

Female and male song rates across breeding stage: testing for sexual and nonsexual functions of female song

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As a textbook example of a sexually selected trait, song in male birds has been extensively examined in the context of female mate choice and male–male competition for access to mates. Female song is also phylogenetically widespread, and probably ancestral. However, we know relatively little about when and why females sing. Female song may be important for female–male communication, e.g. fertility advertisement, mate attraction or coordinating the care of young. Alternatively, female song may function in the context of female–female competition for reproductive resources, e.g. nest sites, year-round territories or parental assistance. We quantified spontaneous song, and song in response to playback of an unfamiliar female song, in female and male superb fairy-wrens, *Malurus cyaneus*, across breeding stages. We found that females and males sang with roughly equal frequency spontaneously; however, females sang much more frequently than males in response to playback of unfamiliar female song. We found no difference in song rates across breeding stage, and no effect of age or the presence of subordinates. In both sexes, song rates increased slightly across the breeding season. Female song rates were also repeatable across the season. Overall, the results suggest that although female song is likely to be a multipurpose trait, as in males, the primary function in superb fairy-wrens appears to be female–female competition.

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Birdsong is among the most important model systems for a wide variety of fields including animal behaviour, evolutionary biology, developmental biology and speciation. The longstanding view is that song is primarily a male trait, and that it evolved in the context of male–male competition over females, either directly via female preferences or indirectly by males competing with other males to acquire and defend resources that females need (Catchpole & Slater, 1995; Searcy & Nowicki, 2010). However, recent work has shown that song is also widespread among females, and is probably the ancestral state for songbirds (Garamszegi, Pavlova, Eens, & Möller, 2006; Odom, Hall, Riebel, Omland, & Langmore, 2014; Price, 2009; Price, Lanyon, & Omland, 2009). Because females are rarely limited by access to genetic partners, this brings into question how song has evolved and persisted, and suggests that other selective mechanisms may be important, e.g. mate attraction, group cohesion or coordination and female–female competition (Langmore, 1998; Odom et al., 2014).

Female song may advertise fertility, solicit male courtship or coordinate offspring care with social partners (Langmore, 1998). In species that reside on year-round territories, female song might also be important for advertising availability as a mate, in the event of a divorce or death of the social male (Langmore, 1998). Alternatively, female song may function in the context of female–female competition for access to resources (e.g. nest sites, territories, offspring care and dominance rank; Langmore, 1998). This form of competition appears to be an important mechanism favouring the expression of traits such as bright colours, aggression and weaponry (Cain & Ketterson, 2012; Cain & Rosvall, 2014; Tobias, Montgomerie, & Lyon, 2012; West-Eberhard, 1983).

To understand which mechanisms underlie the evolution of song, and why females of some species have lost song while males have retained it, we first need to know when and why females sing. Examinations of song rates have provided insights into the selective forces in male song (Catchpole, 1973; Möller, 1991) and sex differences in the function of song (Illes & Yunes-Jimenez, 2009; Levin, 1996). Males sing most when critical reproductive resources are most valuable or threatened, or when mate attraction is most important (Catchpole & Slater, 1995; Searcy & Nowicki, 2010). Thus, understanding the phenology of song rates provides insight into the function. However, female song rate patterns have not been

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well studied (Riebel et al., 2005). As a consequence, it is unclear whether females are using song to communicate with males, to compete with other females, or both. Here, we addressed these broad questions in superb fairy-wrens, *Malurus cyaneus*, by (1) examining female song patterns across the breeding season, (2) contrasting them with male song patterns, and (3) comparing female and male responses to playback of unfamiliar female song.

Superb fairy-wrens are socially monogamous and biparental, and occupy year-round territories (Dunn & Cockburn, 1996; Rowley & Russell, 1997). Females initiate high rates of extrapair matings; extragroup males sire 72% of young (Double & Cockburn, 2000; Dunn & Cockburn, 1999). Males may remain on natal territories as nonbreeding subordinates and assist the breeding pair in nestling feeding and defence (Cockburn et al., 2008). All group members assist in provisioning nestlings; however, dominant males adjust their level of care according to the number of subordinates and their level of paternity (Dunn & Cockburn, 1996). Daughters disperse and must acquire their own territory and mate in order to breed or survive (Cooney & Cockburn, 1995). Female and male fairy-wrens sing a structurally similar year-round song (Fig. 1; Cooney & Cockburn, 1995; Langmore & Mulder, 1992); however, males sing longer songs with more elements (Kleindorfer et al., 2013). In a previous study in this species, Cooney and Cockburn (1995) conducted a detailed, repeated measures analysis of song patterns focusing on the prebreeding ($N = 15$) and nest-building periods ($N = 5$). This study found that females sang more during the breeding season than over winter, suggesting a breeding function. Females also showed a stronger response to foreign females than to neighbours, suggesting a territorial defence function. However, this study did not examine song rates once breeding had begun and did not quantify how the breeding male responded to unfamiliar female playback within the territory.

Here, we built on this study by examining spontaneous song rates in both sexes across the breeding season in a larger sample ($N = 75$ of each sex). We also quantified song rates in both sexes in response to unfamiliar female song playback, simulating a potential female competitor (for the female) or potential mate (for the male). The hypotheses for female song generate contrasting predictions. First, if female song is used to attract a mate, song rates should be highest when females are unpaired, while if song is used to advertise fertility, then song rates should be highest when females are breeding but before they have completed egg laying. Further, unfamiliar female song will have no effect on female song rates, but may affect male song rates. Second, if females use song to

coordinate care with social partners, song rates should be high when there are young, but we would not expect a change in song rates in response to unfamiliar playback from either sex. Finally, if females use song primarily to communicate territory ownership with other females, or to defend social partners or territories, we predict that females will respond robustly to the simulated competitor (unfamiliar female song), while males may show no behavioural changes. Further, if females defend territories in a manner similar to males, we might observe that song rates attenuate over time (Catchpole & Slater, 1995). However, because fairy-wrens nest multiply and resources may become scarcer as the season progresses, territory defence throughout the breeding season may be essential. If so, we may observe that song rates are sustained or increase across the breeding season. We also examined the relationships in song rates within pairs, to determine whether there is an association between female and male song rates, which may reflect coordinated resource defence. Finally, a subset of females were assayed twice to determine repeatability; high repeatability in singing behaviour would suggest consistency within females, and is expected if song reflects territory or female quality, while low repeatability would suggest that song rates are the product of external factors, and is expected if song functions to communicate with potential mates or group members.

METHODS

Study Species and General Field Methods

This study was conducted during the 2012–2013 breeding season (August–January). Adults were uniquely colour-ringed, and all nesting attempts were located and monitored throughout the season. For each breeding group, we determined female age using previous ringing records, and the number of subordinates using field observations. Individuals ($N = 57$ unique pairs) were classified accordingly as first-year breeders or older than first year ($N = 25, 32$ respectively), and as group or pair breeding ($N = 20, 37$ respectively). Nineteen females were assayed twice to estimate repeatability. Breeding stage was categorized as prebreeding (more than 10 days before laying the first egg of the season, $N = 37$), breeding but currently without young (within 10 days of laying, nest building or between nesting attempts, $N = 10$), or breeding with young in the nest (eggs or nestlings, $N = 30$). The study used females from two long-term study sites in native woodland patches 6 km apart in Canberra, southeastern Australia: the Australian Botanic Gardens ($N = 30$; $35^{\circ}16'S, 149^{\circ}06'E$; Cockburn et al., 2008; Mulder, 1997) and Campbell Park ($N = 27$; $149^{\circ}9'E, 35^{\circ}16'S$; Langmore & Kilner, 2007).

Song Recording and Playback Construction

Songs used for playback were recorded using a Sennheiser shotgun microphone (model ME66) and a Zoom digital recorder (model H4N). Songs were recorded opportunistically from spontaneously singing females or in response to a brief song playback (2–3 s). Playback tapes were created in Audacity 2.0.3 (audacity.sourceforge.net) using high-quality recordings, as determined by high signal-to-noise ratio. Selected songs were processed through a high-pass filter to remove low-end noise, with a cutoff of 200 Hz, then normalized so that all songs had the same peak volume (90% of peak amplitude). Playback identity had no effect on song rates ($P = 0.7$), and excluding playbacks made with songs sung in response to brief playback ($N = 3$) had no effect on the results.

Each playback consisted of two unique songs taken from a single bout of song from the same female. Playbacks began with 60 s of silence followed by the first song, repeated three times and with 20 s of silence between each song bout; this was followed with 45 s of

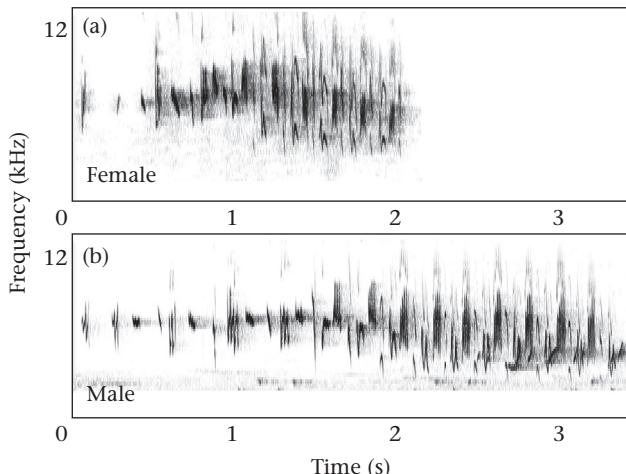


Figure 1. Spectrograms of typical (a) female and (b) male superb fairy-wren song (type 1 song; Langmore & Mulder, 1992).

silence and then three repeats of the second song, again with 20 s between song bouts. This pattern was then repeated (first song \times 3, second song \times 3, silence, first song \times 3, second song \times 3). Each playback was 400 s long with slight variation due to the length of selected songs (mean \pm SE = 402.4 ± 5.8 s). The silence to song ratio and the length of the playback are consistent with observed natural variation in female song (Cooney & Cockburn, 1995). To minimize pseudoreplication we created 36 playback tapes (18 for each population). Females may respond differently to familiar individuals and strangers (Brunton, Evans, Cope, & Ji, 2008; Cooney & Cockburn, 1995; Temeles, 1994), so each female was exposed to a recording of a female from a different population. The playback for a trial was chosen at random; if a playback was used three times it was retired from use.

Quantifying Song Rates

We quantified female and male song rate patterns using a standardized behavioural paradigm that allowed us to quantify both spontaneous song rates and song rates in response to a simulated intruder (Cain, Cockburn & Langmore, 2015). Focal females were identified randomly; thus the observer was blind to female age and breeding stage during the trial (although behaviour occasionally revealed stage). While an equal sample per breeding stage was the goal, owing to predation and random selection of females, this was not achieved (prebreeding, $N = 37$; breeding, no young, $N = 10$; breeding, eggs or chicks in the nest, $N = 30$). A trial began when the focal female was located and included two periods: preplayback (spontaneous song rates) and response (song rates in response to playback stimuli). During the preplayback period, each focal female was observed passively for 10 min and all songs produced by the female and male were tallied separately as spontaneous songs. At the end of this period, a speaker was positioned within 5 m of the female in the immediate area she was observed in, with preference given to areas with good visibility. In the centre of this area we placed an Apple iPod (Apple, Cupertino, CA, U.S.A.) connected to a Pignose amplified speaker (model 7100), hidden in a low bush or high grass, and on the ground with the cone facing up. If birds were disturbed during speaker placement, the trial was aborted ($N = 3$). Once the speaker and observer were in position, a playback of unfamiliar female song (see above) was started and the response period commenced. All songs produced by the focal female or other group members during the playback period (7 min, see playback above) were subsequently tallied from audio recording of the trial. Group composition did not increase from spontaneous to response trial periods; thus changes in song rates are not due to changes in the number of group members present. Male song rate from that trial was excluded if the female was alone during the trial, if the male was not present for the entire trial or if there were multiple males (subordinates) and the identity of the singer could not be determined; there were no differences in female song rates for trials in which males were excluded (ratio = 1.0, $P = 0.3$). To determine repeatability of female responses, a subset of females was assayed twice; trials were at least 2 weeks apart and at a different breeding stage ($N = 19$). If more than one female responded, which may indicate we were inadvertently near a territory border, the trial was aborted ($N = 1$). Females varied in their response, but often approached the speaker and initiated flights and dives in the direction of the speaker, suggesting they were aware of and responding to the playback (Cain et al., 2015).

Ethical Note

This study required nonmanipulative and manipulative behavioural observations. Manipulations were song playbacks, restricted to 7 min, and had no negative impacts on individuals. All

procedures performed in this study were in accordance with the ASAB/ABS 'Guidelines for the treatment of animals in behavioural research and teaching' and the EU Directive 2010/63/EU for animal experimentation. This work was also conducted with approval of the Australian National University Animal Experimental Ethics Committee (A2012/54).

Statistical Analysis

To determine what factors might influence female and male song rates, we used linear mixed models (LMM), which allows random effects, with song rate (number of songs per minute) as the dependent variable. A generalized linear mixed model (GLMM), with Poisson distribution and log link, provided the same qualitative results (Table A1). Initial factors included sex, breeding stage, day of trial, age (first year or past first year), trial order (first or second), group size (pair or group breeding) and breeding status (prebreeding, breeding without young, breeding with young). Because we were interested in sex differences, we also included interactions between these factors and sex. Individual identity, pair identity and population were included as random factors. To maximize our power to detect potential relationships, we chose to simplify the full model using stepwise backward procedures to remove nonsignificant variables ($P > 0.1$ to remove), starting with interactions. However, we present parameter estimates for all initial factors for clarity. All analyses were conducted using R for Mac OSX Version 3.1.1 'Sock it to Me' (R Core Team, 2014), linear mixed models used the function lmer in the package 'lme4' version 1.1 (Bates, Mächler, Bolker, & Walker, 2014).

To determine whether female and male song rates within a pair were related, we examined the correlation between female and male song rates. Because song rates were not normally distributed, we calculated Spearman correlation coefficients, and analysed the spontaneous and response song rates separately.

To estimate repeatability we used the analysis of variance approach recommended by Lessells and Boag (1987). We excluded males, and because we observed strong differences in spontaneous versus response song rates, we examined these measures in two separate models. All repeat trials were done within one population (Botanic Gardens), so we restricted this analysis to that population, and to maintain a balanced design we used only females sampled twice.

RESULTS

Song rates were strongly related to the sex of the singer and context, i.e. whether song rate was measured before or during playback of female song (Tables 1 and 2). These differences were driven by a significant interaction between sex and the context of the songs (Fig. 2). Females showed a marked increase in song rates in response to the simulated intruder, while male song rates were unchanged. There was a slight, but significant, increase in song rates with date in both sexes (Fig. 3a, Table 1). Song rates were unrelated to the breeding stage, age, trial number, group size (pair or group), or interactions between sex and age, sex and date, sex and subordinates, or sex and breeding status (Tables 1 and 2). Female and male song rates were strongly correlated (Fig. 3b; spontaneous: $r_s = 0.4$, $P = 0.001$; response: $r_s = 0.6$, $P < 0.0001$).

Female spontaneous song rates showed low to moderate repeatability across trials; (repeatability sensu Lessells & Boag, 1987; $r = 0.28$, $N = 17$, $F = 1.9$, $P = 0.09$). However, response song rates were highly repeatable ($r = 0.47$, $N = 17$, $F = 2.7$, $P = 0.03$), suggesting that response song rates are more likely to be a property of the individual and may be less affected by other factors.

Table 1

Song rates before and in response to playback of unfamiliar female song

Variable sex	Classification	Spontaneous songs/min (mean±SE)	Response songs/ min (mean±SE)
Group size			
Female	Pair breeding	0.26±0.07	0.45±0.07
	Group breeding	0.34±0.05	0.48±0.08
Male	Pair breeding	0.30±0.07	0.29±0.07
	Group breeding	0.38±0.06	0.29±0.10
Age			
Female	First year	0.30±0.09	0.44±0.09
	Past first year	0.27±0.05	0.47±0.06
Male	First year	0.28±0.06	0.33±0.08
	Past first year	0.37±0.08	0.26±0.08
Breeding stage			
Female	Prebreeding	0.26±0.05	0.33±0.05
	Breeding, no young	0.40±0.27	0.66±0.2
	Breeding with young	0.28±0.06	0.56±0.10
Male	Prebreeding	0.29±0.05	0.20±0.06
	Breeding, no young	0.32±0.20	0.27±0.20
	Breeding with young	0.38±0.10	0.40±0.11

Values are not adjusted for other effects in the final model (e.g. day of trial).

Table 2

Results of the LMM examining potential factors related to song rates of female and male superb fairy-wrens

	Estimated coefficient	SE	F	P
Minimum adequate model				
Intercept	−0.6	—	—	—
Female ^a	0.04	0.06	1.9	0.17
Day of Trial	0.003	0.001	4.7	0.03
Response to playback ^b	0.2	0.06	1.8	0.18
Female*Response	0.2	0.09	5.6	0.02
Excluded variables				
Age (older than first year) ^c	−0.03	0.06	0.6	
Breeding status			0.5	
Trial number	0.002	0.002	0.9	
Age ^c *Female	−0.04	0.12	0.7	
Group breeding ^d	0.06	0.07	0.4	
Subordinates*Female	0.01	0.1	0.5	
Female*Day of trial	0.0002	0.004	0.95	
Female*Breeding status		0.5		

For excluded variables we report estimates and P values from the step prior to exclusion from the final model. Significant P values are in bold.

^a Relative to male song rate.^b Relative to spontaneous song rates.^c Relative to first year.^d Relative to pair breeding.

DISCUSSION

Here we report that female song in superb fairy-wrens is maintained at a similar rate throughout the breeding season, regardless of breeding stage. Further, although male and female song rates did not differ prior to playback of an unfamiliar female's song, female song rates increased in response to female playback, while male song rates did not. Taken together, these results best support the predictions for female song functioning as a signal to other females, rather than to mates, potential mates or social group members. Female–female competition appears to be a primary driver of song rate in this species.

Female–Male Communication

A main function of male song is the attraction and courtship of potential mates and research has suggested some females use song in a similar capacity. In polygynandrous alpine acceptors, *Prunella collaris*, fertile females compete for males by singing whenever they are alone, and female song attracts males (Langmore, Davies, Hatchwell, & Hartley, 1996). In closely related dunnocks, *Prunella modularis*, fertile females produce trill calls, which also attract males

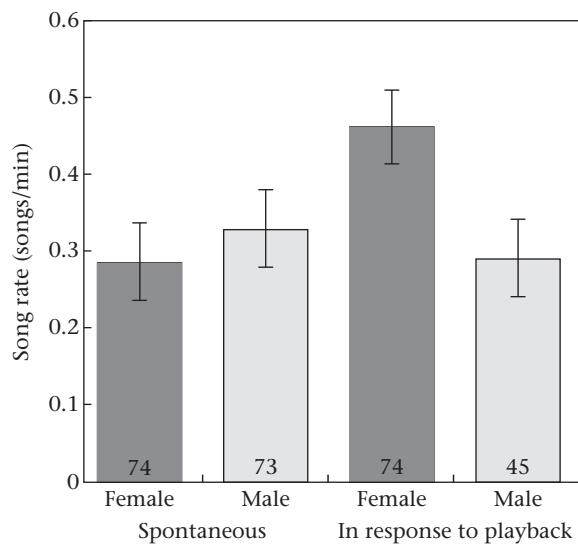


Figure 2. Mean ± 1 SE song rates according to sex and context (spontaneous or response to playback). Values shown are not adjusted for other factors in the model; see Table 2 for full analysis. Numbers in bars are numbers of individual females or males.

(Langmore & Davies, 1997). Female red-cheeked cordon-bleu, an African estrildid, *Uraeginthus bengalus*, sing mainly before egg laying and males respond to female song with courtship behaviours (Gahr & Güttinger, 1986). Further, removal of mates often leads to an increase in female vocalizations (Eens & Pinxten, 1998; Tobias, Gamarra-Toledo, García-Olaechea, Pulgarin, & Seddon, 2011).

Superb fairy-wren females might use song to attract males in three contexts: unpaired, first-year females may sing to attract a mate at the commencement of the breeding season, older females may sing to attract a mate after the death or divorce of their mate, and paired females may sing to attract extrapair mates during their fertile period. In all three contexts, we would expect males to respond to female song. In contrast to this prediction, males did not alter song rates in response to female song. Further, song rates were no higher in first-year females than in older females, and there was no increase in song rate at the commencement of the breeding season or in the days leading up to egg laying. Previous research in fairy-wrens also found that both sexes respond more intensely to a simulated same-sex intruder (Kleindorfer et al., 2013), and that extragroup males do not respond to female song with courtship displays (Cooney & Cockburn, 1995; Kleindorfer et al., 2013).

However, previous work in this population did observe a marked increase in song rates during the pair and territory formation period (Cooney & Cockburn, 1995), and we did not have sufficient sample sizes to test whether song rates were higher in females that had lost their mate or during their brief fertile period (2–4 days before egg laying (Double & Cockburn, 2000)). Thus mate attraction may still play a role in female song. Further, although males did not increase song rates, males might express interest by behaviours other than song, e.g. approaches or displays. We did not explicitly quantify male display or courtship behaviours, and so cannot rule out this possibility; however, we did not observe any courtship behaviours. Taken together, these collective findings suggest that although mate attraction is unlikely to be the primary function of female song, it still may be important for female–male communication.

Group Coordination

Females might use song to communicate with social group members, i.e. to coordinate or solicit parental assistance from the mate or subordinate males, or to maintain group cohesion. For

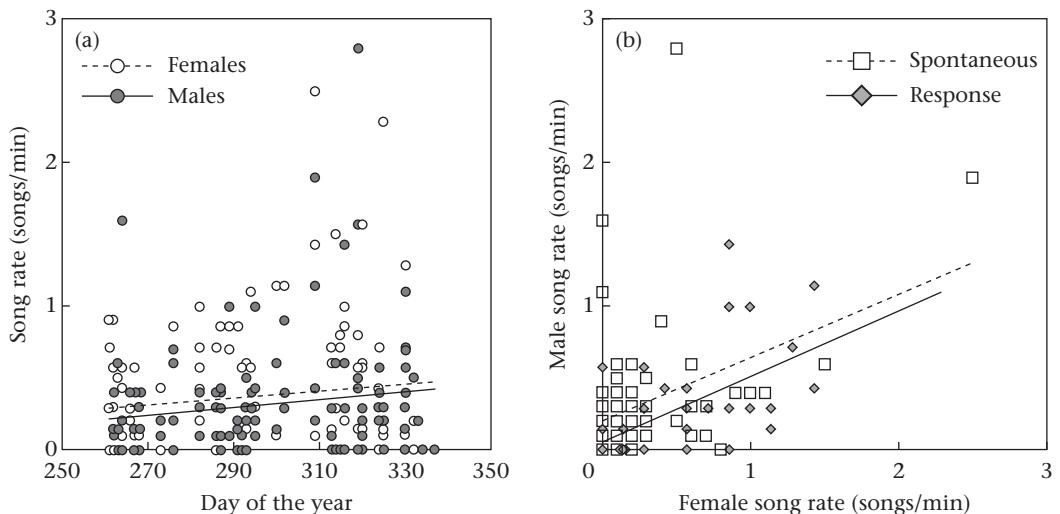


Figure 3. (a) Scatterplot of song rates according to the day of trial and sex. (b) Correlation between female and male song rates within pairs.

example, female black-headed grosbeaks, *Pheucticus melanocephalus*, sing to elicit begging from fledglings (Ritchison, 1983), and female cardinals, *Cardinalis cardinalis*, sing to solicit male nestling feeding (Halkin, 1997). If fairy-wrens use song to elicit nestling provisioning by males, we would predict that song rates would be highest when there are young. In contrast, we found that spontaneous song rates were unrelated to breeding stage; females did not sing more, or less, when there were young in the nest. This suggests that coordination of parental care is also unlikely to be the primary driver of female song in superb fairy-wrens. Moreover, if female song functions to maintain group cohesion, we might predict that song rates would be higher in groups with subordinates, yet this was not the case. Taken together with the results presented above, it is unlikely that female song functions primarily to facilitate female–male communication.

Female–Female Communication/Competition

In migratory species, male song rates tend to be highest in the prebreeding season, when territory boundaries are being delineated and pair formation occurs, then attenuating after pairs and territories are established, or ceasing completely in some non-territorial species. For example, seasonally territorial dark-eyed juncos, *Junco hyemalis*, sing most frequently during the prebreeding season, and maintain a moderate level of song through the breeding season (Titus, 1998), while sedge warblers, *Acrocephalus schoenobaenus*, sing only until paired (Catchpole, 1973). In other words, investment in song is directly dependent on the nature of the resource being defended, and when it is valuable (Lattin & Ritchison, 2009; Marler & Slabbekoorn, 2004; Searcy & Nowicki, 2010). We observed that song rates increased with date in both sexes. Previous research on the New Zealand bellbird, *Anthonis melanura*, also found that female song rates increased as the breeding season progressed (Brunton et al., 2008), while in stripe-headed sparrows, *Peucaea r. ruficauda*, date was unrelated to female response song rates (Illes & Yunes-Jimenez, 2009). In captive European starlings, *Sturnus vulgaris*, females occupying nestboxes sing more than females without one, and sing year-round (Pavlova, Pinxten, & Eens, 2007). In contrast, in female black coucals, *Centropus grillii*, a polyandrous, sex role-reversed species in which females compete for mates, female song rates decreased across the breeding season (Geberzahn, Goymann, Muck, & Cate, 2009). These findings suggest that the relationship between date and song reflects sex and species differences in reproductive strategies.

Female song rates increased in response to the unfamiliar female playback, while males did not change their song rates. A similar pattern has been reported in bellbirds (Brunton et al., 2008), dusky antbirds, *Cercomacra tyrannina* (Morton & Derrickson, 1996), subdesert mesites, *Monias benschi* (Seddon, Butchart, & Odling-Smee, 2002), magpie-larks, *Grallina cyanoleuca* (Mulder et al., 2003), eastern whipbirds, *Psophodes olivaceus* (Rogers, Langmore, & Mulder, 2006), black coucals (Geberzahn et al., 2009), warbling antbirds, *Hypocnemis cantator* (Seddon & Tobias, 2005), and in a different population of superb fairy-wrens (Kleindorfer et al., 2013). In stripe-headed sparrows females also increase song rates in response to unfamiliar female playback (Illes & Yunes-Jimenez, 2009). Further, paired female stripe-headed sparrows sing more frequently and have more complex repertoires than males, and observations of natural song rates suggest that female song is most important for female–female competition (Illes, 2015).

For each of these species, females exhibited stronger responses to female playback than their male partner. This sex-specific response is also consistent with other studies examining female response to simulated competitors during the breeding season. Females are often more aggressive towards simulated female intruders than towards male intruders (Cain, Rich, Ainsworth, & Ketterson, 2011; Mays & Hopper, 2004; Pärn, Lindström, Sandell, & Amundsen, 2008). Taken together, these collective findings suggest that female passerines defend sex-specific resources, or defend them more against same-sex competitors. However, because each of these species is socially monogamous with biparental care, it is unclear whether females are defending a territory, their mate, the mate's parental care efforts, or some combination of all three (Cain, 2014).

Because of the peculiar fairy-wren mating system, it is unlikely that females would defend genetic mates; extrapair paternity is very high (>70%) and females often pair socially with a son or grandson from a previous brood (Cockburn, Osmond, Mulder, Green, & Double, 2003). However, social partnerships are very important, and females are reliant on male partners for assistance with offspring provisioning and nest defence, suggesting that social partners are a resource worth defending (Dunn & Cockburn, 1996; Rowley & Russell, 1997). Anecdotal observations support this possibility. During the breeding season following this study, the death of one male appeared to spur competition for a single remaining male between two neighbouring females; the male moved between the two territories and the spontaneous song rates for those females were 0.9 and 1.1 songs/min when they were unaccompanied by the male, roughly five times the mean spontaneous song

rate reported here (Langmore & Cain, 2013). Further, males differ markedly in the amount of care they provide (Dunn & Cockburn, 1996), suggesting that females might benefit from defending more paternal males. However, the level of paternal care is not a property of the individual. Instead, it appears to be affected by the presence of subordinates and the level of paternity, which the female controls (Dunn & Cockburn, 1996); thus further research is clearly required before we can make any firm conclusions.

Subordinates may also be an important reproductive resource that females defend against other females using song. Subordinates provide parental assistance, which allows females to reduce egg size, reducing the cost of reproduction to the female and increasing life span (A. F. Russell, Langmore, Cockburn, Astheimer, & Kilner, 2007). Subordinates are also associated with an increase in the proportion of extrapair young, suggesting that they allow females greater control of paternity (Mulder, 1997). However, we found no relationship between song rates and the presence of subordinates, suggesting that subordinate defence is unlikely to be the primary driver of female song patterns.

We also observed a strong relationship between female and male song rates, both before the simulated intrusion, and in response to playback. There are a number of underlying factors that could drive this pattern. Pair members may independently defend the territory, but sing at similar rates, e.g. song rates are related to the quality of the territory. This positive relationship might also occur if pairs defend the territory in a cooperative manner, as has been reported in other fairy-wren species (Hall & Peters, 2008). A final possibility is that correlated song rates are due to conflict rather than cooperation. In this scenario, pair members adjust their song output in relation to the perceived level of threat to the partnership, i.e. singing more to block attempts by their partner to attract a replacement (Seddon & Tobias, 2005). However, because females sang even when males were not present, this is unlikely to be the primary reason for the positive relationship. Further work is needed before we can determine which factors are driving this pattern, but the pattern supports that hypothesis that females use song to defend resources.

Female Song Repeatability

Song rates varied considerably among females, but showed substantial individual consistency. Similarly, in captive starlings, female song rates were also repeatable, both within and across years (Pavlova et al., 2007; Pavlova, Pinxten, & Eens, 2010). Repeatability may be the product of high additive genetic variance, and provides an upper limit to heritability (Lessells & Boag, 1987; Nakagawa & Schielzeth, 2010). This suggests that female song rates may be important targets for selection and would be able to respond to selection pressure, if it exists. Alternatively, high repeatability might reflect long-lasting environmental effects (Boake, 1989). Research in captive zebra finches, *Taeniopygia guttata*, suggests that in males, individual differences in song rates are likely to be due to maternal effects rather than genetic factors (Forstmeier, Coltman, & Birkhead, 2004). Understanding sources of individual variation in female song rates and whether female song is a potential quality indicator are important avenues for future research (Pavlova et al., 2007, 2010).

Conclusions

Taken together, these results suggest that although female song may serve multiple functions, as is commonly reported in males, it appears that in superb fairy-wrens the primary function is defence of reproductive resources from same-sex competitors. However, it is difficult to disentangle the relative importance of competition over social partners versus territories as drivers of female song. This

entanglement suggests that differentiating between the different resources important for female reproductive success may be logically very difficult (Cain & Rosvall, 2014; Clutton-Brock, 2009; LeBas, 2006; Tobias et al., 2012). As a consequence, an examination of the functional consequences of song rates is essential to developing a deeper understanding of the mechanisms favouring the evolution and maintenance of female song (Cain & Rosvall, 2014; Odom et al., 2014), and would shed light on other key questions, such as why many northern temperate species have apparently lost female song while it persists in many tropical and southern species (Garamszegi et al., 2006; Odom et al., 2014; Price, 2009; Price et al., 2009).

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Appendix

Song rate was analysed using a linear mixed model. However, because song rate is a count over time and approximates a Poisson distribution we repeated the analysis using a generalized linear mixed model with Poisson error distribution and log link. The results differ quantitatively, but produce the same final model (Table A1).

Table A1

Results of the GLMM (Poisson distribution) examining potential factors related to song rates of female and male superb fairy-wren

Final model	Estimated coefficient	SE	Wald's t	P
Minimum adequate model				
Intercept	-3.3	—	—	—
Female ^a	0.13	0.16	0.8	0.40
Day of trial	0.0064	0.0038	1.7	0.096
Response to playback ^b	0.47	0.15	3.2	0.002
Female*Response	0.64	0.24	-2.7	0.008
Excluded variables				
Age (older than first year) ^c	0.034	0.18	0.85	
Breeding status			0.5	
Trial number	-0.013	0.19	0.95	
Age*Female	-0.20	0.36	0.98	
Group breeding ^d	0.22	0.17	0.20	
Subordinates*Female	0.079	0.34	0.82	
Female*Day of trial	0.004	0.011	0.69	
Female*Breeding status			0.5	

For excluded variables we report estimates and P values from the step prior to exclusion from the final model. Significant P values are in bold; trends ($P < 0.10$) are in italics.

^a Relative to male song rate.

^b Relative to spontaneous song rates.

^c Relative to first year.

^d Relative to pair breeding.