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

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2 ABSTRACT

3 Bird song in temperate zone passerines is a trait under sexual selection in males. Female
4 song is still thought to be rare in this group. Here we show that female song is common in a
5 temperate zone population of house wrens (*Troglodytes aedon*), and we provide evidence for its
6 functional role in defending against male and female conspecifics. We observed that females
7 sang most frequently at the onset of egg laying with song becoming less common as incubation
8 approached. Thus, females sang most during the time when eggs were left unguarded and
9 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 vocalised independently from their partners. However, females were more physically aggressive toward 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 inter-sexual 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.

KEYWORDS

female song, sexual selection, temperate zone songbird, female competition, territory defence, house wren, *Troglodytes aedon*, vocalisation

Analyses of bird song are a cornerstone in the sexual selection literature. Bird song 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 bird song 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). Due to the history of bird song 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 re-written 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* & *Fringillidae* (Garamszegi, Pavlova, Eens, & Møller 2007)). These studies have 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 bird song evolution it is now important to understand why female song is 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 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, European starling, northern

cardinal, red-winged blackbirds), occasionally in some (black-capped chickadees, black-headed grosbeak, dunnock, European robin, song sparrow, tree swallow, white-crowned sparrow, white-stripe morph of the white-throated sparrow, yellow warbler) and rarely in several others (Baltimore orioles, chestnut-sided warbler, common yellowthroat, hooded warbler, indigo bunting, rufous-sided towhee, Wilson's warbler (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, & Freedman-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 their male mates, functioning to redirect male attention back to the female during periods of coordinated behaviour. Like those authors, we found female singing is quite 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 (10-12g), 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 polygyny rates range between 5-45% of males 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 (CA Krieg, unpublished data).

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 collected in this study was in the vicinity of the active nest (≤ 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 a) coordinate pair behaviour, b) solicit copulations, or c) 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 Figure 1) and that females should respond to simulated conspecific 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 (Figure 1a) (Johnson & Kermott 1990b). Female 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 (Figure 1b) (Johnson & Kermott 1989). Females may sing in response to only simulated male conspecifics if songs are designed to solicit extra-pair 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

102 conspecifics pose the biggest risk to female interests (Figure 1c). Conspecific intruders are the
103 biggest threat during the egg laying period. Female house wrens do not begin brooding their
104 eggs until the clutch is complete, so eggs face the greatest threat of ovide prior to incubation
105 when their eggs are left unguarded for long stretches of time. Nest boxes are also likely easiest
106 to usurp during this period for the same reason. Furthermore, if a secondary female begins her
107 clutch around the same time as a primary female, their nestling periods will overlap, and the
108 male will be forced to split his attention (see Supplemental Figure S1). Therefore, a primary
109 female should work particularly hard to repel prospecting females at the beginning of her egg
110 laying period (Slagsvold & Lifjeld 1994). This hypothesis predicts females will sing strongly in
111 response to simulated conspecifics, particularly female conspecifics. We noted all instances of
112 spontaneous female song observed during routine visits across the nesting cycle and conducted a
113 playback experiment during the beginning of egg laying to determine which hypothesis best
114 explained the patterns observed in female house wren song.

Figure 1: Predictions for the timing of female singing if song is used to a) coordinate pair behaviour, b) solicit copulations, or c) defend against conspecific threats to eggs and paternal care. The rectangles represent the fertile period, egg laying period, incubation period, and nestling period during the female's nesting cycle.

METHODS

Study Site

This study was conducted at the Lux Arbor Reserve, Kellogg Biological Station in Barry County, MI (42°29'N, 85°28'W). This reserve is a 529 ha protected area containing grasslands,

wetlands, forest, and fragmented agricultural fields. Prior to the return of the house wrens from migration in April, we set up wooden nest boxes near forest edges on 59 territories. Each territory contained a cluster of 3 boxes between 5-10 m apart and each cluster was roughly 100 m from its neighbour, allowing one male to easily defend a single cluster but making it difficult to defend more than one. This population has been established for the last fifteen years (Dubois & Getty 2003) and attracts roughly 100 adults each year that we colour-band for individual identification.

Female Song

We define female song as a stereotyped female vocalisation lasting longer than one second. Female song in this species ranges from a collection of buzz-like broadband syllables to songs that are nearly indistinguishable from male songs (Supplemental Figure S2). These female songs are distinct from both the chattering calls females give when the nest is disturbed by predators and the high pitched calls given sometimes during courtship (CK, personal observation). Recordings from Supplemental Figure S2 are available in the online song repository <http://www.xeno-canto.org>.

We identified female song types by either directly observing a color-banded female singing or by matching the structure of the song to a female song previously verified in such a fashion. Visual confirmation was possible during the majority of observations. Nearly all female songs are structurally distinct from male song and quite easy to distinguish by ear. For the one female that sang a very male-like song, we were even more strict about attributing songs to the female. Each song was either given when the female was directly visible or given from a location where we saw the female disappear during which time her mate was clearly present in a different location. We never observed a third house wren on this territory.

Spontaneous Female Song

During the summers of 2012 and 2013, we checked nest boxes for activity every 1-4 days and noted spontaneous female song any time it occurred. We define spontaneous song as a song that was not provoked by experimental house wren playback. We measured spontaneous song in three different nest visit scenarios (standard box checks, nestling measurements, pre-playback period of trials) using three criteria that allowed us to compare across these contexts. First, we limited our data set to songs that occurred during the first 5 minutes spent within 30 m of the nest that day. Second, all three contexts involved a brief approach to the nest and thus a similar level of disturbance. Third, for each day no spontaneous songs were measured after house wren playback was used or nestlings were temporarily removed. During standard box checks, an observer listened for all vocal activity as they approached the territory and took notes on the status of the nest, the vocal behaviour of the male and female resident, the closest distance each bird approached, and the identity of each bird. During nestlings measurements, the same data was taken and nestling were measured for five points in 2012 (days 2, 4, 6, 8, and 10 after hatching) and four points in 2013 (days 4, 6, 8, and 10). The playback experiment is explained in further detail below (see “*Playback Experiment*”).

It is possible that some females sang in direct response to the human observer near the nest. However, house wrens at our study site are regularly exposed to humans throughout the breeding season. When agitated, house wrens typically respond with chattering alarm calls (CK, personal observation). They appear to habituate quickly to human presence when observers retreat some distance from the nest and remain quiet, allowing observers to view typical courtship, nest building, incubation, and feeding behaviours.

We used the date that the first egg was laid by each female (defined as day 0) to determine the day in her nesting cycle on which these spontaneous songs occurred. We define “nesting cycle” as a period stretching between the nest-building phase until nestling fledging. For the purposes of this study, the nesting cycle was limited to 5 days prior to egg laying (day -5) until 28 days after the first egg was laid (day 28). The location of most females was not known prior to day -5 and nests were not visited after day 28 to prevent startling nestlings into early fledging. Cycle days do not perfectly correspond to calendar date within the breeding season as females settle asynchronously and typically have two clutches per season. Each time a new clutch was initiated, we considered this a new nesting cycle.

Playback Experiment

To evaluate song responses to different types of simulated intrusions, we tested each female with playback from a female house wren, a male house wren, and a heterospecific control (described below). All subsequent references to “trials” refer to one of these tests. For each trial a speaker was attached to a tripod 1.5m off the ground and positioned within 2 m of the active nest box. For male and female playback trials, we placed a painted wooden carving of a house wren on top of the tripod to give birds a potential target for aggression. House wrens are sexually monomorphic in both size and colouration, so we used the same model for both male and female trials. Each playback trial consisted of a 2 minute set-up period during which no data was recorded, a 5 minute silent pre-playback period, a 5 minute playback period, and a 5 minute silent post-playback period. An observer (CK) with a Marantz PMD 660 solid state digital recorder attached to a Sennheiser ME62 omnidirectional microphone and a Minerooff parabolic reflector recorded all vocal responses from the focal pair and narrated any physical attacks

females directed toward the playback set-up. The sex of responding birds was easy to determine using acoustic characteristics and leg-band colours.

All females were tested with only one of the three trial types each day until all three trial types were completed. We conducted tests between sunrise and 12:30 EST within the first four days of the egg laying period with trial order assigned randomly. We tested most birds on 3 three consecutive days, however, some birds experienced a one day gap due to weather or time constraints. In 2012 we tested 53 females, and in 2013 we tested 56 females, 17 of which were also tested in 2012. Some birds received an additional set of trials, however, we only included the first set in this analysis. Some birds did not receive all trial types due to uncontrolled nest destruction (12.8% of trial sets).

We constructed each playback stimulus from a loop of six different high quality songs given by the same individual. Each song was separated by 5 seconds of silence to approximate natural singing rates. In the first year of playback studies (2012), we constructed six unique female stimuli and six unique male stimuli each from recordings of a single known individual from 2011. In the following year (2013), we expanded the stimulus set to include 16 female recordings 14 male recordings made from known individuals from both 2011 and 2012. The six unique control stimuli used in both years were each composed of six high quality songs from six different cup-nesting species recorded at the study site in 2011 (*Turdus migratorius*, *Dumetella carolinensis*, *Pipilo erythrophthalmus*, *Melospiza melodia*, *Spizella passerina*, *Spizella pusilla*). We filtered out all noise below 1 kHz and normalised all songs to a peak amplitude of 1.4 kU using Raven Pro v. 1.4 (Bioacoustics Research Program 2011). Birds were never tested with their own song, the song of their mate, song stimuli they were tested with in a previous year, or

the song of neighbours that shared a territory boundary. The results presented here were qualitatively similar for 2012 and 2013 and are therefore pooled for all subsequent analyses.

House Wren Ovicide

Throughout the season, we tracked the status of the nest box and noted the cause of any egg destruction. Wren ovicide leaves tell-tale signs. We classified eggs as destroyed by ovicide if eggs a) were found cracked but unconsumed, b) were found with beak-sized punctures, c) were found unconsumed on the ground in front of the box, or d) were missing on the day that a new wren moved on to the territory. We classified eggs as destroyed by predators if a) shells were found in the nest, b) the nest or nest box was clearly disturbed or damaged, or c) a nest predator was found living in the box. We classified the cause of destruction as “unknown” if none of these criteria applied.

Statistical Analysis

We used a chi-squared goodness-of-fit test to determine if visits with spontaneous female song occurred more often on particular days in the female’s nesting cycle than expected by chance, given our observational effort. We visited nests more frequently during certain periods of the female’s cycle (e.g. egg laying) than others (e.g. incubation). The number of nest visits we made on each day in the cycle was used to calculate the number of songs expected if there were an equal probability of female song occurring on each visit. We restricted our chi-squared analysis to the period between -5 days and +8 days, because including the low number of expected songs during the incubation and nestling period violates the assumptions of the chi-squared test (day of the first egg was set at 0 days and females laid between 5 and 8 eggs per clutch). The three hypotheses about the function of female song differ most in their predictions

during this period. A day with a chi-squared value greater than 3 was considered to contribute strongly to the lack of fit with the random expectation.

We then used a negative binomial generalised linear mixed model with a log link and Tukey post-hoc contrasts to test if female song occurred more often during some stages of the playback trials than others. The dependent variable was the number of female songs, the independent variable was playback stage, and female identity was included as a random effect.

Finally, we used a Wilcoxon signed-rank test to determine if females initiated more vocalisation bouts following playback for both the control, female, and male trials. We applied a Holm family-wise error rate correction to the p-values from these three tests to correct for multiple comparisons (Holm 1979). Females in our experiment sang 1) solos, 2) songs that were followed by male songs upon their conclusion, 3) songs that were given after male songs concluded, as well as 4) songs that overlapped with male songs. When female songs occurred 3 seconds or less from the start of the nearest male partner song, we considered these vocalisations initiated by the sex that sang first, regardless of whether these vocalisations actually overlapped. All other songs were considered female solos. Vocalisation bouts initiated by females as well as female solos were considered female-initiated vocalisations. When two house wren songs start within 3 seconds of one another, these vocalisations either overlap or occur in close sequence. Reducing this cut-off to 1 second or expanding it to 6 seconds does not change the significance of our results. These distinctions allowed us to determine whether females were sometimes operating independently when deciding to vocalise or whether they were exclusively following their mate's lead. All tests were two-tailed. We performed all statistical tests with R version 3.0.2 (R Core Team 2013; package "glmmADMB" (Fournier et al. 2012; Skaug, Fournier,

Bolker, Magnusson, & Nielsen 2015); package “multcomp” (Hothorn, Bretz, & Westfall 2008); package “car” (Fox & Weisberg 2011); package “MuMIn” (Barton 2015)).

Ethical Note

This research was approved by the Michigan State University’s IACUC panel, followed the ASAB/ABS Guidelines for the Use of Animals in Research, and followed appropriate federal and state permits (Michigan State University IACUC #04/11/076-00; US Fish and Wildlife Service Federal Banding Permit #23587; Michigan Department of Natural Resources Michigan Scientific Collectors Permit #SC 1432). Female reactions to recorded song were similar to their reactions to ambient natural song, and they returned to pre-trial behaviour within a half hour. No birds abandoned territories following our tests. Females were either trapped on the nest during incubation or in mist nets that were monitored continuously using procedures deemed appropriate by MSU’s IACUC panel, the US Fish and Wildlife Service, and the Michigan Department of Natural Resources. No birds suffered adverse effects during brief capture and measurement.

RESULTS

Prevalence of Female Song

Female song is a common phenomenon in our population of house wrens. Out of the 108 adult females that were present during 2012 and/or 2013, 72 females (66.7% of the study population) were observed singing in at least one of these contexts described below. Thirty-one females were observed singing spontaneous female song according to the methods outlined in this study (28.7% of studied females). In response to playback, 60 of the 92 tested females sang during at least one trial (65.2% tested females). An additional 17 birds not included in the

analyses above were observed singing either spontaneous song during longer observations on focal territories (15 birds) or provoked song during mist net attempts using house wren playback (2 birds) (see Supplemental Table S1). Like most temperate zone birds, however, male house wrens still sang more frequently. All males sang at some point, and we heard male songs during 33% of nest visits compared to 2% for female songs.

Figure 2: The number of nest visits with spontaneous female song across the nesting cycle (solid line). Visits with songs are more common during early egg laying than expected if song is equally probable on each nest visit (dashed line) ($P < 0.0001$). Black dots represent days when songs are more common and white dots represent days when songs are less common than expected ($\chi^2 > 3$). Light grey dots after day 8 were not included in the chi-square analysis because of low sampling effort and expected values. Numbers in parentheses indicate the number of nest visits made during each stage.

298 *Spontaneous Female Song*

299 Females sang during significantly more visits on particular days than would be expected
300 by chance (Figure 2, $\chi^2_{13} = 48.54$, $P < 0.0001$). Most visits with spontaneous female song
301 occurred at the beginning of the egg laying period. Visits with spontaneous female song were
302 rare on days prior to egg laying and then spiked dramatically by the day of the second egg (cycle
303 day 1). By the end of the egg laying period, song declined once again to low levels that were
304 maintained for the remainder of the nesting cycle.

305 The timing of this increase in female song does not appear to be merely a result of
306 increased vocal vigilance on days following prior house wren playback. During the peak of
307 singing (day 0-3), we observed 24 visits with spontaneous song before any house wren playback
308 was used on the territory and 20 visits with spontaneous song after house wren playback had
309 been used on a previous day.

310 The pattern of singing across the nesting cycle is consistent with both the copulation-
311 solicitation and the defence-against-conspecifics hypothesis (see Figure 1b, c). However, it
312 should be noted that songs are significantly less common than expected during visits on the day
313 before the first egg is laid, which is well within the female's fertile period. The defence-against-
314 conspecifics hypothesis is supported further by the results from our playback experiment.

315

Figure 3: The mean number of female songs recorded ($\pm$ SE) during each 5 minute playback stage. Females sing significantly more following conspecific playback compared to control playback (** $P < 0.01$, * $P < 0.05$). Letters represent Tukey's posthoc comparisons.

Female Response to Playback

Both male and female playback prompted dramatic increases in female house wren singing. Females sang significantly more during and after both female and male playback compared to the playback stage of control trials (Figure 3, during female playback: $Z = 6.77$, $P < 0.001$; post female playback: $Z = 6.07$, $P < 0.001$; during male playback: $Z = 6.04$, $P < 0.001$; post male playback: $Z = 3.07$, $P = 0.049$). The majority of female songs occurred following conspecific playback, and females that sang gave more songs on average following conspecific playback than during control playback or silence (Table 1). Furthermore, females were not exclusively following their partner's vocal response when engaging with conspecifics (Figure 4). Females initiated the majority of songs during and after both female ($V = 857$, $N = 108$, corrected

331 $P < 0.0001$) and male playback ($V = 662.5$, $N = 97$, corrected $P = 0.005$). However, during and
 332 after control playback, the number of songs females started independently (female-initiated) and
 333 the number songs females gave immediately following songs of their mates (male-initiated) did
 334 not differ ($V = 53$, $N = 106$, corrected $P = 0.266$). Previous house wren playback did not
 335 significantly change female singing responses to subsequent house wren trials. Including
 336 whether the trial was performed before or after a previous house wren trial as a model coefficient
 337 does not improve the model fit or alter the significance of the results presented here.

338 While females responded to both male and female playback with singing, female songs
 339 provoked the strongest physical response. A total of 16 different females (17.4% of tested
 340 females) attacked the playback by swooping down within inches of the model or speaker,
 341 sometimes making direct physical contact. Female playback received the majority of these
 342 attacks (94.7%) (Table 1).

343
 344 Figure 4: The mean number of female-initiated female songs compared to male-initiated female
 345 songs ($\pm$ SE) during the playback period (5 min) and post-playback period (5 min) of each trial

type. Females initiate significantly more songs following female and male playback (***) $P < 0.001$, * $P < 0.05$).

Table 1: The number of attacks and female songs during each stage of playback trials

Trial Type	During and after playback			Pre-playback
	Female ^a	Male ^b	Control ^c	All
# of attacks	36	2	0	0
attacks per attacking female (X ± SE)	2.4 ± 0.57	1 ± 0	-	-
# of songs	601	369	58	122
songs per singing female (X ± SE)	13.98 ± 2.36	8.39 ± 1.94	4.24 ± 1.61	3.94 ± 1.17

^a 108 trials, 91 individuals

^b 97 trials, 82 individuals

^c 106 trials, 89 individuals

Reproductive Consequence of Female Song

To further evaluate the defense-against-conspecifics hypothesis, we asked whether females that sang more during simulated intrusions were better at defending their eggs (binomial generalized linear model, fixed effects: songs + year). We found that females that sang more songs during the playback and post playback period of the male and female trials lost significantly fewer eggs to house wren ovicide (Figure 5; model $R^2 = 0.25$, songs: $Z = -3.34$, $P = 0.0008$). The rate of ovicide was significantly higher in 2013 than 2012 (year: $Z = 6.3$, $P < 0.0001$). In 2013 we carried out a different experiment that briefly increased the number of

363 floating house wrens. The population was also larger in 2013 (27% more females). While these
 364 factors likely increased ovicide rates in 2013, the relationship between song and ovicide is
 365 qualitatively similar in 2012 (see Figure 5). Although female song may also prevent secondary
 366 females from settling, rates of polygyny were too low in our population to evaluate this
 367 dimension of the defense-against-conspecifics hypothesis.

368
 369 Figure 5: Females that sang more songs during and after male and female house wren playback
 370 lost significantly fewer eggs to ovicide by other house wrens (binomial generalized linear model:
 371 model $R^2 = 0.25$, songs $P < 0.001$). Ovicide was less common in 2012 but still affected females

with low song rates. Lines represent predicted values for each year in the model $\pm$ 95% confidence intervals.

DISCUSSION

Here we present evidence of temperate zone females using their songs in a similar fashion to temperate zone males. Female house wren song appears to play a role in defending against reproductive threats from both male and female rivals. Females sang most frequently at the onset of egg laying, during which conspecific intruders are the biggest threat to vulnerable eggs and future paternal care. This behaviour decreased dramatically as incubation approached and remained at a low level for the rest of the nesting cycle. Furthermore, simulating conspecific intruders by playing male or female playback elicited strong song responses from female house wrens. These females were not merely following the defence efforts of males. Females initiated the majority of their song bouts following conspecific playback in contrast to the control condition when they are equally likely to follow the male's lead. Finally, this female behaviour had measurable reproductive consequences. Females that gave more songs in response to simulated male and female intruders lost significantly fewer eggs to house wren ovicide.

While females were equally vocal to male and female stimuli, females were more aggressive toward female stimuli. Nearly all physical attacks were directed exclusively at female playback songs. This suggests that females may have perceived other females as a greater threat than other males. During the egg laying period, both male and female residents benefit from driving away other males who may usurp territories and destroy eggs. Female intruders pose a unique threat to resident females because they will not only destroy eggs but may also settle as a secondary female. Secondary females are the biggest threat when they begin their clutch around

the same time as a primary female (Slagsvold & Lifjeld 1994). In this scenario, the period of nestling provisioning will overlap for both females, and males must split their attention (see Supplemental Figure S1). While primary females may also benefit from preventing female settlement at the beginning incubation, the time constraints of incubation likely limit their defensive efforts.

In the tropics where both sexes generally maintain their territories year-round, females frequently use song to defend territories (for examples see Brunton, Evans, Cope & Ji 2008; Cooney & Cockburn 1995; Farabaugh 1982; Hall 2004; Illes & Yunes-Jimenez 2009; Illes 2015; Levin 1996). In temperate zone species, female song also appears to play a role in defence (for examples see Arcese, Stoddard & Hiebert 1988; Baptista, Trail, Dewolfe, & Morton 1993; Beletsky 1983; Hobson & Sealy 1990; Langmore 1998, 2000; Sandell & Smith 1997). Although vocal displays during conspecific conflicts by temperate zone males, tropical females, and temperate zone females take the same form, the functions of these displays can be very different. While males certainly use song to defend non-sexual resources, this behaviour is frequently studied in the context of sexual selection. Temperate zone males singing to defend temporary breeding territories accrue benefits typically not sought by temperate zone females- defence of a resource to attract mates and prevention of extra-pair fertilisations by neighbouring males (Catchpole & Slater 2008; Morton 1996). In contrast, tropical birds of both sexes often defend year-round territories and form long-term pair bonds, making territories and mates particularly valuable resources to both males and females (Farabaugh 1982; Morton 1996; Slater & Mann 2004). In one sense, female house wrens behave in a fashion similar to males when singing to protect eggs, nesting cavities, and/or paternal investment from conspecific threats. In another sense, this behaviour differs in important ways.

Like female house wrens, other females in the wren family (*Troglodytidae*) use their songs during inter and intra-sexual competition. The wren family contains a wide range of female singing styles, culminating in species that perform complex, antiphonal duets (Mann, Dingess, Barker, Graves, & Slater 2009). In temperate zone species, female song is thought to be absent (marsh wren: Brenowitz, Nalls, Kroodsma & Horning 1994; Carolina wren: Nealen & Perkel 2000) or its function is unknown (canyon wren: Benedict, Rose, & Warning 2013). In tropical species where its function has been investigated, female song appears to play a role in inter- and/or intra-sexual territory defense (buff-breasted wren: Gill, Alfson, & Hau 2007; bay wren: Levin 1996; black-bellied wren: Logue & Gammon 2004; rufous-and-white wren: Mennill 2006; happy wren: Templeton, Rivera-Cáceres, Mann, & Slater; but see banded wren: Hall, Rittenbach, & Vehrencamp 2015). With the wide range of singing styles and natural histories found in *Troglodytidae*, this family may be particularly useful model for investigating the evolution of female song.

Although the results here suggest females use their song to defend nest areas from conspecifics, this may not be the only function of this behaviour. Female house wren song occurs occasionally throughout the entire nesting cycle, even during periods where conspecifics are not significant threats to reproductive activities. Females may also use song differently at territory edges or off their territories, for instance, to defend territory boundaries or seek extra-pair copulations. Without more systematic measurement of female vocal behaviour throughout a female's range, we are unable to offer an exhaustive determination of all the possible functions of female song. Instead, we offer one previously unknown function of female song in a species where female song has received little attention. Female house wrens may sing both to communicate with their mates, as suggested by Johnson and Kermott (1990b), as well as to

441 defend eggs, nesting cavities, and/or paternal investment from conspecifics, as our data suggests.
442 Like male song, female house wren song likely plays a role in both intra- and inter-sexual
443 communication.

444 The nature of female house wren vocal behaviour highlights challenges facing
445 researchers studying other temperate zone singers. Although the majority of the females in our
446 population were observed singing, this behaviour has only been documented once before
447 (Johnson & Kermott 1990b). Why has this behaviour been largely overlooked? First, house
448 wrens are sexually monomorphic. Because song is only expected to occur in temperate zone
449 males, field biologists may be likely to assume that a singing bird of unknown sex is a male
450 (Langmore 1998). This appears to have been the case in black-capped chickadees, another
451 monomorphic species (Hahn et al. 2013). Second, the majority of female house wren song is
452 very vocally distinct from male house wren song. Unless one first clearly observes a female
453 making this unique sound, it would be extremely easy to dismiss female song as an unknown
454 vocalisation from a different species (see Nolan 1958 for a similar case). Third, female house
455 wren song is common during a very specific window of the breeding season and is used in a
456 specific social context. If observers are not in the right place at the right time, it is easy to miss
457 entirely. Male house wrens sing most when attempting to attract females to their territories, and
458 they dramatically reduce both the quantity and amplitude of singing during egg laying (Johnson
459 & Kermott 1991b). Biologists focused only on male house wren vocal behaviour could easily
460 miss the peak of female singing. If other female singers are using their songs differently than
461 males, this may be difficult to detect without specific focus on females. To understand the broad
462 patterns of female song evolution, we need to understand the selective forces favouring the

463 maintenance these vocalisations. To accomplish this, however, we may first need to re-evaluate
464 which temperate zone species truly lack female singers and which hold unexpected surprises.

465 Predicting which species likely possess female song requires a more detailed examination
466 of the relevant natural history characteristics. When females compete for valuable breeding
467 resources, selection should favour aggressiveness as well as signals used in aggressive
468 encounters in a process analogous to sexual selection on males (Clutton-Brock 2009; Clutton-
469 Brock & Huchard 2013; Rosvall 2011; Tobias, Montgomerie, & Lyon 2012; West-Eberhard
470 1983). Female house wrens lack many of the characteristics associated with female song to date
471 (tropical breeding, year-round territoriality, social monogamy, sedentary behaviour) (Odom et al.
472 2015; Price 2009; Price et al. 2009; Slater & Mann 2004). However, as facultatively polygynous
473 secondary cavity nesters, they are in direct competition with other females for limited nesting
474 cavities and valuable paternal care. Polygynous females are expected to face high levels of
475 intrasexual competition (Slagsvold & Lifjeld 1994). Many temperate zone species with female
476 song also demonstrate occasional polygyny (for partial review see Langmore 1998, 2000;
477 additional species: Carey & Nolan 1975; Clemmons 1994; Flood 1985; Powell & Jones 1978;
478 Quinney 1983). Rival females may pose an additional threat in secondary cavity nesting species,
479 which typically face intense competition for suitable nesting sites (von Haartman 1957). Under
480 natural conditions, only a portion of house wren males have access to these supplemental nests
481 (Czapka & Johnson 2000; Johnson & Kermott 1991a). Ovicide by nearby females likely further
482 reduces the number of viable cavities. Intriguing, European starlings, which demonstrate
483 frequent female singing, are also facultatively polygynous cavity nesters that elevate singing
484 rates when defending nest boxes from other females (Pavlova, Pinxten, & Eens 2007; Sandell &
485 Smith 1997). These additional dimensions of female competition in house wrens may explain

why a species with multiple characteristics associated with the loss of female singing still possess functional female song.

Most studies to date have investigated factors that differ dramatically between temperate zone and tropical species when considering the evolution of female song, such as migratory behaviour or broad natural history changes associated with tropical environments (Odom et al. 2015; Price 2009; Price et al. 2009; Slater & Mann 2004). Here we show that female song also has a function for certain migratory, temperate zone species. Our results suggest that additional factors more intimately related to the possible function of female song, for instance the degree of intra- and inter-sexual competition for resources, may do a better job of explaining the presence of female song in certain temperate zone species. A more exhaustive examination of the natural history characteristics related to the putative selective forces shaping female song may shed more light on the presence and absence of this classically male trait in female organisms.

REFERENCES

Arcese, P., Stoddard, P. K., & Hiebert, S.M. (1988). The form and function of song in female song sparrows. *The Condor*, 90, 44-50. (doi: 10.2307/1368431)

Baptista, L. F., Trail, P. W., Dewolfe, B. B., & Morton, M. L. (1993). Singing and its functions in female white-crowned sparrows. *Animal Behaviour*, 46, 511-524. (doi:10.1006/anbe.1993.1219)

Barton, K. (2015). MuMIn: multi-model inference. R package version 1.13.4. <http://CRAN.R-project.org/package=MuumIn>

509

510 Beletsky, L. D. (1982). Vocalizations of female northern orioles. *The Condor*, 84, 445-447. (doi:

511 10.2307/1367454)

512

513 Beletsky, L. D. (1983). Aggressive and pair-bond maintenance songs of female Red-winged

514 Black-birds (*Agelaius phoeniceus*). *Zeitschrift fur Tierpsychologie*, 63, 47-54.

515

516 Belles-Isles, J., & Picman, J. (1986). House wren nest-destroying behavior. *The Condor*, 88, 190-

517 193. (doi:10.2307/1368914)

518

519 Benedict, L., Rose, A., & Warning, N. (2013). Small song repertoires and high rate of song-type

520 sharing among canyon wrens. *The Condor*, 115, 874-881. (doi: 10.1525/cond.2013.130025)

521

522 Bioacoustics Research Program. (2011). Raven Pro: Interactive Sound Analysis Software

523 (Version 1.4) [Computer software]. Ithaca: The Cornell Lab of Ornithology. Available from

524 <http://www.birds.cornell.edu/raven>.

525

526 Brenowitz, E. A., Nalls, B., Kroodsma, D. E., & Horning, C. (1994). Female marsh wrens do not

527 provide evidence of anatomical specializations of song nuclei for perception of male song.

528 *Journal of Neurobiology*, 25, 197-208. (doi: 10.1002/neu.480250210)

529

530 Brunton, D. H., Evans, B., Cope, T., & Ji, W. (2008). A test of the dear enemy hypothesis in
 531 female New Zealand bellbirds (*Anthornis melanura*): female neighbors as threats. *Behavioral*
 532 *Ecology*, 19, 791-798. (doi:10.1093/beheco/arn027)
 533
 534 Byers, B. E., & King, D. I. (2000). Singing by female chestnut-sided warblers. *Wilson Bulletin*,
 535 112, 547-550. (doi:10.1676/0043-5643(2000)112[0547:SBFCSW]2.0CO;2)
 536
 537 Carey, M., & Nolan, V. (1975). Polygyny in indigo buntings: a hypothesis tested. *Science*, 190,
 538 1296-1297. (doi:10.1126/science.190.4221.1296)
 539
 540 Catchpole, C. K., & Slater, P. J. (2008). The study of bird song: biological themes and variations
 541 (2nd ed.) New York, NY: Cambridge University Press.
 542
 543 Clemmons, J. R. (1994). Multiple cases of polygyny in the black-capped chickadee: a possible
 544 advantage to the primary female. *The Condor*, 96, 1113-1114. (doi:10.2307/1369126)
 545
 546 Clutton-Brock, T. (2009). Sexual selection in females. *Animal Behaviour*, 77, 3-11.
 547 (doi:10.1016/j.anbehav.2008.08.026)
 548
 549 Clutton-Brock, T. H., & Huchard, E. (2013). Social competition and selection in males and
 550 females. *Philosophical Transactions of the Royal Society B*, 368, 20130074.
 551 (doi:10.1098/rstb.2013.0074)
 552

553 Cooney, R., & Cockburn, A. (1995). Territorial defense is the major function of female song in
 554 the superb fairy-wren, *Malurus cyaneus*. *Animal Behaviour*, 49, 1635-1647. (doi:10.1016/0003-
 555 3472(95)90086-1)

556

557 Czapka, S. J., & Johnson, L. S. (2000). Consequences of mate sharing for first-mated females in
 558 a polygynous songbird, the house wren. *Wilson Bulletin*, 112, 72-81. (doi:10.1676/0043-
 559 5643(2000)112%5B0072:COMSFF%5D2.0.CO;2)

560

561 Drilling, N. E., & Thompson, C. F. (1991). Mate switching in multibrooded house wrens. *The*
 562 *Auk*, 108, 60-70.

563

564 Dubois, N. S., & Getty, T. (2003). Empty nests do not affect female mate choice or maternal
 565 investment in house wrens. *The Condor*, 105, 382-387. (doi: 10.1650/0010-
 566 5422(2003)105[0382:ENDNAF]2.0.CO;2)

567

568 Farabaugh, S. M. (1982). The ecological and social significance of duetting. In D. E. Kroodsma,
 569 & E. H. Miller (Eds.), *Acoustic communication in birds*. Vol. 2. (pp. 85-125). New York, NY:
 570 Academic Press.

571

572 Flood, N. J. (1985). Incidences of polygyny and extrapair copulation in the northern oriole. *The*
 573 *Auk*, 102, 410-413. (doi:10.2307/4086790)

574

575 Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., et al. (2012).
 576 AD model builder: using automatic differentiation for statistical inference of highly
 577 parameterized complex nonlinear models. *Optimization Methods and Software*, 27, 233-249.
 578 (doi:10.1080/10556788.2011.597854)
 579
 580 Fox, J., & Weisberg, S. (2011). An R companion to applied regression (2nd ed.). Thousand Oaks,
 581 CA: Sage Publ. URL: <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>.
 582
 583 Garamszegi, L. Z., Pavlova, D. Z., Eens, M., & Møller, A. P. (2007). The evolution of song in
 584 female birds in Europe. *Behavioral Ecology*, 18, 86-96. (doi:10.1093/beheco/ar1047)
 585
 586 Gilbert, G. M., & Carroll, A. F. (1999). Singing in a mated female Wilson's warbler. *Wilson*
 587 *Bulletin*, 111, 134-137.
 588
 589 Gill, S. A., Alfson, E. D., & Hau, M. (2007). Context matters: female aggression and testosterone
 590 in a year-round territorial neotropical songbird (*Thryothorus leucotis*). *Proceedings of the Royal*
 591 *Society of London B*, 274, 2187-2194. (doi: 10.1098/rspb.2007.0457)
 592
 593 Hahn, A. H., Kryslar, A., & Sturdy, C. B. (2013). Female song in black-capped chickadees
 594 (*Poecile atricapillus*): Acoustic song features that contain individual identity information and sex
 595 differences. *Behavioural Processes*, 98, 98-105. (doi: 10.1016/j.beproc.2013.05.006)
 596

597 Hall, M. L. (2004). A review of hypotheses for the functions of avian duetting. *Behavioral*
598 *Ecology and Sociobiology*, 55, 415-430. (doi: 10.1007/s00265-003-0741-x)
599

600 Hall, M. L., Rittenbach, M. R. D., & Vehrencamp, S. L. (2015). Female song and vocal
601 interactions with males in a neotropical wren. *Frontiers in Ecology and Evolution*, 3, 12. (doi:
602 10.3389/fevo.2015.00012)
603

604 Hobson, K. A., & Sealy, S. G. (1990). Female song in the yellow warbler. *The Condor*, 92, 259-
605 261. (doi: 10.2307/1368416)
606

607 Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal*
608 *of Statistics*, 6, 65-70.
609

610 Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inferences in general parametric
611 models. *Biometrical Journal*, 50, 346-363. (doi:10.1002/bimj.200810425)
612

613 Illes, A. E. (2015). Context of female bias in song repertoire size, singing effort, and singing
614 independence in a cooperatively breeding songbird. *Behavioral Ecology and Sociobiology*, 69,
615 139-150. (doi: 10.1007/s00265-014-1827-3)
616

617 Illes, A. E., & Yunes-Jiménez, L. (2009). A female songbird out-sings male conspecifics during
618 simulated territorial intrusions. *Proceedings of the Royal Society of London B*, 276, 981-986.
619 (doi:10.1098/rspb.2008.1445)

620

621 Johnson, L. S., & Kermott, L. H. (1989). Territorial intrusions in the house wren *Troglodytes*
622 *aedon*: evidence for the sperm competition hypothesis. *Ornis Scandinavica*, 20, 89-92. (doi:
623 10.2307/3676873)

624

625 Johnson, L. S., & Kermott, H. L. (1990a). Possible causes of territory takeovers in a north-
626 temperate population of house wrens. *The Auk*, 107, 781-784. (doi: 10.2307/4088013)

627

628 Johnson, L. S., & Kermott, H. L. (1990b). Structure and context of female song in a north-
629 temperate population of house wrens. *Journal of Field Ornithology*, 61, 273-284.

630

631 Johnson, L. S., & Kermott, H. L. (1991a). Effect of nest-site supplementation on polygynous
632 behavior in the house wren (*Troglodytes aedon*). *The Condor*, 93, 784-787.
633 (doi:10.2307/1368219)

634

635 Johnson, L. S., & Kermott, L. H. (1991b). The functions of song in male house wrens
636 (*Troglodytes aedon*). *Behaviour*, 116, 190-209. (doi:10.1163/156853991X00030)

637

638 Johnson, L. S., & Searcy, W. A. (1996). Female attraction to male song in house wrens
639 (*Troglodytes aedon*). *Behaviour*, 133, 357-366. (doi:10.1163/156853996X00495)

640

641 Kendeigh, S. C. (1941). Territorial and mating behavior of the house wren. *Illinois Biological*
642 *Monographs*, 18, 1-120.

643

644 Langmore, N. E. (1998). Functions of duet and solo songs of female birds. *Trends in Ecology*
645 *and Evolution*, 13, 136-140. (doi:10.1016/S0169-5347(97)01241-X)

646

647 Langmore, N. E. (2000). Why female birds sing. In Y. Espmark, T. Amundsen, & G. Rosenqvist
648 (Eds.), *Animal Signals: Signalling and signal design in animal communication*. (pp. 389-399).
649 Trondheim, Norway: The Foundation Tapir Publishers.

650

651 Levin, R. N. (1996). Song behavior and reproductive strategies in a duetting wren, *Thryothorus*
652 *nigricapillus*: II. Playback experiments. *Animal Behaviour*, 52, 1107-1117.
653 (doi:10.1006/anbe.1996.0258)

654

655 Logue, D. M., & Gammon, D. E. (2004). Duet song and sex roles during territory defence in a
656 tropical bird, the black-bellied wren, *Thryothorus fasciatoventris*. *Animal Behaviour*, 68, 721-
657 731. (doi: 10.1016/j.anbehav.2003.10.026)

658

659 Lowther, J. K., & Falls, J. B. (1968). White-throated sparrow. In A. C. Bent, *Life histories of*
660 *northern cardinals, grosbeaks, towhees, finches, sparrows, and allies*. Part 3. (pp. 1364-1392).
661 Washington, DC: US National Museum Bulletin, No 337.

662

663 Mann, N. I., Dingess, K. A., Barker, F. K., Graves, J. A., & Slater, P. J. B. (2009). A
664 comparative study of song form and duetting in neotropical *Thryothorus* wrens. *Behaviour*, 146,
665 1-43. (doi:10.1163/156853908X390913)

666

667 Mennill, D. J. (2006). Aggressive responses of male and female rufous-and-white wrens to stereo
668 duet playback. *Animal Behaviour*, 71, 219-226. (doi: 10.1016/j.anbehav.2005.05.006)

669

670 Morton, E. S. (1996). A comparison of vocal behavior among tropical and temperate passerine
671 birds. In D. E. Kroodsma, & E. H. Miller (Eds.), *Ecology and evolution of acoustic*
672 *communication in birds* (pp. 258-268). Ithaca, NY: Comstock Publ.

673

674 Nealen, P.M., & Perkel, D.J. (2000). Sexual dimorphism in the song system of the Carolina wren
675 *Thryothorus ludovicianus*. *The Journal of Comparative Neurology*, 418, 346-360. (doi:
676 10.1002/(SICI)1096-9861(20000313)418:3%3C346::AID-CNE8%3E3.0.CO;2-K)

677

678 Nice, M. M. (1943). Studies in the life history of the song sparrow II. The behavior of the song
679 sparrow and other passerines. *Transactions of the Linnean Society of New York*, 6, 127-132.

680

681 Nolan, V. (1958). Singing by female indigo bunting and rufous-sided towhee. *The Wilson*
682 *Bulletin*, 70, 287-288.

683

684 Odom, K. J., Hall, M. L., Riebel, K., Omland, K. E., & Langmore, N. E. (2014). Female song is
685 widespread and ancestral in songbirds. *Nature Communications*, 5, 3379.
686 (doi:10.1038/ncomms4379)

687

- Odom, K. J., Omland, K. E., & Price, J. J. (2015). Differentiating the evolution of female song and male-female duets in the New World blackbirds: Can tropical natural history traits explain duet evolution? *Evolution*, 69, 839-847. (doi:10.1111/evo.12588)
- Ogden, L. J. E., Neudorf, D. L. H., Pitcher, T. E., & Stutchbury, B. J. M. (2003). Female song in the hooded warbler. *Northeastern Naturalist*, 10, 457-464. (doi: 10.2307/3858662)
- Pavlova, D. Z., Pinxten, R., & Eens, M. (2007). Seasonal singing patterns and individual consistency in song activity in female European starlings (*Sturnus vulgaris*). *Behaviour*, 144, 663-680. (doi:10.1163/156853907781347835)
- Powell, G. V. N., & Jones, H. L. (1978). An observation of polygyny in the common yellowthroat. *Wilson Bulletin*, 90, 656-657.
- Price, J. J. (2009). Evolution and life-history correlates of female song in the New World blackbirds. *Behavioral Ecology*, 20, 967-977. (doi:10.1093/beheco/arp085)
- Price, J. J. (2015). Rethinking our assumptions about the evolution of bird song and other sexually dimorphic signals. *Frontiers in Ecology and Evolution*, 3, 40. (doi: 10.3389/fevo.2015.00040)

Price, J. J., Lanyon, S. M., & Omland, K. E. (2009). Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. *Proceedings of the Royal Society of London B*, 276, 1971-1980. (doi: 10.1098/rspb.2008.1626)

Quinney, T. E. (1983). Tree swallows cross a polygyny threshold. *The Auk*, 100, 750-754.

R Core Team. (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing [Computer software]. Vienna, Austria. Available from <http://www.R-project.org>.

Riebel, K., Hall, M. L., & Langmore, N. E. (2005). Female songbirds still struggling to be heard. *Trends in Ecology and Evolution*, 20, 419-420. (doi:10.1016/j.tree.2005.04.024)

Rosvall, K. A. (2011). Intrasexual competition in females: evidence for sexual selection? *Behavioral Ecology*, 22, 1131-1140. (doi: 10.1093/beheco/arr106)

Sandell, M. I., & Smith, H. G. (1997). Female aggression in the European starling during the breeding season. *Animal Behaviour*, 53, 13-23. (doi: 10.1006/anbe.1996.0274)

Sharman, M. Y., Robertson, R. J., & Ratcliffe, L. M. (1994). Vocalizations of the tree swallow (*Tachycineta bicolor*) during the prelaying period: a structural and contextual analysis. *American Midland Naturalist* 132:264-274. (doi:10.2307/2426582)

732 Skaug, H., Fournier, D., Bolker, B., Magnusson, A., & Nielsen, A. (2015). Generalized linear
 733 mixed models using AD model build. R package version 0.8.1.
 734

735 Slagsvold, T., & Lifjeld, J. T. (1994). Polygyny in birds: the role of competition between females
 736 for male parental care. *American Naturalist*, 143, 59-94. (doi:10.1086/285596)
 737

738 Slater, P. J. B., & Mann, N. I. (2004). Why do the females of many bird species sing in the
 739 tropics? *Journal of Avian Biology*, 35, 289-294. (doi:10.1111/j.0908-8857.2004.03392.x)
 740

741 Taff, C. C., Littrell, K. A., & Freeman-Gallant, C. R. (2012). Female song in the common
 742 yellowthroat. *Wilson Journal of Ornithology*, 124, 370-374. (doi: 10.1676/11-182.1)
 743

744 Templeton, C. N., Rivera-Cáceres, K. D., Mann, N. I., & Slater, P. J. B. (2011). Song duets
 745 function primarily as cooperative displays in pairs of happy wrens. *Animal Behaviour*, 82, 1399-
 746 1407. (doi: 10.1016/j.anbehav.2011.09.024)
 747

748 Thorpe, W. H. (1964). Singing. In A. L. Thomson (Ed.), *A new dictionary of birds*. (pp. 739-
 749 750). New York, NY: McGraw-Hill Book Company.
 750

751 Tobias, J. A., Montgomerie, R., & Lyon, B. E. (2012). The evolution of female ornaments and
 752 weaponry: social selection, sexual selection and ecological competition. *Philosophical*
 753 *Transactions of the Royal Society B*, 367, 2274-2293. (doi:10.1098/rstb.2011.0280)
 754

755 von Haartman, L. (1957). Adaptation in hole-nesting birds. *Evolution*, 11, 339-347. (doi:
756 10.2307/2405797)
757
758 West-Eberhard, M. J. (1983). Sexual selection, social competition,, and speciation. *Quarterly*
759 *Review of Biology*, 58, 155-183. (doi:10.1086/413215)