a function in resource and/or mate defense. Consistent with an adaptive, territorial function, females of multiple temperate species sing most often during aggressive interactions with rival females (Langmore 1998), and recent evidence suggests that female song rate is positively related to fitness in some species (Cain et al. 2015, Brunton et al. 2016).

Dark-eyed juncos are socially monogamous (Nolan et al. 2002, Price et al. 2008, Atwell et al. 2014), which is consistent with our observations of paired males readily courting an intruding female while also being chased away from the intruding female by their aggressive, singing (female) mate. As such, female song during the early breeding season may also serve a specific function in preventing polygyny by acting as an aggressive signal to rival females, the female's social mate, or both. Whether female song also functions in territory defense against rival males remains unknown in juncos, but has been observed in other species (Langmore 1998, Illes and Yunes-Jimenez 2009). Future experiments that simulate separate intrusions by a female and male conspecific to the same junco pairs throughout the breeding season are essential for determining the specific functions of female song in mate and territory defense.

Female juncos that are induced to sing with exogenous testosterone produce trilled, male-like songs (Konishi 1964), which makes the structural similarities between female and male song observed here unsurprising. Females did not differ detectably from males in song length, trill rate, maximum frequency, or frequency bandwidth, but females sang at a significantly lower minimum and peak frequency. The difference in minimum frequency is notable because males in this

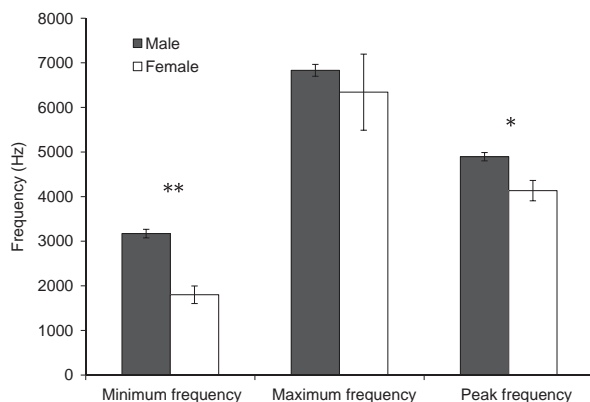


Figure 2. Mean (\pm SE) frequency characteristics of male ($n=33$) and female ($n=3$) songs recorded in the presence of a live, caged female conspecific. ** $p=0.001$. * $p < 0.05$.

urban population are known to sing at a significantly higher minimum frequency than males from a nearby montane population that experiences substantially less low-frequency, anthropogenic noise (Slabbekoorn et al. 2007, Cardoso and Atwell 2011a). Collectively, these observations suggest that female song may be poorly optimized for transmission through the local urban environment, and raises the question of why females produce a lower frequency song? Mechanistically, body size cannot explain this difference as females are smaller than males, which would predict a higher frequency song, and body size does not correlate with male song frequency in this population (Cardoso et al. 2008). If females predominantly sing at lower amplitude than males, which was a qualitative observation in this study, then the higher minimum frequency of male song may be partially explained by the Lombard Effect, which relates to a physiological constraint linking acoustic amplitude and frequency (Brumm and Zollinger 2011, but see Cardoso and Atwell 2011b).

From an ultimate perspective, the effects of masking by environmental noise may be insufficient to select for higher frequencies in females because female song appears to function in short-range, territorial interactions, which reduces the need for effective transmission over long distances (Reichard et al. 2011). The potential lack of selection for long-distance transmission may be further supported by the observation that female songs appear to have more energy in the upper harmonics than male song (Fig. 1; DGR unpubl.). This difference suggests that the female vocal tract may not filter those upper harmonics as effectively as the male vocal tract, which is thought to be an adaptation driven by selection favoring the effective, long-distance transmission of male songs in other oscine birds (Riede et al. 2006, Riede and Suthers 2009).

The junco population studied here was established by a well-documented colonization event in which a subset of overwintering juncos apparently ceased migrating and began year-round residency along the urban California coast in the early 1980s (Rasner et al. 2004). This novel coastal environment is drastically different than the habitat of other *J. h. thurberi* populations that most typically inhabit higher elevation, montane forests. Our research group and others have documented the population's subsequent phenotypic and genetic divergence in the novel environment, as compared to representative ancestral, migratory populations (Rasner et al. 2004, Yeh and Price 2004, Atwell et al. 2014). Thus, the occurrence of female song in this population may represent yet another divergent trait. Gains of migratory behavior are often associated with the loss of elaborate female traits, including song (Friedman et al. 2009, Price et al. 2009, Logue and Hall 2014), but losses of migration do not always result in gains of female song (Najar and Benedict 2015). This junco population may provide an excellent system for studying the potential proximate and ultimate links between migration and female song. However, an essential first step will involve conducting comparable observations in the ancestral race as well as other migratory junco subspecies to test for the presence of female song across *Junco* lineages

and closely related taxa. Female song may be common and widespread during the early breeding season in all dark-eyed juncos, and future researchers must avoid the erroneous assumption that all singing juncos are male.

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