



Not just for males: females use song against male and female rivals in a temperate zone songbird



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ARTICLE INFO

Article history:

Received 11 September 2015
Initial acceptance 13 October 2015
Final acceptance 17 November 2015
Available online
MS. number: A15-00786

Keywords:

female competition
female song
house wren
sexual selection
temperate zone songbird
territory defence
Troglodytes aedon
vocalization

Birdsong in temperate zone passerines is a trait under sexual selection in males. Female song is still thought to be rare in this group. Here we show that female song is common in a temperate zone population of house wrens, *Troglodytes aedon*, and we provide evidence for its functional role in defending against male and female conspecifics. We observed that females sang most frequently at the onset of egg laying, with song becoming less common as incubation approached. Thus, females sang most during the time when eggs were left unguarded and susceptible to conspecific attack. We also conducted playback experiments to test whether conspecific stimuli would induce female song in focal individuals. Playback from both male and female conspecifics elicited strong song responses from resident females, who often vocalized independently from their partners. However, females were more physically aggressive towards female songs than male songs. Finally, females that sang more during these simulated conspecific intrusions ultimately lost fewer eggs to house wren ovicide. These results suggest that female house wren song may have evolved, at least in part, for use in intra- and intersexual competition. These results also highlight how investigating these traditionally male behaviours in female animals can lead to key insights regarding the evolution of sexual dimorphism.

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Analyses of birdsong are a cornerstone in the sexual selection literature. Birdsong is a classic example of a male trait under both intrasexual selection for territory defence and intersexual selection for mate attraction (Catchpole & Slater, 2008). In contrast to male song, female song is much less common in temperate zone breeding species (Langmore, 1998; Morton, 1996; Slater & Mann, 2004). The earliest and most thoroughly studied birdsong systems come from temperate zone species where females are largely songless (Catchpole & Slater, 2008; Slater & Mann, 2004). In contrast to their temperate zone counterparts, many tropical females are prolific singers, performing coordinated vocal duets with males that function to defend territorial resources, guard their mate against intruding females, solicit copulations from their mates and/or coordinate pair and reproductive behaviour (for review see Farabaugh, 1982; Hall, 2004; Langmore, 1998). Because of the history of birdsong studies, songless temperate zone females have been seen as the archetypal condition whereas tropical singers have been seen as a derived state.

Recent phylogenetic work has rewritten this narrative. A survey of 34 songbird families conducted by Odom, Hall, Riebel, Omland, and Langmore (2014) reconstructed female song as an ancestral state for all oscine passerines. This large-scale pattern is consistent with new findings for several avian families (Icteridae: Odom, Omland, & Price, 2015; Price, 2009; Price, Lanyon, & Omland, 2009; Muscicapidae and Fringillidae: Garamszegi, Pavlova, Eens, & Møller, 2007). These studies found that female song is an ancestral condition that has been repeatedly lost as species adopt a temperate zone or migratory breeding pattern. To understand the full picture of birdsong evolution, it is important to understand why female song was lost or maintained in temperate zone lineages, not merely why tropical females sing (Price, 2015; Riebel, Hall, & Langmore, 2005).

Two major hurdles stand in the way of this goal. The first is the shortage of systematic studies of female song in temperate zone breeding species (Garamszegi et al., 2007). Anecdotes of temperate zone female singing have historically been dismissed as the by-product of abnormally high steroid hormone levels (Byers & King, 2000; Gilbert & Carroll, 1999; Nice, 1943; Ogden, Neudorf, Pitcher, & Stutchbury, 2003; Thorpe, 1964), although this hypothesis is rarely supported by hormonal sampling. This lack of hormonal evidence makes it difficult to determine whether this

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behaviour is truly a biological abnormality or merely an unexpected natural phenomenon. The second major hurdle is the lack of data on the function of temperate zone female song. A number of temperate zone species are known to possess female song. This behaviour occurs regularly in several species (alpine accentor, *Prunella collaris*, European starling, *Sturnus vulgaris*, northern cardinal, *Cardinalis cardinalis*, red-winged blackbird, *Agelaius phoeniceus*), occasionally in some (black-capped chickadee, *Poecile atricapillus*, black-headed grosbeak, *Pheucticus melanocephalus*, dunnock, *Prunella modularis*, European robin, *Erithacus rubecula*, song sparrow, *Melospiza melodia*, tree swallow, *Tachycineta bicolor*, white-crowned sparrow, *Zonotrichia leucophrys*, white-throated sparrow (white-striped morph), *Zonotrichia albicollis*, yellow warbler, *Setophaga petechial*) and rarely in several others (Baltimore oriole, *Icterus galbula*, chestnut-sided warbler, *Setophaga pensylvanica*, common yellowthroat, *Geothlypis trichas*, hooded warbler, *Setophaga citrina*, indigo bunting, *Passerina cyanea*, rufous-sided towhee, *Pipilo erythrophthalmus*, Wilson's warbler, *Cardellina pusilla*) (see Langmore, 1998, for partial review; additional species: Beletsky, 1982; Byers & King, 2000; Gilbert & Carroll, 1999; Hahn, Kryslar, & Sturdy, 2013; Lowther & Falls, 1968; Nolan, 1958; Ogden et al., 2003; Sharman, Robertson, & Ratcliffe, 1994; Taff, Littrell, & Freeman-Gallant, 2012). For most of these species, however, the function of song remains unknown.

Here we examine several possible functions of female song in a temperate zone population of house wrens, *Troglodytes aedon*. Female house wren song has only been reported in one previous temperate zone population during a larger study on male vocal behaviour (Johnson & Kermott, 1990b). These authors concluded that female song is directed at the female's mate, functioning to redirect male attention back to the female during periods of coordinated behaviour. Like those authors, we found that female singing is common in our population. However, we also observed that it is frequently performed in the absence of males. Based on this new observation, we examined additional possible functions of song in female house wrens.

Both male and female house wrens compete to obtain and defend valuable breeding resources. House wrens are small (10–12 g), facultatively polygynous migratory songbirds that nest in secondary cavities (Kendeigh, 1941). Both males and females compete separately for access to limited nest cavities (Johnson & Kermott, 1990a; Johnson & Searcy, 1996). Each year we observe several instances of male–male and female–female replacements on territories. Males frequently advertise for secondary mates once the primary female begins incubating (Johnson & Kermott, 1991a), although 5–45% of males may be polygynous depending on the population and year (Drilling & Thompson, 1991; Johnson & Kermott, 1991a, 1991b; Kendeigh, 1941). House wrens also engage in ovicide. Prior to laying their own eggs, both male and female house wrens will puncture and toss any undefended songbird eggs they find in other nests nearby (Belles-Isles & Picman, 1986). Ovicide directed at other wrens also occurs in conjunction with attempted or successful territory take-overs, resulting in the destruction of 4–15% of the eggs in our population each year (Krieg, n.d.).

We focus on three possible functions of female house wren song that parallel the functions of song in male songbirds (Slater & Mann, 2004). All female song data for the present study were collected in the vicinity of active nests (≤ 30 m). Therefore, we limited the hypotheses to those we could address by measuring song near the nest. We asked whether female house wren song works to (1) coordinate pair behaviour, (2) solicit copulations or (3) defend against conspecific threats to eggs and paternal care. Each of these hypotheses predicts that female singing should peak at different times of the female nesting cycle (see Fig. 1) and that

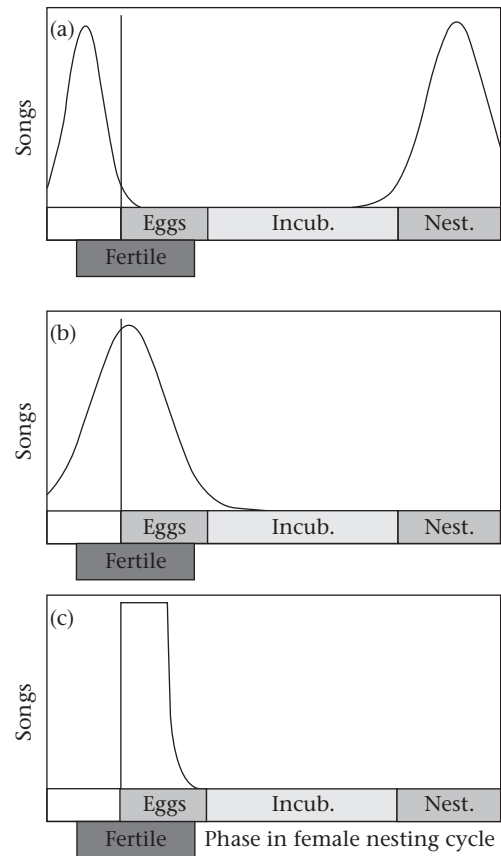


Figure 1. Predictions for the timing of singing by female house wrens if song is used to (a) coordinate pair behaviour, (b) solicit copulations or (c) defend against conspecific threats to eggs and paternal care, for each phase of the female's nesting cycle (fertile period, egg-laying period, incubation period and nestling period).

females should respond to simulated conspecifics in different ways. If females sing to coordinate pair behaviour, songs should peak prior to egg laying and during the nestling period when house wren pair behaviour is highly coordinated (Fig. 1a) (Johnson & Kermott, 1990b). Females should not sing in response to simulated conspecifics under this hypothesis. If instead females sing to solicit copulations, songs should peak during the female's fertile period that starts several days prior to egg laying and lasts through the day of the penultimate egg (Fig. 1b) (Johnson & Kermott, 1989). Females may only sing in response to simulated male conspecifics if songs are designed to solicit extrapair copulation or fail to sing if solicitation songs are directed only at her social mate. Finally, if females sing to ward off conspecific threats, songs should peak when conspecifics pose the biggest risk to female interests (Fig. 1c). Conspecific intruders are the biggest threat during the egg-laying period. Female house wrens do not begin brooding their eggs until the clutch is complete, so eggs face the greatest threat of ovicide prior to incubation when their eggs are left unguarded for long stretches of time. Nestboxes are also likely easiest to usurp during this period for the same reason. Furthermore, if a secondary female begins her clutch around the same time as a primary female, their nestling periods will overlap, and the male will be forced to split his attention (see Supplementary Fig. S1). Therefore, a primary female should work particularly hard to repel prospecting females at the beginning of her egg-laying period (Slagsvold & Lifjeld, 1994). This hypothesis predicts that females will sing strongly in response to simulated conspecifics, particularly female conspecifics. We noted all instances of spontaneous female song observed during routine

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