

RESEARCH ARTICLE

Loss of complex female song but not duetting in the ancestors of Carolina wrens

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Abstract

Female singing and coordinated male–female duetting are often but not always found in the same species. Both behaviors are more common in tropical than temperate songbirds, but few studies have differentiated between the factors selecting for each. Here we investigate the evolution of female vocal complexity and male–female vocal coordination in Carolina wrens (*Thryothorus ludovicianus*), one of the few non-tropical members of a songbird family (Troglodytidae) that is well known for producing coordinated male–female duets. Female Carolina wrens are not known to sing; rather, they produce relatively simple, sex-specific chatters, often during territorial encounters. We analyzed field recordings to show that females coordinate these chatters with male songs at rates similar to those observed in some tropical duetting wren species. We then used phylogenetic comparative methods to show that the evolutionary ancestors of Carolina wrens had female songs that were more acoustically complex than the vocalizations of current females, suggesting past selection against female vocal complexity. Levels of vocal coordination with males, in contrast, have changed relatively little from those of tropical ancestors. Our results suggest that these two aspects of female behavior, acoustic complexity and vocal coordination with males, have evolved independently and have different functions in communication.

KEYWORDS

ancestral state, dimorphism, duet, female vocalizations, phylogeny, *Thryothorus ludovicianus*

1 | INTRODUCTION

Past studies of the use and evolution of passerine bird song have focused largely on males (Catchpole & Slater, 2008; Darwin, 1859). Recent research, however, has revealed that female singing is surprisingly widespread (Garamszegi et al., 2007; Odom et al., 2014; Odom & Benedict, 2018; Webb et al., 2016), especially among tropical songbird species (Slater & Mann, 2004; Stutchbury & Morton, 2001). Phylogenetic studies have further shown that females sang in the ancestors of all modern songbirds and that current differences in singing behavior between the sexes have generally evolved through past losses of complex song in females rather than gains in males (Odom et al., 2014; Price et al., 2009). Thus, the role of sexual selection and other factors in the evolution of bird

song appears more complicated than previously thought (Austin et al., 2021; Price, 2019; Rose et al., 2022).

Both males and females may produce solo songs, or they may combine their vocalizations to produce vocal duets (Langmore, 1998). Duetting is defined as the coordination of vocalizations by two individuals such that their elements alternate or overlap (Farabaugh, 1982; Hall, 2009). Studies of female singing behavior have frequently focused on species that perform coordinated male–female duets (reviewed by Hall, 2009), presumably in part because the existence of female song in these species is relatively obvious. Species in which both sexes sing typically have low levels of sexual dichromatism (Webb et al., 2016), making males and females difficult to distinguish, so female solo singers have frequently been mistaken for males (Odom & Benedict, 2018). Indeed, given this and

other potential biases (Austin et al., 2021; Haines et al., 2020; Rose et al., 2022), it is clear that female songbirds have been generally underrepresented in studies of avian vocal behavior.

Female singing and duetting are both more common in tropical than temperate songbird species (Slater & Mann, 2004; Stutchbury & Morton, 2001). Both behaviors are associated with life history characteristics that are relatively common in the tropics, such as long-term monogamy and defense of year-round territories, and they have been attributed to similar selection pressures (Hall, 2004; Langmore, 1998; Slater & Mann, 2004). Yet, female singing and male–female duetting are not equivalent, and they occur together in only a small subset of avian taxa (Hall, 2009; Mitchell et al., 2019; Odom et al., 2015). The males and females of many avian species produce complex solo songs without coordinating them (Odom et al., 2014; Price, 2009; Price et al., 2008), and a variety of taxa perform duets by combining vocalizations that are not generally considered songs (Benedict, 2008; Hall, 2009).

Only a handful of studies have directly compared the evolution of female song and duets. Odom et al. (2015) showed that duetting behavior has evolved multiple times in the New World blackbird family (Icteridae), but only in lineages where female song was already present, thus suggesting that female singing is a precursor for the evolution of vocal duets. Similarly, in a study of New World warblers (Parulidae), Mitchell et al. (2019) found that duetting has evolved multiple times and is frequently but not exclusively associated with female song. These patterns are consistent with other studies suggesting that the factors selecting for complex female song and for coordinated vocal duetting largely overlap but nevertheless are not the same (Hall, 2009; Keenan et al., 2020; Langmore, 1998; Logue & Hall, 2014; Price, 2009). Given that duetting has tended to evolve in species with female song (Odom et al., 2015), while female singing behavior has been lost repeatedly during the evolutionary history of songbirds (Odom et al., 2014; Price et al., 2009), should we expect duetting to be lost when complex female song is lost?

Here, we investigate the evolution of female vocal complexity and vocal coordination in Carolina wrens (*Thryothorus ludovicianus*), one of the few non-tropical members of the New World wren family (Troglodytidae). Neotropical wren species are well known for their highly coordinated duets (Keenan et al., 2020; Mann et al., 2009). In Carolina wrens, however, only males are reported to sing (Haggerty & Morton, 2020). Females produce relatively simple, sex-specific trills referred to as ‘chatters’ (Benedict, 2008; Haggerty & Morton, 2020), often during territorial encounters while their male mate is singing (Figure 1). Distinguishing songs and calls in a species can be problematic (Austin et al., 2021; Rose et al., 2022), especially for vocalizations like female chatters that appear to be used in the same contexts as male song. We refer to these vocalizations as chatters rather than songs or calls to avoid imposing this distinction. Haggerty and Morton (2020) noted that female chatters often overlap male song, though with no consistent timing. Shuler (1965) and Benedict (2008) referred to these overlapping vocalizations as a duet. Mann et al. (2009) described overlapping as occurring only rarely, and Keenan et al. (2020) did not categorize Carolina wrens

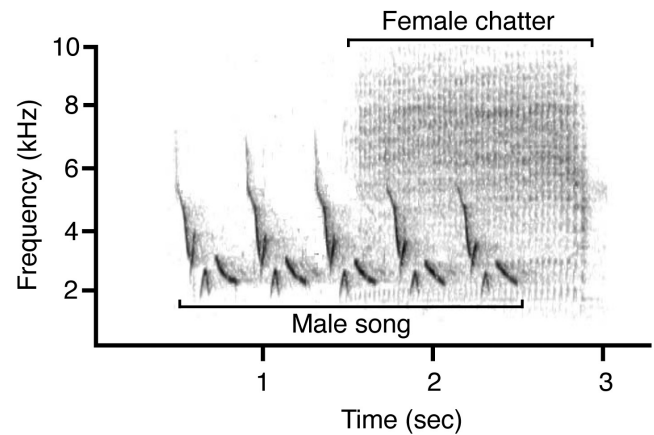


FIGURE 1 Spectrogram showing a male's song and a female's chatter. Female Carolina wrens overlap their mates' songs with their chatters more often than expected by chance. Recording courtesy of Dustin G. Reichard.

as a duetting species. Whether such vocal overlapping can be considered as an intentional duet is largely dependent upon whether it occurs more often than expected by chance (Masco et al., 2016); however, this possibility has not been previously tested.

We used two different approaches in our study. First, we collected field recordings of territorial Carolina wren pairs to test the hypothesis that males and females actively coordinate their vocalizations as a duet. Second, we included this information plus data from other wren species in a phylogenetic comparative analysis to reconstruct the evolution of female vocal complexity and duet coordination in the ancestors of Carolina wrens. These reconstructions addressed two main questions: (1) Did the ancestors of Carolina wrens lose complex female song, as in other songbird lineages (Odom et al., 2014), or do the simple chatters of current females represent an ancestral state during the evolution of more elaborate female vocalizations in other wren taxa? (2) Likewise, if Carolina wrens actively coordinate their vocalizations, did this behavior evolve recently or has it been retained from duetting wren ancestors? Addressing these questions is an important step towards understanding and discriminating between the functions of female vocal complexity and duetting in this and other songbird species.

2 | METHODS

2.1 | Vocal coordination in Carolina wrens

We recorded the vocalizations of nine territorial pairs of Carolina wrens on the campus of St. Mary's College of Maryland, St. Mary's City, MD (38.188°N, 76.426°W), and at North Point State Park, Edgemere, MD (39.232°N, 76.444°W), from October 2020 to March 2021 using a Marantz PMD 670 digital recorder and Sennheiser ME67 microphone. All recordings were conducted when pairs were active in the morning <2h after sunrise. Carolina wrens defended territories and vocalized year-round on

our study sites. Males and females are sexually monomorphic; however, although some sounds are produced by both sexes, only males are known to sing and only females chatter (Haggerty & Morton, 2020), so the sexes were easily distinguished in our recordings. We generated spectrograms using Raven Pro v1.65 (<http://www.birds.cornell.edu/brp/raven>), digitized at 48 kHz (frequency resolution = 135 Hz; time resolution = 10.7 ms).

To assess whether males and females actively overlapped their vocalizations more or less than expected by chance, we used the Song Overlap Null model Generator (SONG) package (Masco et al., 2016) implemented in R (<http://www.r-project.org/>). We selected 14 clear recordings for this analysis that had minimal background noise and that included multiple male songs and female chatters (mean \pm SE duration = 128.5 ± 18.4 s, male songs = 14.7 ± 1.6 , female chatters = 9.9 ± 1.0). For three male–female pairs, we analyzed 2–3 recordings each that had been made on different occasions. The SONG package uses resampling randomization to predict the expected levels of overlap due to chance, using the start and end times of each male and each female vocalization within each recording, which were then compared to observed levels of overlap to obtain a *p*-value. Following Masco et al. (2016), a low $p < .025$ indicated active overlapping, whereas a high $p > .975$ indicated the active avoidance of overlapping. Either of these outcomes could be considered evidence that pairs coordinate their vocalizations. These procedures had been used previously by Masco et al. (2016) to verify the presence of overlapping duetting in a tropical wren species, the rufous-and-white wren (*Thryophilus rufalbus*), allowing us to compare our results to theirs.

In the SONG package, a vocalization is considered to overlap another vocalization if it begins while the ‘reference’ vocalization is in progress (Masco et al., 2016). We ran analyses with male songs as the reference to test the hypothesis that females actively coordinate with males, and with female chatters as the reference to test whether males actively coordinate with females. We calculated effect sizes using Cohen's *W*. These analyses included four different resampling methods available in SONG: (1) SampleGaps, which randomizes the interval lengths between vocalizations; (2) KeepGaps, which randomizes the order of both vocalizations and intervals; (3) KeepSongOrder, which randomizes just the order of intervals; and (4) the Duty Cycle method of Ficken et al. (1974), in which the probability of overlap is determined simply by the proportion of time spent vocalizing (Masco et al., 2016). We categorized an interaction as overlapping or avoiding overlap if this was supported by at least two of these four analysis methods.

Finally, for each occurrence of vocal overlapping between the sexes, we noted whether the male or the female vocalization occurred first, and we tested whether this order differed from chance expectations using a X^2 test.

2.2 | Scoring female vocal characters

We collected information for our comparative analyses from species accounts in the Birds of the World database (Winkler et al., 2020) and

other published sources (e.g., Benedict, 2008; Keenan et al., 2020; Mann et al., 2009), and by examining spectrograms available at the Cornell Lab of Ornithology Macaulay Library (<https://www.macaulaylibrary.org/>). For each species, we scored two aspects of female vocalizations, vocal complexity and coordination with male song, as well as breeding latitude. We did not include taxa for which any of these characteristics were not clearly described and/or apparent in literature and spectrograms. Conversely, for house wrens (*Troglodytes aedon*), which are reported to exhibit a range of female vocal behaviors and occupy the broadest latitudinal range of any native New World passerine (Johnson, 2020), we assigned more than one score for vocal coordination and breeding latitude. Altogether, we scored the vocal behaviors of 42 wren species, including Carolina wrens. Character scores and source information are listed in Table S1.

Female vocal complexity was scored as (1) simple or (2) complex based on the number of different note types in a typical song or other similar vocalization (see below), based on spectrograms and detailed literature descriptions. In spectrograms, we classified any clearly defined units of a vocalization with similar frequency and temporal characteristics as being the same note type. Simple vocalizations had just one or two note types, usually repeated as a trill, whereas complex vocalizations included three or more note types. The songs of most wren species are easily recognized as stereotyped, frequently repeated vocalizations that are notably louder than their other sounds (Winkler et al., 2020). Whenever possible we focused on female vocalizations specifically described as ‘song’ in species accounts (Mann et al., 2009; Winkler et al., 2020). If no female song was described, we focused on vocalizations reported to be given in similar contexts (e.g., during territorial interactions) or recorded most frequently in females.

We scored vocal coordination between males and females as either (1) uncoordinated or (2) coordinated based on quantitative assessments of duet coordination conducted here and in previous studies (Hathcock & Benedict, 2018; Keenan et al., 2020; Masco et al., 2016) or based on written descriptions in the literature (e.g., Mann et al., 2009; Winkler et al., 2020). Species explicitly described as not duetting were scored as uncoordinated. Species described as duetting or regularly overlapping their territorial vocalizations were scored as coordinated. Duetting wren species vary considerably and seemingly continuously in their levels of male–female coordination and consistency (Keenan et al., 2020), from species that regularly but loosely overlap their songs (rufous-and-white wrens: Mennill & Vehrencamp, 2005) to species that perform antiphonal duets or choruses with exceptional levels of precision (plain-tailed wrens, *Pheugopedius euophrys*: Mann et al., 2006; Coleman et al., 2021). All these various forms of male–female duetting were scored as coordinated.

Finally, we scored breeding ranges of species as either (1) temperate or (2) tropical based on whether the majority (>80%) of their breeding ranges occurred above or below 23.5° north latitude (Winkler et al., 2020). House wrens were an exception, with multiple studies in both temperate and tropical regions (Johnson, 2020), so this species was scored as both temperate and tropical.

2.3 | Reconstructing ancestral character states

We reconstructed the evolution of female vocal characters in Mesquite v3.61 (Maddison & Maddison, 2019), using a molecular phylogeny of the 42 wren species generated as a majority rule consensus of 1000 randomly sampled phylogenies from Jetz et al. (2012). This tree corresponded to genus-level relationships reported by Barker (2017). We used two ancestral state reconstruction models to estimate ancestral characteristics, unordered parsimony and Markov k-state one-parameter maximum-likelihood, which allowed us to test the robustness of our results to different evolutionary assumptions. Parsimony is the simpler model, resolving discrete ancestral states that minimize the number of character changes. Maximum likelihood has advantages over parsimony in that it indicates degrees of uncertainty in possible ancestral states and uses branch lengths, reflecting levels of genetic divergence among taxa. Neither method allows more than one character score for any single taxon, so we divided house wrens into two closely related taxa in these evolutionary reconstructions.

We used both parsimony and maximum-likelihood methods to reconstruct evolutionary changes in female vocal complexity, vocal coordination between the sexes, and breeding latitude, focusing on the four nodes of the wren phylogeny that represented direct ancestors of Carolina wrens.

3 | RESULTS

In more than half of our recorded Carolina wren interactions (8 out of 14), female chatters overlapped the songs of their mates significantly more often than expected by chance ($p < .025$), supported by at least two randomization methods with males used as the reference (Table 1a). In each of the pairs that were sampled more than once (pairs 3, 4, and 5 in Table 1), males and females exhibited significant overlapping in some recordings but not in others, similar to rufous-and-white wrens (Masco et al., 2016). Thus, our analyses show that female Carolina wrens frequently, but not invariably, time their chatters non-randomly in coordination with the songs of their mates to form a duet (Figure 1).

When overlapping occurred, males typically led the interaction, with females beginning their chatters partway through the male song. In 95 recorded overlapping interactions, 82 (86.3%) involved the male vocalizing before the female, significantly more than expected by chance ($X^2 = 50.116$, two-tailed, $p < .001$), indicating that duets are typically created by females coordinating their vocalizations with males rather than the reverse. In the few cases in which a female chatter began before an overlapping male song, we observed the female abruptly stopping her vocalization as soon as the male's song began. Likewise, when female chatters were used as the reference in our randomization methods rather than male song (Table 1b), relatively high $p > .999$ indicated that males actively avoided beginning their songs during a female's chatter.

Evolutionary reconstructions showed that the ancestors of Carolina wrens had female vocalizations that were more acoustically complex than the simple chatters of current females (Figure 2a). Maximum-likelihood analyses reconstructed ancestral female vocalizations as relatively complex at all directly ancestral nodes on the tree (82%–90% likelihood), suggesting that female vocalizations diverged from male songs and became simpler in recent evolutionary ancestors. In contrast, levels of male–female vocal coordination appear to have changed relatively little from those of ancestral taxa (Figure 2b), with maximum-likelihood reconstructions strongly suggesting that recent ancestors performed coordinated vocal duets (98%–99% likelihood). Maximum-likelihood also suggested that the ancestors of Carolina wrens were tropical (81%–91% likelihood; Figure 2c).

Parsimony reconstructions agreed with maximum-likelihood in resolving ancestral taxa with coordinated male–female duets; however, parsimony did not resolve the ancestral states for female vocal complexity or breeding latitude in the direct ancestors of Carolina wrens. Reconstructions of all ancestral states are available in Figures S1–S3.

4 | DISCUSSION

Female Carolina wrens actively overlap their mates' songs with their chatters, supporting previous suggestions that these combined vocalizations constitute a territorial duet (Benedict, 2008; Shuler, 1965). As in many other duetting species (Hall, 2009), including most wrens (Mann et al., 2009), the duets of Carolina wrens are led by males and instigated by females responding to their partners' songs. Other duetting wren species exhibit a wide range in their levels of male–female coordination (Keenan et al., 2020; Mann et al., 2009), from antiphonal duets that are remarkably coordinated and precise (Coleman et al., 2021; Mann et al., 2006; Templeton et al., 2013) to loosely overlapping vocalizations that are less consistently combined (Mennill & Vehrencamp, 2005). Our analysis suggests that Carolina wrens belong in the latter category, similar to some Neotropical duetting wrens but unlike other temperate-breeding North American wren species that are not known to duet at all (Benedict, 2008; Hathcock & Benedict, 2018; Winkler et al., 2020). Indeed, patterns of overlapping in our analysis were remarkably similar to those found by Masco et al. (2016): see their table 2 in their analysis of rufous-and-white wrens, a tropical species that is well known for its male–female duets (Mann et al., 2009; Mennill & Vehrencamp, 2005).

Our phylogenetic comparative analyses strongly indicated that duetting behavior in female Carolina wrens was retained from evolutionary ancestors (Figure 2b), which were likely tropical and performed duets that were at least as coordinated. Interestingly, this retained behavior is exhibited even at an early age in female Carolina wrens, as noted by Haggerty and Morton (2020) who recounted that “a 52-day-old, hand-raised female spontaneously produced female

TABLE 1 Tests for vocal coordination above chance levels by either (a) females with respect to males or (b) males with respect to females in nine territorial pairs using four analysis methods

Pair	Interaction	SampleGaps	KeepGaps	KeepSongOrder	Duty cycle
(a) Female behavior with respect to males					
1	Neither	.522	.565	.583	.501
2	Overlap	.004	.008	.005	.018
3	Neither	.218	.234	.116	.408
3	Overlap	<.001	<.001	<.001	<.001
4	Overlap	.003	.011	.031	.293
4	Overlap	.014	.013	.020	.409
4	Neither	.513	.419	.450	.631
5	Neither	.204	.064	.117	.143
5	Overlap	.003	.035	.012	<.001
5	Overlap	.007	.020	.007	<.001
6	Neither	.030	.064	.056	<.001
7	Overlap	.032	.004	<.001	.166
8	Neither	.302	.246	.213	.725
9	Overlap	<.001	.005	.008	.004
(b) Male behavior with respect to females					
1	Neither	.597	.443	.458	.728
2	Neither	.910	.885	.887	.168
3	Neither	.121	.121	.125	.863
3	Avoid	>.999	>.999	>.999	.009
4	Neither	.217	.094	.038	.630
4	Neither	.830	.880	.929	.436
4	Neither	.175	.153	.247	.474
5	Avoid	>.999	>.999	>.999	.416
5	Neither	.464	.438	.438	.800
5	Avoid	>.999	>.999	>.999	.211
6	Avoid	>.999	>.999	>.999	.108
7	Avoid	>.999	>.999	>.999	.169
8	Neither	.322	.357	.367	.764
9	Avoid	>.999	>.999	>.999	.380

Note: For each interaction, the bird's behavior was categorized as overlapping or avoiding overlap if at least two methods resulted in significant p -values ($p < .025$ or $p > .975$, respectively)^a, highlighted in bold.

^aEffect sizes using Cohen's W ranged from 0.01 to 0.59 (mean \pm SE = 0.16 ± 0.02), available in Table S2.

chatter" in response to tape recordings of male song. The existence of duetting in Carolina wrens is consistent with comparative studies of other species showing that duetting behavior is associated with year-round territoriality and long-term monogamous-pair bonds, regardless of latitude (Benedict, 2008, Logue & Hall, 2014; Mitchell et al., 2019). In a previous comparison of neotropical wren species, Keenan et al. (2020) found that levels of duet coordination are positively associated with breeding season length, presumably reflecting levels of cooperation and pair-bond stability. Carolina wren pairs defend their territories year round and appear to maintain long-term pair bonds much like tropical taxa, though their breeding seasons are shorter than those of many tropical wren species (Haggerty & Morton, 2020). The relatively loosely coordinated duets of Carolina

wrens may function to signal commitment or coalition strength to mates and neighboring conspecifics (Hall, 2004; Keenan et al., 2020).

Along this same evolutionary lineage, in which the ancestors of Carolina wrens appear to have moved from tropical to temperate habitats, our reconstructions suggest that female vocalizations became less complex (Figure 2a). Phylogenetic studies in other avian groups have revealed similar historical losses of complex female song with transitions from tropical to temperate breeding habitats (Price et al., 2009, Odom et al., 2014, also see the reverse pattern shown by Najar & Benedict, 2015). In New World blackbirds, for instance, female singing is associated with a suite of life-history traits that are commonly found in the tropics, including social monogamy, lack of migration, and dispersed nest sites, while repeated losses of female

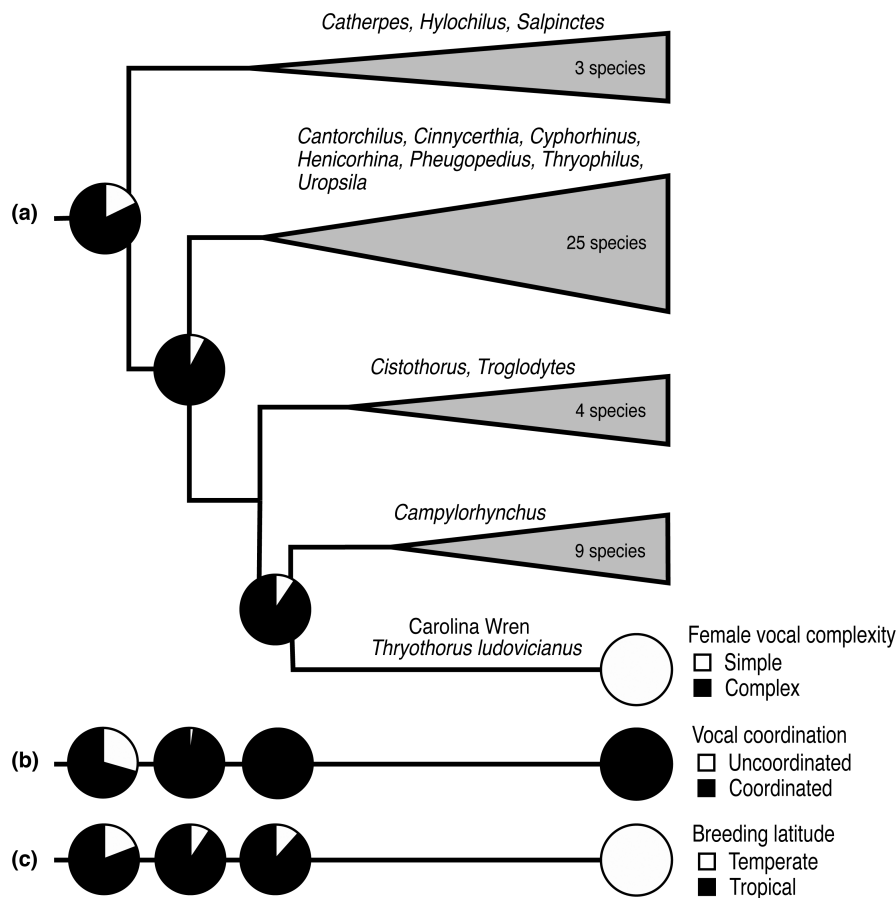


FIGURE 2 Maximum-likelihood reconstructions of (a) female vocal complexity, (b) vocal coordination between males and females, and (c) breeding latitude in Carolina wrens and their evolutionary ancestors (Markov k-state one parameter model). Black-and-white fill in pie charts indicate proportional likelihoods of ancestral states at three nodes on the phylogeny. Other clades in the wren family (Troglodytidae), representing 15 genera including 41 species, are condensed and shown as gray triangles.

song have been associated with evolutionary transitions away from any of these characteristics (Price, 2009). Carolina wrens exhibit the same characteristics associated with female song in blackbirds—they are monogamous, sedentary, and defend nest sites that are widely dispersed (Haggerty & Morton, 2020)—yet they are one of the few wren species that lack complex female song. This apparent loss of female vocal complexity with their change in breeding latitude suggests the existence of additional, as-yet-undefined factors that have selected against female vocal complexity while favoring vocal coordination with males in this lineage. Perhaps the shorter breeding seasons of temperate habitats selected against female song (Price et al., 2009; Slater & Mann, 2004), while duetting was maintained for year-round territory defense (Hall, 2004; Logue & Hall, 2014).

The evolution of complex birdsong has involved changes in specialized brain regions (Catchpole & Slater, 2008), and such past neuroanatomical changes are clearly evident in comparisons among wren species (Brenowitz, 1997). Carolina wrens have brains that are strikingly dimorphic, with males having much larger song control regions (SCRs) than females (Nealen & Perkel, 2000), unlike tropical duetting wren species that have relatively monomorphic brains in which both sexes have large SCRs (Brenowitz & Arnold, 1986). These SCR volumes are strongly associated with levels of vocal output and complexity (Brenowitz, 1997). In bay wrens (*Cantorchilus nigricapillus*) and buff-breasted wrens (*C. leucotis*), for instance, females duet with males using complex song repertoires and have SCR volumes

similar to males, whereas in rufous-and-white wrens, females have song repertoires half the size of males and likewise have significantly smaller SCRs (Brenowitz et al., 1985; Brenowitz & Arnold, 1986). Carolina wrens are exceptional among wren species in that males have song repertoires and SCR volumes that are both unusually large, whereas females do not sing and have no detectable SCRs (Nealen & Perkel, 2000). Selection therefore appears to have favored not just the loss of female song in this species but also a corresponding gain in male singing complexity, a striking sexual divergence that might reflect the division of labor associated with shorter breeding seasons in comparison to most other wrens (Keenan et al., 2020; Kleindorfer et al., 2016).

While the brain regions underlying song learning and production are relatively well studied in songbirds (Catchpole & Slater, 2008), much less is known about the neural pathways involved in vocal coordination to produce duets (Hall, 2009). Recordings of neurophysiological activity in the SCRs of plain-tailed wrens have revealed complex neural mechanisms mediating the production of precise, antiphonal duets (Coleman et al., 2021; Fortune et al., 2011); however, large female SCRs do not appear necessary for all forms of duetting, as illustrated by Carolina wrens and other birds in which pairs duet but females are not known to sing (Benedict, 2008; Hall, 2009). Comparing the brains of closely related duetting and non-duetting taxa would be an interesting avenue for future research, especially in combination with fine-scale comparisons of behaviors and

life-history traits. Such comparisons could include female Carolina wrens, which duet but do not produce complex song, as well as female canyon wrens (*Catherpes mexicanus*), which produce complex songs but do not duet with their mates (Hathcock & Benedict, 2018). Both species exhibit year-round territories and long-term monogamy, yet females use different strategies in territorial defense.

Adequately addressing these issues will require better documentation of female behavior in general (Odom & Benedict, 2018). In our study, for example, several key members of the wren family could not be included, and thus some ancestral states could not be resolved, because we lack published information about female vocal behavior (Winkler et al., 2020). In Bewick's wren (*Thryomanes bewickii*), a southwestern North American species that is the Carolina wren's closest phylogenetic relative (Barker, 2017), male song has been well studied but surprisingly little has been reported about female vocalizations (Kennedy & White, 2020). Likewise, in the tropical subspecies of Carolina wren (white-browed wren, *Thryothorus l. albinucha*), almost nothing has been reported about female vocalizations (Haggerty & Morton, 2020; Mann et al., 2009). Collecting information from these and other wren taxa would provide important new insights into how female song and duetting behavior have evolved in the family.

Our study adds to previous evidence that the evolution of female song and vocal duets involve separate but largely overlapping selection pressures (Hall, 2009; Keenan et al., 2020; Langmore, 1998; Logue & Hall, 2014; Mitchell et al., 2019; Odom et al., 2015; Price, 2009). Our findings do not necessarily contradict the suggestion that female song is often a precursor for the evolution of duetting (Odom et al., 2015); rather, they are consistent with the idea that either behavior can be gained or lost independently (Mitchell et al., 2019). The apparent loss of female vocal complexity in Carolina wrens, while at the same time maintaining vocal coordination with males, raises interesting questions for future investigations into the factors selecting for or against these behaviors in this and other species.

AUTHOR CONTRIBUTIONS

R.W.P. collected field recordings and performed statistical analyses of vocal overlapping; M.T.W. collected species information for scoring characters and conducted phylogenetic comparative analyses; and J.J.P. conceived the project and wrote the paper. All authors edited and approved the manuscript.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All analyzed data are available as supplemental material or from the authors upon request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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