A female songbird out-sings male conspecifics during simulated territorial intrusions

Anya E. Illes^{1,*} and Laila Yunes-Jimenez²

¹Department of Biology, University of Washington, Post Box 351800, Seattle, WA 98195, USA

²Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apartado Postal 70-399, México 04510 DF, México

While birdsong is a model system for animal communication studies, our knowledge is derived primarily from the study of only one sex and is therefore incomplete. The study of song in a role-reversed species would provide a unique opportunity to study selective pressures and mechanisms specific to females, and to test the robustness of current theories in an empirically novel manner. We investigated function of female song in stripe-headed sparrows (*Aimophila r. ruficauda*), a Neotropical, duetting passerine, and found that during simulated territorial intrusions by a female, male or duetting pair, females: (i) sang more than males to same-sex and duet playback, (ii) played a leading singing role in all contexts, and (iii) showed a longer term song response than males. These results suggest that females sing competitively against other females, and that intrasexual selection may be greater among females than among males. This is the first songbird study to show a stronger vocal role in territory defence for females than males. Stripe-headed sparrows are group-living cooperative breeders, and preliminary data suggest that polyandry and/or resource defence may explain strong female singing behaviour. Stripe-headed sparrows may be a useful study species for expanding our knowledge of vocal communication in female animals.

Keywords: birdsong; female song; duetting; sexual selection; role reversal; cooperative breeding

1. INTRODUCTION

Birdsong is an important model system for a variety of research areas, including sexual selection, vocal learning, neurophysiology and endocrinology. Much of our knowledge of song is restricted to male songbirds, and males are usually credited as being much stronger singers than females. This sex bias limits the model's predictive power. A recent increase in published studies on female singers suggests that females may sing more than previously thought, and that the biased perspective greatly under-represents the diversity of selective pressures and mechanisms in passerine song systems (Langmore 1998; Amundsen 2000; Riebel 2003; Riebel *et al.* 2005).

For sexual selection studies, the study of song function in females could reveal important information on sources of selection on females. In male birds, common functions of song are mate attraction and territory defence (Andersson 1994; Catchpole & Slater 2008), which suggests that acquiring and defending a mate are driving forces behind male ornamentation. Recent studies have shown that some females sing for similar reasons, and that females also duet with their mates in order to guard mates or to cooperatively defend territories (Langmore 1998; Amundsen 2000; Hall 2004). Other studies also hypothesize that because females often bear a larger direct cost of reproduction than males, such elaboration in females is especially adaptive in contexts of resource defence (Lebas 2006; Heinsohn 2008; Clutton-Brock

2009). Therefore, territorial female birds may be likely to use elaborate singing behaviour to defend against female competitors, or in the case of duetting species, against competing pairs. Given females' sensitivity to resource availability, one would almost expect to find species where females sing as much as or more than males for resource defence. Thorough study of a role-reversed species would be extremely useful for understanding song in females, and for testing the robustness of current theories in an empirically novel manner.

In our study, we investigated the function of song in stripe-headed sparrows (*Aimophila r. ruficauda*, family Emberizidae) in the context of conspecific territorial intrusion. Stripe-headed sparrows are a Neotropical, sexually monochromatic, cooperatively breeding passerine whose singing behaviour was previously known only via cursory observation of unmarked individuals (Wolf 1977; Stiles & Skutch 1989). We limited our study to test 'chatter song' (Wolf 1977), which is sung year-round by both sexes as solos and duets (figure 1). Males also sing 'trilled song,' but since trills are sung almost exclusively in contexts of mate attraction (A. Illes, personal observation) we did not test them here. We simulated conspecific intrusions by broadcasting female, male and duet chatter song within a mated pair's territory, and observed responses of both males and females. We predicted that if females sing to defend resources related to reproduction, they would respond more strongly to same-sex than to opposite-sex intrusion and most strongly to intrusion by pairs. Alternatively, we predicted that if mate attraction were a more important function for female song, we would either see no sex bias (all subjects were already mated) or stronger response to male stimuli. We also made similar

* Author for correspondence (ailles@u.washington.edu).

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Figure 1. Spectrograms of *A. r. ruficauda* chatter song and ticking calls. (a) female chatter, (b) male chatter, (c) chatter duet and (d) ticking calls. Sex differences in song characteristics are consistent and enabled us to reliably sex individuals. Duets are overlapping bouts of chatter in which onset and termination are the only coordinated features; degree of coordination is extremely variable.

predictions for males, and predicted that male song responses would be higher than female responses, as in almost all other species studied to date.

Here, we report results that support the resource-defence hypothesis for female song and the surprising result that females exhibited a stronger singing response to simulated same-sex territorial intrusion than did males. This is the first experimental study to describe such a role reversal in a songbird. We compare our results with those of other studies, suggest hypotheses for why female stripe-headed sparrows exhibit such strong singing behaviour and discuss the significance of the discovery of such a species for disciplines that use birdsong as a model.

2. MATERIAL AND METHODS

Stripe-headed sparrows are found from west-central Mexico through northwestern Costa Rica. Our study took place in the lowland tropical dry forest of Santa Rosa National Park of the Guanacaste Conservation Area of northwestern Costa Rica. In Santa Rosa, stripe-headed sparrows defend territories year-round and breed seasonally (June–October). We colour-banded all subjects to facilitate individual identification, and sexed birds via sex differences in song structure, body size and the presence of brood patch (A. Illes, unpublished data). The dominant male and female in groups were identified via their tendency to remain in close proximity and to duet during counter-singing interactions. We conducted all playbacks in 2007, during pre-breeding (5–25 May) and breeding seasons (26 May–8 September). For recording techniques, see electronic supplementary material.

(a) Playback stimuli

We constructed stimuli using SYRINX (John Burt, www.syrinxpc.com), and adjusted each stimulus to the same peak amplitude in ADOBE AUDITION (Adobe Systems, San Jose, CA, USA). Each stimulus track consisted of two alternating renditions of one song type repeated six times each, for a total of 12 songs. Duet stimuli contained two renditions of a pair singing one duet type. All treatment types presented one shorter rendition (4–6 s) and one longer rendition (6–9 s) separated by an intersong interval of 10 s. Average duration of entire stimuli was 189 ± 10 s (range 174–214 s). A single lure track consisted of stripe-headed sparrow ‘ticking’ calls (figure 1d), with which we attracted pairs to the playback area. Both sexes produce ticking calls in contexts of movement or mild alarm, and spectral qualities of each sex’s ticking calls

do not obviously differ. The 5 min lure track consisted of six different ticking bouts from one individual randomly repeated (interbout interval: 4.9 ± 1.1 s.d.; bout duration: 3.0 ± 1.7 s.d.; note production rate: 3.5 notes per s ± 0.8 s.d.).

We used a total of 8 duets, 9 female solo and nine male solo stimuli on 17 pairs. Because we used most stimuli on only two pairs, we could not test for effect of source stimuli. However, we feel that the number used was sufficient for avoiding pseudoreplication. Subjects received only stimuli recorded from more than two territories away. Each treatment for each pair was from a different source pair. All pairs received the same lure track in all trials.

(b) Playback design, sequence and response measures

We presented 17 pairs with three playback treatments each for a total of 51 trials. Treatments consisted of duet, female solo and male solo. Each pair received each treatment in separate trials conducted on different days; each trial was separated by 2–4 days. Treatment presentation order was randomized (number of treatments given first: duet, 7; female, 5; male, 5; second: duet, 5; female, 6; male, 6; third: duet, 5; female, 6; male, 6). All trials began between 06.30 and 09.00.

Each trial consisted of four periods: pre-playback control (5 min); variable-duration lure; experimental playback and post-playback I combined (approx. 3+5 min); and post-playback II (5 min, starting 20 min after playback initiation). We combined experimental and post-playback I periods because *post hoc* analysis showed that response intensity was generally equal during these consecutive periods. We delayed initiation of post-playback II because we were interested in long-term responses. Playback setup consisted of a lure speaker and a stimulus speaker placed 25–30 m apart, with the lure closer to the territory centre than the stimulus (for additional playback setup details see electronic supplementary material).

We began the pre-playback period by broadcasting four renditions of a heterospecific call recorded in the study area (spot-bellied bobwhite quail, *Colinus leucopogon*), and used this playback to calibrate the speakers to a natural stripe-headed sparrow peak sound-pressure level (87 dB at 1 m, measured with a RadioShack Realistic 33–2050 sound pressure level meter). The lure period started with playback of the lure, which usually attracted subjects to the playback area within 5 min. Within 15 s of the pair arriving within 5 m of the lure speaker and perching 1 m or less apart, we began experimental playback from the stimulus speaker.

If subjects did not approach the lure after 5 min of playback, we waited for 5 min and then rebroadcast the lure. If both pair members did not approach within 20 min, the trial was aborted and attempted on another day ($n=2$ pairs); if a pair did not approach on two separate days, we eliminated it from analysis (the same two pairs above). Two observers on opposite sides of and 15 m from the experimental speaker recorded all vocal responses, flights and time that birds spent within 10 m of the speaker. We also noted latency to first approach, initial approach distance and the closest approach distance. All distances reflected horizontal distance.

Vocal response measures included proportion of time spent singing, proportion of time spent soloing (time spent singing alone both during solos and duets), number of solo bouts, song latency and sex of the first bird to sing in response to playback. For duets, we recorded sex of the first bird to sing (the duet 'initiator'). For more details on song response measures, see electronic supplementary material.

(c) Statistical analyses

To analyse normally distributed response measures, we used a mixed-model ANOVA with restricted maximum-likelihood estimation of model parameters. Pair and subject nested within pair were entered as random effects. This approach accounts for non-independence of data arising from multiple trials conducted on each pair and on each individual. Each response measure was initially modelled with sex, treatment type, trial order (1, 2 or 3), a sex by treatment interaction, an order by treatment interaction, time of day and season (prebreeding or breeding). Non-significant terms were sequentially removed from the model. To determine the differences between treatments, we used *post hoc* Tukey and Student's *t*-tests (both at $\alpha=0.05$). For data transformations, see table 1 in the electronic supplementary material.

We analysed various measures separately, but then used a principal components analysis to summarize the overall singing and approach responses to playback. We report all eigenvalues greater than 1. We generated PC1, a 'song response' factor, PC2 an 'approach response' factor and PC3 a 'fly and time close' factor (table 1, electronic supplementary material). High PC1 values indicate greater time spent singing, greater time singing alone in a greater number of bouts and a greater likelihood to initiate duets. Low PC2 values describe subjects who approached more quickly, more closely and who ultimately approached the closest. High values of PC3 describe individuals who spent more time close to the speaker and who made more flights.

We used non-parametric Wilcoxon matched-pairs signed-rank tests to determine the differences between non-normally distributed post-playback period II data. We Bonferroni-corrected the various tests, but also presented effect sizes (see table 1). When comparing song output among different playback periods, we averaged each individual's three measures across treatments and performed Wilcoxon tests on these averages. For all analyses, we used JMP v. 6 for Windows. Proportions are expressed as percentages, medians with lower (Q_1) and upper (Q_3) quartiles, and means with standard errors. All tests are two tailed.

3. RESULTS

Pairs sang vigorously and approached in response to playback in all trials. Males sang trills in two cases, but only one rendition each (<1% of song response),

and both more than 10 min after the end of playback. Usually, only dominant individuals sang. Occasionally subordinate males sang, and in a few cases we could not distinguish between dominant and subordinate male song. Therefore, subordinate male song may be included in the measures of male song response and may overstate individual male response. In no cases did subordinate females sing.

(a) Pre-playback song output and initial response to playback

Many individuals did not sing prior to playback (51 trials, females, 34 cases; males, 45 cases). However, females sang more than males during pre-playback ($n=17$ Wilcoxon $Z=-26.0$, $p=0.042$, figure 2a). Both sexes increased song output during playback ($n=17$; females: Wilcoxon $Z=76.5$, $p=0.000$; males: Wilcoxon $Z=76.5$, $p=0.000$, figure 2a). Females almost always sang first (females first in 16 out of 17 duet trials, 17 out of 17 female solo trials and 15 out of 17 male solo trials; $\chi^2=20.2$, $p<0.0001$). For analysis of sex to approach first, we eliminated one trial each from duet and female treatment groups, because males and females approached simultaneously. Both sexes were equally likely to be the first to approach duet and female playbacks (binomial tests; first approaches in duet trials: female, 9; male, 7; $p=0.804$; female trials: female, 11; male, 5; $p=0.210$), but males were more likely to approach male playback first (male trials: female, 4; male, 13; $p=0.049$). Pairs approached female and duet treatments ($F_{2,68}=3.89$, $p=0.003$, figure 2b) and second or third trials ($F_{2,58}=3.80$, $p=0.028$) more quickly. Season, sex by treatment and treatment by order interactions for approach latency had no effect ($p>0.250$). While the sex differences were not significant, on average females approached male stimuli almost twice as slowly as males (females = 32.1 ± 12.6 s, males = 18.1 ± 4.7 s).

(b) Response during combined playback and first post-playback period

The final model for PC1 song response showed that females generally responded more strongly than males (sex effect, $F_{1,16}=24.0$, $p=0.0002$), that females responded more strongly than males during duet and female treatments, and the same as males during male treatments (sex by treatment interaction, $F_{1,63}=15.5$, $p<0.0001$; for all PC analyses, see figure 3). Order, season and the order by treatment interaction did not affect PC1 ($p \geq 0.145$). Close inspection of each of the song response measures that comprise PC1 (figure 4) showed that, on average, females sang 30 per cent more than males during duet playback, twice as much as males during female playback, but during male playback males and females sang equally. Females also sang thrice as many solos and initiated twice as many duets as males did in response to same-sex playback. For PC2 approach response pairs approached duet playback more quickly and closely than male playback, but there was no difference between male and female playback (treatment effect, $F_{2,62}=6.34$, $p=0.003$). Pairs responded more strongly to the third treatment than the first (order effect, $F_{2,62}=3.76$, $p=0.029$), but there were no significant interaction or season effects ($p \geq 0.245$). PC3 fly and time close showed no significant effects ($p>0.200$).

Figure 2. (a) Proportion time spent singing according to playback period and sex. Boxplots represent median, inter-quartile range and 10th percentiles. (b) Effect of treatment and sex on approach latency. Levels not connected by a letter are significantly different. Grey bars, female; white bars, male.

(c) *Response during the second post-playback period*

Twenty minutes after the end of playback, both males and females were still singing at greater than pre-playback levels ($n=17$; females: Wilcoxon $Z=68.5$, $p=0.000$; males: Wilcoxon $Z=68.0$, $p=0.000$, figure 2a). However, females sang more than males, regardless of treatment (female = $13 \pm 1.9\%$, male = $5.6 \pm 1.1\%$, $F_{1,16} = 17.9$, $p=0.0006$). For other vocal responses, females responded more strongly than males in all treatments (table 1). There were no sex differences in time spent close to the speaker or number of flights.

4. DISCUSSION

In our study, female stripe-headed sparrows played a leading role in a pair's singing response to simulated territorial intrusions: when first responding to playback, females almost always sang before males and across all treatments initiated more singing bouts than males. In addition, female song response to pair and same-sex intrusions was higher than male song response to male intrusions. Lastly, the duration of this elevated female response was sustained: 20 min after the end of playback, females were still leading and singing more than males, even after male solo playback. These data suggest that females perceive territorial intrusions as more threatening than their mates do, and that females are the primary territory defenders in this species.

The function of chatter song appears to overlap partially, however, in both sexes. Increased song output over baseline, coupled with approach to any chatter playback, suggests that both sexes perceived chatter as a

Figure 3. Effects of playback type on principal component response measures of both male (white bars) and female (grey bars) subjects.

threat. In addition, both sexes responded with chatter. These results are consistent with a territory defence function for both sexes, and with a possible mate-guarding function in duets (Hall 2004). Because neither sex sang more in the presence of the opposite sex, it appears that neither uses chatter to attract potential mates, at least when they are already mated or in an intrusion context. It is important to note, however, that males use a different kind of song for mate attraction (§1).

The data show that pairs reacted to intrusions of any sort in a coordinated physical fashion, yet females were much more vocally aggressive, especially to the same sex. Males, on the other hand, showed no change in singing behaviour according to treatment, and only neared female song output during male treatments. The approach responses of both sexes rarely differed. Similar approach latencies and equal number of flights suggest that individuals immediately followed if their mate flew. Both sexes also showed that they perceived two individuals (duet playback) as a greater threat by approaching duets more quickly and closely. An order effect for the PC2 approach response indicates that the subjects also considered repeated intrusion as an increasing threat.

The most popular hypothesis for the mechanism of elaborate song evolution in birds is sexual selection (Andersson 1994; Catchpole & Slater 2008). In stripe-headed sparrows, two results suggest *greater* intrasexual competition among females than among males: the degree to which female singing response surpassed male singing

Figure 4. Effect of playback type on separate song response measures (mean $\pm$ s.e.). Statistical tests were performed on these combined measures as a principal component (figure 3). Grey bars, female; white bars, male.

Table 1. Post-playback II response data, Wilcoxon signed-rank test and effect sizes. (Median, $\bar{x}$; interquartile range = Q_1 – Q_3 . For each test, $n = 17$. Italicized p values are significant before Bonferroni correction; asterisks indicate significance after Bonferroni correction.)

		female		male				
response measure	treatment	$\bar{x}$	Q_1 – Q_3	$\bar{x}$	Q_1 – Q_3	z	p -value	effect size ^a $r = z/\sqrt{n}$
<i>song</i>								
per cent time singing solo	duet	4.6	0.7–12	0.0	0.0–2.3	–58.0	0.000*	–9.94
	female	5.6	0.6–15	0.0	0.0–4.6	–52.0	0.000*	–8.92
	male	2.3	0.0–12	0.3	0.0–2.0	–32.5	0.021	–5.57
number of solos	duet	4.0	0.0–13	0.0	0.0–1.5	–38.0	0.005*	–6.52
	female	6.0	0.5–18	0.0	0.0–0.5	–45.0	0.000*	–7.72
	male	2.0	0.0–12	0.0	0.0–2.0	–28.0	0.049	–4.80
number of duets initiated	duet	1.0	0.0–7.0	0.0	0.0–0.0	–27.5	0.002*	–4.72
	female	1.0	0.0–4.0	0.0	0.0–0.0	–27.5	0.002*	–4.72
	male	2.0	0.0–5.0	0.0	0.0–1.5	–27.0	0.014*	–4.63
<i>approach</i>								
time in 10 m	duet	0.0	0.0–23	0.0	0.0–41	0.50	1.00	0.09
	female	0.0	0.0–1.3	0.0	0.0–0.0	–2.00	0.500	–0.34
	male	0.0	0.0–17	0.0	0.0–17	–0.50	1.00	–0.09
number of flights	duet	2.0	0.0–2.5	1.0	0.0–2.0	–3.00	0.250	–0.51
	female	2.0	0.0–3.0	2.0	0.0–3.0	1.00	1.00	0.17
	male	1.0	0.0–3.0	1.0	0.0–4.0	5.00	0.313	0.86

^aField (2005).

response, and the fact that it did so mainly in same-sex contexts. For intrasexual selection to be greater among females than males, variance in reproductive success should be greater among females (Andersson 1994). In this group living, cooperatively breeding species, possible sources of high reproductive variance among females may be competition for breeding territories, breeding status and/or male parental care. Preliminary observation suggests that reproductive suppression and polyandry may be important factors in this system. Our future studies will investigate these issues.

Our study adds to increasing evidence that territory or resource defence may be an important function of female birdsong. Among passerines, both female superb fairywrens (Cooney & Cockburn 1995) and New Zealand bellbirds (Brunton *et al.* 2008) sing to defend territories. Among non-passerines, female greater Vasa parrots *Caracopsis vasa* (Ekstrom *et al.* 2007) sing to ensure male parental care, and female black coucals *Centropus grillii* (Goymann *et al.* 2004) sing to defend territories. Other recent examples of aggressive resource defence in female birds include tree swallows *Tachycineta bicolor*

(Rosvall 2008), *Eclectus* parrots (Heinsohn 2008) and wattled jacanas *Jacana jacana* (Emlen & Wrege 2004). For *A. r. ruficauda*, the fitness benefit of aggressive behaviour may lie in the acquisition of breeding territories and breeding status (A. Illes, unpublished data).

To our knowledge, this is the first study to show a stronger vocal role in territory defence for females than males. Observational studies found that females sang more frequently than males in streaked-backed orioles *Icterus pustulatus* (Price *et al.* 2008), in breeding New Zealand bellbirds *Anthornis melanura* (Brunton & Li 2006) and Cocos flycatchers *Nesotriccus ridgwayi* (Kroodtsma *et al.* 1987), but all three studies lack information on sex differences in territorial response. An additional study of female bellbirds found that the subjects used song in territory defence (Brunton *et al.* 2008), but the oriole and flycatcher studies lack information on song function. Other studies of female singers have either not found that females out-sing males, or have not compared female with male song output. It is unclear whether this lack of song role reversals is due to research bias towards males, such as is documented in European birds (Garamszegi *et al.* 2007), or if this trait is actually rare. It is likely that both 'research bias' and 'rarity' explanations have merit, but more study is needed to explain the lack of data.

Stripe-headed sparrows belong to a group of birds (oscine passerines) whose vocal behaviour is a model for understanding acoustic communication in many taxa, even humans. Despite many years of investigation, little is known about the function, ontogeny, mechanism and evolution of female song, making the system an incomplete model. We feel that the high expression of song in female stripe-headed sparrows makes them a particularly useful study species for understanding female aspects in all of these study areas. We also anticipate that, as researchers continue to investigate additional monomorphic and/or tropical species, they will discover many more singing females, showing that the importance of female birdsong is greatly underestimated.

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