Female song can be as long and complex as male song in wild House Finches (*Haemorhous mexicanus*)

Ar Kornreich, 1,2 Mason Youngblood, 1,3 Paul C. Mundinger, 1† and David C. Lahti 1,3*

ABSTRACT—In temperate zone avian species, female song is typically less common and structurally complex than male song. Although anecdotal accounts suggest that female House Finch (*Haemorhous mexicanus*) song is less complex, it has never been compared quantitatively with male song. We analyzed songs from 2 House Finch populations in southern New York to investigate the degree of sexual dimorphism in complexity, as measured by concavity, frequency excursion, and length of song. We found that, although females sing at a significantly higher mean frequency and lower bandwidth, there is no significant sex difference in the structural complexity of song. Future research should investigate whether female House Finch song has an unrecognized function, or whether the retention of complexity is a byproduct of selection on a correlated trait. *Received 28 October 2019. Accepted 16 March 2021.*

Key words: Carpodacus, female song, Fringillidae, sexual dimorphism, vocal communication.

El canto femenino puede ser tan largo y complejo como el canto masculino en los Haemorhous mexicanus

RESUMEN (Spanish)—En especies de aves de la región templada, el canto de las hembras es típicamente menos común y estructuralmente complejo que el canto de los machos. Aunque reportes anecdóticos sugieren que el canto de la hembra del gorrión *Haemorhous mexicanus* es menos complejo, éste nunca ha sido comparado cuantitativamente con el de los machos. Analizamos los cantos de 2 poblaciones de estos gorriones en el sur de Nueva York para investigar el grado de dimorfismo sexual en complejidad, medida en términos de concavidad, frecuencia de excursión y longitud de canto. Encontramos que, aunque las hembras cantan a una frecuencia significativamente más alta y a una amplitud de banda más baja, no hay diferencia significativa en la complejidad estructural del canto. Futuras investigaciones deben investigar si el canto de las hembras de este gorrión tiene una función no reconocida o si la retención de esta complejidad es consecuencia de la selección en una característica correlacionada.

Palabras clave: canto de hembras, Carpodacus, comunicación vocal, dimorfismo sexual, Fringillidae.

Female bird song is an intriguing and challenging phenomenon in contemporary ornithology. Although singing in both sexes is apparently the ancestral state in oscine birds (Odom et al. 2014), the incidence of female song decreases within clades with shifts from tropical to temperate ranges (Price et al. 2009). Indeed, female song in temperate birds (which include the most extensively studied species) has been considered the exception rather than the rule. Also, sexual selection theory has been more readily and successfully employed to explain male than female song, whether the selection is intrasexual (competition) or intersexual (choice), and whether the expected benefits to receivers of attending to song are indirect (e.g., mate quality) or direct (resources) (Falls 1998, Nowicki et al. 1998, Catchpole and Slater 2008). Female song has thus been

Despite the traditional focus on sexual selection on males, male and female song might share the same adaptive functions in some cases, such as territorial defense or mate attraction. However, if the traditional adaptive functions of bird song are less applicable to females than males, then female song might not exhibit the same parameters we expect for a male of the same species. For instance, in birds with complex songs, the degree of complexity in male song can be an honest signal of neural development and has frequently been found to be under sexual selection (Nowicki et al. 1998, DeVoogd 2004). In such a species, if males do not attend to female song complexity as females do to male song, we might expect female

understudied historically (Garamszegi et al. 2007, Krieg and Getty 2016). This situation has been changing in recent decades with an increased study of tropical and southern hemisphere birds, many of which duet (Hall 2004), and with increased understanding of how female song functions (Langmore 1998). A better understanding of the evolution and function of bird song depends on continued documentation of female song, particularly in the temperate zone where it is less common and might be overlooked.

¹ Department of Biology, Queens College, City University of New York, New York, NY, USA

² Department of Biological Sciences and Graduate School of Arts and Sciences, Fordham University, New York, NY, USA

³ The Graduate Center, City University of New York, New York, NY, USA

[†] Deceased

^{*} Corresponding author: david.lahti@qc.cuny.edu

song to be less complex than male song. This relationship has in fact been reported (Garamszegi et al. 2007), particularly in temperate species. Males may have longer songs and more syllable types (Langmore et al. 1996, Cain and Langmore 2015), more complex syllables (Pavlova et al. 2005), or more song-types in their repertoires (Sethi et al. 2012) than females do.

Here we test the hypothesis that male song is more complex than female song by comparing male and female songs in the House Finch (Haemorhous mexicanus). The House Finch is a gregarious, partially migratory, socially monogamous species native to the Southwest of North America, particularly California and Mexico (Moore 1939, Badyaev et al. 2020). The species was introduced to the temperate East Coast of the United States and has since spread throughout much of the country. House Finches socially learn their songs (Mundinger 1975, Mann et al. 2021). They are not considered territorial, so males do not appear to use song for the purpose of territory defense (Thompson 1960, but see Ciaburri and Williams 2019). House Finch song is composed of a variety of syllables rapidly delivered over the course of 2 or more seconds with little repetition (Mundinger 1975, Ju et al. 2019). The complexity of this song, perhaps in terms of the number of syllables or the overall length, seems to predict mate choice (Nolan and Hill 2004, Mennill et al. 2006, Ciaburri and Williams 2019).

Female song in the House Finch has been documented but is thought to be uncommon. Females have been observed to sing the same song types as the males in their neighborhood, and to produce mating solicitation calls immediately before their songs (Mundinger 1975). Female song in this species is associated with intense solicitation of courtship feeding and copulation, and then recurs at the end of incubation (Mundinger 1975, Bitterbaum and Baptista 1979), although females have also been observed singing when alone (Thompson 1960). The structure of female song in House Finches has been described as "simple" and "incomplete" (Thompson 1960). Another study, which used testosterone treatments to induce female singing behavior, concluded that females had fewer song types in their repertoires than males did, but that the structure of female song could be either simpler than or similar to typical male song, depending on the female (Bitterbaum and Baptista 1979). However, no previous study has quantitatively described female song in this species.

Considering prior observations of female House Finch song and the general pattern of diminishing of female song in temperate songbird lineages, we hypothesized that female song would be less complex than male song in this species. We compared male and female House Finch song, and particularly looked for differences in several measures of complexity in a song: the number of syllables, the number of unique syllable types, the changes in concavity in frequency-time space (Ju et al. 2019), and the length of the frequency-time excursion (Ju 2015, Podos et al. 2016). Since studies in other birds have found differences in frequency parameters between male and female songs (Mennill and Vehrencamp 2005, Koloff and Mennill 2013, Fishbein et al. 2018), we also compared frequency and bandwidth. We analyzed songs recorded in the mid-1970s from 2 House Finch populations in southern New York state.

Methods

Recordings

We selected House Finch songs from digitized field recordings collected by Paul Mundinger (PM). All individuals were visually identified during recording. Females were identified by plumage as well as their soliciting behavior associated with singing, which was never seen in males (as in Mundinger 1975); PM verbally reported these identifications in the original audio streams of the recordings. The songs used were from 5 males and 4 females in Rye, Westchester County, New York, in April 1974, and 5 males and 5 females in Nassau County, Long Island, New York, in June 1975. Examples of both female and male song can be seen in Figure 1. For a map showing the geographic distribution of the individuals, see Supplemental Figure S1. We used data collected from nearby locations within a 2 year period to avoid effects of temporal and spatial variation in song (Mundinger 1975). The number of recorded songs per individual ranged from 3 to 28 ($\bar{x} = 10.26$, SD = 7.078). In total, we analyzed 195 songs (F = 49, M = 146) from 19 individuals (F = 9, M = 10). Each individual was dummy coded by a third party so that we were blind to the sex and location of the singer during analysis. Our

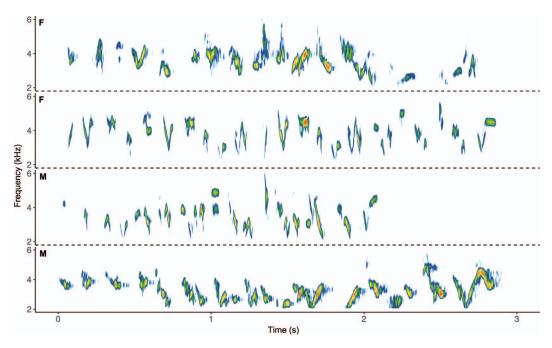


Figure 1. Sample spectrograms of songs from 2 female (top 2 rows) and 2 male (bottom 2 rows) House Finches from southern New York. Time in seconds is on the *x*-axis, and frequency in kHz is on the *y*-axis. The warmth of the color of the signal corresponds to relative amplitude (dB).

data most likely do not comprise full song repertoires, especially of individuals represented by only a few songs (Mundinger 1975, Ju et al. 2019).

PM used a Nagra III reel-to-reel tape recorder (9.5 cm/s) and Sennheiser 804 shotgun microphone to record the birds. In 2013, the Cornell Laboratory of Ornithology's Macaulay Library of Natural Sounds cleaned and repaired these tapes and converted the recordings to an uncompressed digital format (PCM 32-bit float, 96 kHz sample rate), while correcting for tape speed and other irregularities. We parsed the House Finch songs from the audio stream visually and cleaned them using Audacity 2.1.0 (Audacity Team 2020). Cleaning involved a high-pass filtered at 2 kHz with a 48 dB/octave roll-off, and noise reduction using an FFT and spectral noise gating algorithm. In cases where heterospecific vocalizations appeared in the recording but did not overlap in frequency with House Finch song (n = 24), we removed them using spectral editing in Raven 1.3 (Center for Conservation Bioacoustics 2011).

Acoustic parameters and syllable classification

Following concealment of the sex of the individuals, one of us (AK) visually inspected

the spectrographs for distinctive syllables or phrases, with the intention of comparing their incidence between the sexes. We especially aimed to keep account of the long broadband "terminal buzzes" that are typical of the species, as we thought these might be more common in males than in females. In the process we revised this terminology because our data contained 2 protracted buzzy syllable types: a flat or slightly upticked type, and a shorter, narrower downward type, neither of which was always terminal (Fig. 2).

We analyzed the songs in FinchCatcher (Ju 2015), a program developed for analyzing House Finch song that automates feature extraction to characterize syllables (as in Ju et al. 2019, Mann et al. 2021). We set the program to extract the following parameters for each song across all syllables: (1) mean frequency, (2) bandwidth, (3) concavity, (4) frequency excursion, (5) length, and (6) number of unique syllables. Concavity is the number of changes per time in the sign of the slope of frequency change of the spectrographic trace, i.e., the number of critical points in the derivative of the signal (Ju et al. 2019). Excursion is the total

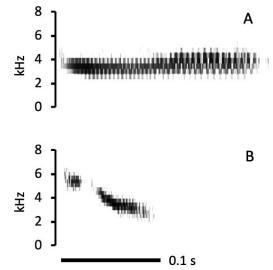


Figure 2. Examples of the 2 long buzz types of House Finches found in our dataset: (A) flat type and (B) downward type. Males sang these more often than females, and males sang the flat type more often than the downward type.

path length of a signal in the frequency and time domains (Ju 2015, Podos et al. 2016, Ju et al. 2019). We measured song length in both numbers of syllables and time in seconds. However, these values correlated so heavily (R = 0.48, P = 0.038) that we included only one of these values in subsequent analyses. We ran the analyses both ways and found no differences in the results. Here we present the results with song length measured in time. To generate individual-level parameters for the statistical analysis, we averaged each songlevel parameter across all of the songs recorded from each individual, for all parameters except for minimum and maximum frequency; these were calculated from the minimum and maximum frequency across all of the songs recorded from each individual. Parameter values were averaged to correct for variation in the number of songs collected from each individual (e.g., rare syllables from more heavily sampled birds could inflate bandwidth).

Syllables from all analyzed songs were classified using the *dynamicTreeCut* package in R 1.63–1 (Langfelder et al. 2016). This uses the unweighted pair group method with arithmetic mean (UPGMA) clustering to classify syllables based on their start frequency, end frequency,

mean frequency, highest frequency, lowest frequency, bandwidth, duration, excursion, mean slope, and concavity. Hybrid adaptive tree cut was used to identify clusters in the resulting dendrogram (cluster height = 3, minimum cluster size = 5, maximum scatter of core for cluster = 1, minimum cluster gap = 0.5) and revealed 225 syllable types across all of the recordings (see Supplemental Fig. S2).

Statistical analyses

In order to identify which variables were predictive of sex, we conducted Bayesian logistic regression using Markov chain Monte Carlo (MCMC) simulations in the rstanarm package in R 2.17.4 (Goodrich et al. 2018). Bayesian methods were used instead of traditional logistic regression because of the separation issues that can result from low sample sizes. Mean frequency, bandwidth, concavity, excursion, song length, and unique syllables were the predictor variables, and sex was the outcome variable. The default, weakly informative prior probability distributions were used for the intercept (normal, location = 0, scale = 10) and all parameters (normal, location = 0, scale = 2.5) (Goodrich et al. 2018). The default scale for each parameter was adjusted by rstanarm to match its range (see Supplemental Table S1). The analysis was conducted with 4 MCMC chains of 5,000 iterations each, after a warm-up period of the same length. Effects were considered statistically significant if the 95% highest posterior density interval (HDPI) did not include zero. Several post hoc tests were also conducted to aid in the interpretation of the main effects of the Bayesian logistic regression.

All analyses were conducted in R 3.4.4 (R Core Team 2014). Sample songs, raw data, R scripts, and cluster results have been deposited in the Harvard Dataverse (https://dataverse.harvard.edu/dataset.xhtml?persistentId=doi:10.7910/DVN/00PDOV).

Results

Both male and female House Finches sang long complex warbles, with features summarized in Table 1. Females and males differed the most in mean frequency, with females singing at a higher frequency. In all other parameters, including those

Table 1. Means and standard deviations for acoustic parameters of female and male House Finch songs recorded in southern New York, by individual. Mean frequency, minimum frequency, maximum frequency, and bandwidth are measured in Hz. Song length in time is measured in seconds. Excursion is the total path length in the frequency (Hz) and time (s) domains. The SD of minimum frequency was 0 due to the 187.5 Hz frequency resolution (96 kHz sample rate divided by 512 FFT size).

	Females $(n = 9)$ Males $(n = 10)$ mean (SD)	
Avg freq	3814.82 (206.48)	3529.06 (153.67)
Min freq	2125.00 (93.75)	2062.50 (0)
Max freq	5666.67 (395.28)	6168.75 (503.50)
Bandwidth	2867.95 (361.30)	3287.55 (531.70)
Concavity	20.07 (5.67)	17.15 (3.00)
Excursion	661.55 (126.02)	553.63 (176.14)
Song length (Time)	2.17 (0.83)	2.41 (0.41)
Song length (Syls)	15.48 (5.19)	21.17 (6.90)
Unique syls	11.78 (3.43)	13.79 (2.33)

related to frequency, song length (in syllables or time), or complexity (concavity, excursion, or unique syllables in a song), the males and females overlapped substantially, such that one standard deviation from the male mean encompassed the female mean. Long buzzy (atonal, broadband) syllables are distinctive in House Finch song, and are often noticed at the end of songs.

In our dataset, of a total of 49 songs sung by 9 females, 5 (10%) had 1 buzz each, sung by 2 of the 9 individuals. Of a total of 146 songs sung by 10 males, 55 (38%) had buzzes, including 20 songs with more than 1; 9 out of 10 males sang songs with buzzes. Male buzzes were usually (71/88, 81%) of the long flat type, with the remainder being of the downward type (17/88, 19%), whereas all female buzzes were of the downward type (Fig. 2). Although appearing generally toward the end of a song, buzzes were only terminal 40% of the time in male songs (35/88). Of the 5 female buzzes documented, 1 was terminal.

The posterior distributions for the Bayesian logistic regression can be seen in Figure 3. Positive effects indicate that a parameter predicts an individual is female, whereas negative effects indicate that a parameter predicts an individual is male. Based on the positive upper and lower bounds of its 95% HDPI, mean frequency was a significant positive predictor of sex (median = 0.0165; 95% HDPI: [0.0049, 0.0308]; Fig. 3),

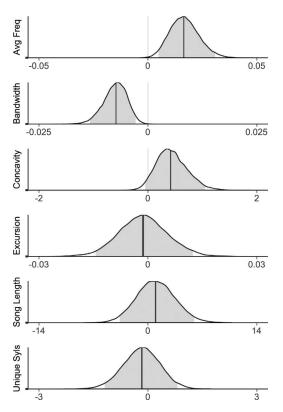


Figure 3. The posterior distributions for each acoustic parameter in a Bayesian logistic regression of male and female House Finch songs from southern New York. Each distribution is drawn from 4 MCMC chains of 5,000 iterations each (after warm-up). The x-axis corresponds to the model estimate and the y-axis corresponds to the density of probability. The direction of the model estimate corresponds to the influence of that parameter on the outcome variable (sex). Positive estimates (to the right) predict that an individual is female, whereas negative model estimates (to the left) predict that an individual is male. The dark centered lines indicate median point estimates, while the lighter shaded areas indicate the 95% HDPI. Effects were considered statistically significant if the 95% highest posterior density interval (HDPI) did not include zero. In this case, mean frequency significantly predicted that an individual was female, while bandwidth significantly predicted that an individual was male.

indicating that females may sing at a higher mean frequency. Conversely, bandwidth was a significant negative predictor of sex (median = -0.0073; 95% HDPI: [-0.0133, -0.0028]; Fig. 3), indicating that males may sing with a higher frequency bandwidth. Concavity, excursion, song length, and unique syllables were not significant predictors of sex (Table 2 and Fig. 3), although concavity

Table 2. The median point estimate, odds ratio, upper and lower bounds of the 95% HDPI, effective posterior sample size (ESS), and \hat{R} , for each acoustic parameter in a Bayesian logistic regression of the songs of male and female House Finches from southern New York. The estimate indicates the direction of the effect, which is only significant if the 95% interval does not include 0 (asterisks). The odds ratio (OR) indicates how a unit increase in the parameter changes the odds that the individual is male (OR < 1) or female (OR > 1). For example, for each unit increase in mean frequency, the odds that the individual is female increase by 1.65%. In all cases the ESS is above 1000 and \hat{R} is close to 1, indicating sufficient independent samples and convergence.

		Bayesian logistic regression					
	Estimate	OR	2.5%	97.5%	ESS	Ŕ	
Avg freq*	0.0165	1.0166	0.0049	0.0308	13,597	1	
Bandwidth*	-0.0073	0.9927	-0.0133	-0.0028	13,155	1	
Concavity	0.4162	1.5162	-0.049	1.0468	14,708	1	
Excursion	-0.0012	0.9987	-0.0144	0.0124	16,505	1	
Song length	0.9833	2.6733	-3.6248	5.9488	12,645	1	
Unique syls	-0.1673	0.8459	-1.1892	0.8092	12,451	1	

trended toward a positive effect, suggesting concavity might be higher in female song. Independent samples t-tests indicated that, although males and females do not differ in minimum frequency (t = -2, df = 8, P = 0.08), males have a higher maximum frequency than females (t = 2.43, df = 16.72, P < 0.05). An additional independent samples t-test indicated that syllable rate (syllables per second) is not significantly different between males and females (t = 1.34, df = 12.17, P = 0.20).

Diagnostic variables for the Bayesian logistic regression can be seen in Table 2. For all parameters the effective posterior sample size (ESS) is >1,000 and \hat{R} is close to 1, indicating sufficiently independent samples and that the 4 MCMC chains have converged. For visual diagnostics of the Bayesian logistic regression, see Supplemental Figure S3–S5.

Discussion

We characterized female song in the House Finch, hypothesizing that it would be less complex than male song. Specifically, we investigated whether female songs were shorter, had fewer unique syllables per song, or were less convoluted in terms of concavity or excursion in frequency—time space. The results did not support our hypothesis. Instead, we found little evidence of sexual dimorphism in any aspects of song complexity. This is puzzling, as female song output is low in natural contexts. The reasons female songs should be as complex as the much

more frequent songs of males is not obvious, and challenges views on song complexity that have been based primarily on studies of males.

The female House Finches in our sample sang at a higher mean frequency than the males. This effect has been found in several other species, including Rufous-and-white Wrens (Thryothorus rufalbus; Mennill and Vehrencamp 2005), Rufousnaped Wrens (Campylorhynchus rufinucha; Bradley and Mennill 2009), Barred Antshrikes (Thamnophilus doliatus; Koloff and Mennill 2013), and Chestnut-backed Antshrikes (Thamnophilus palliatus; Fishbein et al. 2018). The difference may simply reflect difference in body size between males and females (Ryan and Brenowitz 1985), as females are smaller in this species (Badyaev and Martin 2000). This frequency difference could also be a result of sexual dimorphism of bill structure (Podos and Nowicki 2004, Giraudeau et al. 2014). Male House Finch song also appears to exhibit higher frequency bandwidth than female song. Frequency bandwidth for a given syllable repetition rate has often been considered a proxy for vocal performance, of potential relevance to sexual selection (Podos 1997, Podos et al. 2009). Alternatively, such frequency differences may communicate the singer's sex. Several passerines, such as Black-bellied Wrens (Pheugopedius fasciatoventris; Logue et al. 2007), Black-capped Chickadees (Poecile atricapillus; Hahn et al. 2013), and Northern Cardinals (Cardinalis cardinalis; Yamaguchi 1998), have sexually dimorphic structural differences in their songs that communicate sex and identity to conspecifics without

necessarily differing in structural complexity. The frequency-related differences we observed in song are not likely to be caused by dimorphism in auditory sensitivity, which is similar in male and female House Finches, and more variable within than between the sexes at all frequencies (table 1 in Dooling 1978). Finally, males were much more likely than females to sing the long buzzy notes (either flat or downward) that are commonly recognized as part of House Finch song; the function or communicative value of these syllables is unknown. These differences do not exhaust the possibilities for sexual dimorphism in male and female song; a more expansive study of features at the syllable, song, and repertoire levels might reveal additional differences.

This study faced a number of limitations that affect our interpretation of the results. We were restricted in the number of female individuals for which song data could be found, due to the elusiveness of female song behavior in this species. We were also unable to test amplitude in this study, due to the lack of microphone calibration and varying distances from the subjects. Song amplitude may relate to function. Songs used for intrapair communication are directed at the mate alone, and therefore may tend to be low-amplitude for discreet short-distance transmission (Barker et al. 2009), especially to avoid drawing the attention of predators or brood parasites (Kleindorfer et al. 2016). In contrast, songs defending mates and territories are more likely to be conspicuous, higher-amplitude signals (Sogge et al. 2007, Illes and Yunes-Jimenez 2009). Because many more male songs could be used in our study than female songs, we could not accurately assess sexual dimorphism in repertoire size. These questions could have been addressed if more female songs recorded per bird were usable. House Finches are known to share at least some of their syllables in sequence between the sexes (Mundinger 1975), and laboratory studies on testosterone-implanted California House Finch females found females to have smaller repertoires of song types than males (Bitterbaum and Baptista 1979).

The lingering question is why female House Finches sing. This question is intensified by the finding that their songs are as complex as those of males in our sample. The 3 general possibilities are that it is a relict (holdover from ancestors in which

it was adaptive), a byproduct (maintained indirectly by selection on correlated traits of the other sex), or adaptive (currently functional). The relict hypothesis is plausible for 2 reasons. First, the range of the House Finch extends into the tropics, where it may have originated (Wang et al. 2003), and where female bird song is more typical. Second, females in the House Finch's only 2 congeners (Purple Finch [Haemorhous purpurea] and Cassin's Finch [H. cassinii]) have been reported to sing as well (Stratton 1967 and Hahn 1996, respectively). Hahn (1996) reports both a personal observation and a reference to Samson (1978) for female song in Cassin's Finch. However, neither Samson (1978) nor any other publication by that author cited in Hahn (1996) mentions female song in this species. The claim here is therefore based solely on Hahn's personal observation. However, the relict hypothesis might be difficult to test: *Haemorhous* is a clade about 10 million years old (Smith et al. 2013) and is sister to a large cardueline assemblage of dozens of species (Zuccon et al. 2012).

The byproduct hypothesis would posit that if female House Finches evaluate and even recognize males on the basis of song, as appears to be the case (Mundinger 1975, Nolan and Hill 2004, Mennill et al. 2006, Ciaburri and Williams 2019), then they probably engage in song learning to some extent. In fact, we do know from an experimental lab study that female House Finches learn songs for production (Mann et al. 2021). Female production of song might involve a relatively minor physiological adjustment that evolved for another function. For example, female testosterone levels might have increased due to selection for dominance over males (Thompson 1960), or for intraspecific competition, which incidentally triggered female song. Another possibility is that dominance interactions among males have led to high testosterone, and female testosterone became high as a consequence (Ketterson et al. 2005), either merely as a byproduct or to increase testosterone investment in eggs to enhance male offspring dominance.

The third general possibility, that female song is adaptive in House Finches, was favored by the 2 previous studies that considered this question (Mundinger 1975, Bitterbaum and Baptista 1979). The function proposed by those authors is intrapair communication for the purposes of

individual recognition and maintenance of the pair bond, based mostly on the context within which females tended to sing: in the presence of their mates and while physically oriented toward them (Mundinger 1975). Likewise, PM observed during recording of the data presented here that female song occurred usually, but not always, in the presence of a male, usually the mate. Both in this study and in Mundinger (1975), females were observed commonly soliciting males for courtship feeding and copulation. Furthermore, female House Finch song has been observed alongside male song in volleys, if not quite duets (F. Geller, pers. comm. 2016). Bitterbaum and Baptista (1979) additionally proposed that female song learning enables matching of her song to that of her mate for recognition and pair-bonding functions, following Mundinger's (1970) discovery of this phenomenon in 2 other cardueline finches. The use of female vocalizations for intrapair communication in the service of pair bonding has been documented in other species, such as Eastern Bluebird (Sialia sialis; Rose et al. 2019), Blackheaded Grosbeak (Pheucticus melanocephalus; Ritchison 1983), Red-winged Blackbird (Agelaius phoeniceus; Beletsky and Orians 1985), Northern Cardinal (Ritchison 1986, Halkin 1997, Vondrasek 2006), and Cuban Grassquits (Tiaris canorus; Baptista 1978).

Regardless of functional considerations, the facts remain that House Finch females sing, and that although female song is rarer than male song, when they do sing, their songs can be as long and as complex as those of males. Females in both congeners apparently sing as well, but no research has been performed on those phenomena. This situation highlights the importance of looking and listening for female birdsong as an elusive and often overlooked behavior in the temperate zone that might challenge established views on birdsong complexity.

Acknowledgments

We are grateful for the present and past members of the Lahti Lab for ideas and critique, especially B. Habig, A. Richards, D. Mann, F. Geller, W. Castillo, E. Roginek, and student researchers on the House Finch cultural evolution project. C. Ju developed the FinchCatcher software. Cornell Laboratory of Ornithology's Macaulay Library of Natural Sounds digitized the original analog recordings. Funding for this project was provided by the Queens College Foundation's Mundinger Biology Fund.

Literature cited

- Audacity Team. 2020. Audacity: Free audio editor and recorder. Version 2.1.0. https://audacityteam.org/
- Badyaev AV, Belloni V, Hill GE. 2020. House Finch (Haemorhous mexicanus), version 1.0. In: Poole AF, editor. Birds of the world. Ithaca (NY): Cornell Lab of Ornithology. https://doi.org/10.2173/bow.houfin.01
- Badyaev AV, Martin TE. 2000. Sexual dimorphism in relation to current selection in the House Finch. Evolution. 54:987–997.
- Baptista LF. 1978. Territorial, courtship and duet songs of the Cuban Grassquit (*Tiaris canora*). Journal für Ornithologie. 119:91–101.
- Barker NKS, Dabelsteen T, Mennill DJ. 2009. Degradation of male and female Rufous-and-white Wren songs in a tropical forest: Effects of sex, perch height, and habitat. Behaviour. 146:1093–1122.
- Beletsky LD, Orians GH. 1985. Nest-associated vocalizations of female Red-winged Blackbirds, *Agelaius phoeniceus*. Ethology. 69:329–339.
- Bitterbaum E, Baptista LF. 1979. Geographical variation in songs of California House Finches (*Carpodacus mexicanus*). Auk. 96:462–474.
- Bradley DW, Mennill DJ. 2009. Solos, duets and choruses: Vocal behaviour of the Rufous-naped Wren (Campylo-rhynchus rufinucha), a cooperatively breeding Neotropical songbird. Journal of Ornithology. 150:743–753.
- Cain KE, Langmore NE. 2015. Female and male song rates across breeding stage: Testing for sexual and nonsexual functions of female song. Animal Behaviour. 109:65– 71.
- Catchpole CK, Slater PJP. 2008. Bird song: Biological themes and variations. Cambridge (UK): Cambridge University Press.
- Center for Conservation Bioacoustics. 2011. Raven Pro: Interactive sound analysis software. Version 1.3. Ithaca (NY): Cornell Lab of Ornithology. http:// ravensoundsoftware.com/
- Ciaburri I, Williams H. 2019. Context-dependent variation of House Finch song syntax. Animal Behaviour. 147:33–42.
- DeVoogd T. 2004. Neural constraints on the complexity of avian song. Brain, Behavior, & Evolution. 63:221– 232.
- Dooling R. 1978 Behavior and psychophysics of hearing in birds. Journal of the Acoustical Society of America. 64:S4. https://doi.org/10.1121/1.2004237
- Falls JB. 1988. Does song deter territorial intrusion in White-throated Sparrows (*Zonotrichia albicollis*)? Canadian Journal of Zoology. 66:206–211.
- Fishbein AR, Löschner J, Mallon JM, Wilkinson GS. 2018. Dynamic sex-specific responses to synthetic songs in a duetting suboscine passerine. PLOS One. 13:e0202353.
- Garamszegi LL, Pavlova D, Eens M, Møller AP. 2007. The evolution of song in female birds in Europe. Behavioral Ecology. 18:86–96.
- Giraudeau M, Nolan PM, Black CE, Earl SR, Hasegawa M, McGraw KJ. 2014. Song characteristics track bill

- morphology along a gradient of urbanization in House Finches (*Haemorhous mexicanus*). Frontiers in Zoology. 11:83.
- Goodrich B, Gabry J, Ali I, Brilleman S. 2018. rstanarm: Bayesian applied regression modeling via Stan. R package version 2.17.4. http://mc-stan.org/
- Hahn AH, Krysler A, Sturdy CB. 2013. Female song in Black-capped Chickadees (*Poecile atricapillus*): Acoustic song features that contain individual identity information and sex differences. Behavioural Processes. 98:98–105.
- Hahn TP. 1996. Cassin's Finch (Haemorhous cassinii), version 2.0. In: Poole AF, Gill FB, editors. Birds of North America. Ithaca (NY): Cornell Lab of Ornithology. https://doi.org/10.2173/bna.240
- Halkin SL. 1997. Nest-vicinity song exchanges may coordinate biparental care of Northern Cardinals. Animal Behaviour. 54:189–198.
- Hall ML. 2004. A review of hypotheses for the functions of avian duetting. Behavioral Ecology and Sociobiology. 55:415–430.
- Illes AE, Yunes-Jimenez L. 2009. A female songbird outsings male conspecifics during simulated territorial intrusions. Proceedings of Royal Society B. 276:981– 986
- Ju C. 2015. Cultural evolution in natural populations: A quantitative bioacoustic analysis [dissertation]. New York (NY): City University of New York. https:// academicworks.cuny.edu/gc_etds/1000
- Ju C, Geller FC, Mundinger PC, Lahti DC. 2019. Four decades of cultural evolution in House Finch songs. Auk: Ornithological Advances. 136:uky012.
- Ketterson ED, Nolan V Jr, Sandell M. 2005. Testosterone in females: Mediator of adaptive traits, constraint on sexual dimorphism, or both? American Naturalist. 166:S85–S98.
- Kleindorfer S, Evans C, Mahr K. 2016. Female in-nest chatter song increases predation. Biology Letters. 12:20150513.
- Koloff J, Mennill DJ. 2013. Vocal behaviour of Barred Antshrikes, a Neotropical duetting suboscine bird. Journal of Ornithology. 154:51–61.
- Krieg CA, Getty T. 2016. Not just for males: Females use song against male and female rivals in a temperate zone songbird. Animal Behaviour. 113:39–47.
- Langfelder P, Zhang B, Horvath S. 2016. dynamicTreeCut:

 Methods for detection of clusters in hierarchical clustering dendrograms. R package version 1.63–1.

 https://CRAN.R-project.org/package=dynamicTreeCut
- Langmore NE. 1998. Functions of duet and solo songs of female birds. Trends in Ecology and Evolution. 13:136–140.
- Langmore NE, Davies NB, Hatchwell BJ, Hartley IR. 1996.
 Female song attracts males in Alpine Accentor *Prunella collaris*. Proceedings of the Royal Society. 263:141–146.
- Logue DM, Droessler EE, Roscoe DW, Vokey JR, Rendall D, Kunimoto RM. 2007. Sexually antithetical song structure in a duet singing wren. Behaviour. 144:331– 350.

- Mann DC, Lahti DC, Waddick L, Mundinger PC. 2021. House Finches learn canary trills. Bioacoustics. 30:215–231.
- Mennill DJ, Badyaev AV, Jonart LM, Hill GE. 2006. Male House Finches with elaborate songs have higher reproductive performance. Ethology. 112:174–180.
- Mennill DJ, Vehrencamp SL. 2005. Sex differences in singing and duetting behavior of Neotropical Rufousand-white Wrens (*Thryothorus rufalbus*). Auk. 122:175–186.
- Moore RT. 1939. A review of the House Finches of the subgenus *Burrica*. Condor. 41:177–205.
- Mundinger PC. 1970. Vocal imitation and individual recognition of finch calls. Science. 168:480–482.
- Mundinger PC. 1975. Song dialects and colonization in the House Finch, *Carpodacus mexicanus*, on the East Coast. Condor. 77:407–422.
- Nolan PM, Hill GE. 2004. Female choice for song characteristics in the House Finch. Animal Behaviour. 67:403–410
- Nowicki S, Peters S, Podos J. 1998. Song learning, early nutrition and sexual selection in songbirds. American Zoologist. 38:179–190.
- Odom KJ, Hall ML, Riebel K, Omland KE, Langmore NE. 2014. Female song is widespread and ancestral in songbirds. Nature Communications. 5:3379.
- Pavlova D, Pinxton R, Eens M. 2005. Female song in European Starlings: Sex differences, complexity, and composition. Condor. 107:559–569.
- Podos J. 1997. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). Evolution. 51:537–551.
- Podos J, Lahti DC, Moseley DL. 2009. Vocal performance and sensorimotor learning in songbirds. Advances in the Study of Behavior. 40:159–195.
- Podos J, Moseley DL, Goodwin SE, McClure J, Taft BN, et al. 2016. A fine-scale, broadly applicable index of vocal performance: Frequency excursion. Animal Behaviour. 116:203–212.
- Podos J, Nowicki S. 2004. Beaks, adaptation, and vocal evolution in Darwin's finches. BioScience. 54:501– 510.
- Price JJ, Lanyon SM, Omland KE. 2009. Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. Proceedings of the Royal Society. 276(1664):1971–1980.
- R Core Team. 2014. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. http://www.R-project.org/
- Ritchison G. 1983. The function of singing in female Black-headed Grosbeaks: Family group maintenance. Auk. 100:105–116.
- Ritchison G. 1986. The singing behavior of female Northern Cardinals. Condor. 88:156–159.
- Rose EM, Cross DA, Haines CD, Danquah SA, Studds CE, Omland KE. 2019. Why do females sing? – Pair communication and other song functions in Eastern Bluebirds. Behavioral Ecology. 30:1653–1661.
- Ryan MJ, Brenowitz EA. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. American Naturalist. 126:87–100.

- Samson FB. 1978. Vocalizations of Cassin's Finch in northern Utah. Condor. 80:203–210.
- Sethi VK, Bhatt D, Kumar A. 2012. Structure and context of female song in a tropical bird, the Pied Bush Chat. Current Science. 103:827–832.
- Smith BT, Bryson RW Jr, Chua V, Africa L, Klicka J. 2013. Speciational history of North American *Haemorhous* finches (Aves: Fringillidae) inferred from multilocus data. Molecular Phylogenetics and Evolution. 66:1055–1059.
- Sogge MK, Koronkiewicz TJ, van Riper C, Durst SL. 2007. Willow Flycatcher nonbreeding territory defense behavior in Costa Rica. Condor. 109:475–480.
- Stratton L. 1967. Notes on nesting of Purple Finch at Oxford. Kingbird. 17:19.

- Thompson WL. 1960. Agonistic behavior in the House Finch. Part I: Annual cycle and display patterns. Condor. 62:245–271.
- Vondrasek JR. 2006. Social factors affect the singing rates of female Northern Cardinals *Cardinalis cardinalis*. Journal of Avian Biology. 37:52–57.
- Wang ZS, Baker AJ, Hill GE, Edwards SV. 2003. Reconciling actual and inferred population histories in the House Finch (*Carpodacus mexicanus*) by AFLP analysis. Evolution. 57:2852–2864.
- Yamaguchi A. 1998. A sexually dimorphic learned birdsong in the Northern Cardinal. Condor. 100:504–511.
- Zuccon D, Prys-Jones R, Rasmussen PC, Ericson PGP. 2012. Phylogenetic relationships and generic limits of finches (Fringillidae). Molecular Phylogenetics and Evolution. 62:581–596.

Copyright of Wilson Journal of Ornithology is the property of Wilson Ornithological Society and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.