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Title:

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

ABSTRACT

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 likely 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 across breeding stages (*Malurus cyaneus*). 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 season. Overall, the results suggest that though female song is likely to be a multi-purpose trait, as in males, the primary function in superb fairy-wren appears to be female-female competition.

24

25 **Keywords:** bird song, female song, *Malurus*, fairy-wren, female competition,
26 resource defence, territoriality, social selection, song rate, vocal communication

27

28

29 **INTRODUCTION**

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

43

44 Female song may advertise fertility, solicit male courtship, or coordinate offspring
45 care with social partners (Langmore, 1998). In species that reside on year-round
46 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 favoring the expression of traits such as bright colours, aggression, and
weaponry (Cain & Ketterson, 2012; Cain & Rosvall, 2014; Tobias, Montgomerie, &
Lyon, 2012; West-Eberhard, 1983).

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

70

71 Superb fairy-wrens are socially monogamous and bi-parental, and occupy year-
72 round territories (Dunn & Cockburn, 1996; Rowley & Russell, 1997). Females
73 initiate high rates of extra-pair matings; extra-group males sire 72% of young
74 (Double & Cockburn, 2000; Dunn & Cockburn, 1999). Males may remain on natal
75 territories as non-breeding subordinates and assist the breeding pair in nestling
76 feeding and defence (Cockburn et al., 2008). All group members assist in
77 provisioning nestlings, however, dominant males adjust their level of care according
78 to the number of subordinates and their level of paternity (Dunn & Cockburn, 1996).
79 Daughters disperse and must acquire their own territory and mate in order to breed
80 or survive (Cooney & Cockburn, 1995). Female and male fairy-wrens sing a
81 structurally similar year-round song (Figure 1)(Cooney & Cockburn, 1995;
82 Langmore & Mulder, 1992), however males sing longer songs with more elements
83 (Kleindorfer et al., 2013). In a previous study in this species Cooney and Cockburn
84 (1995) conducted a detailed, repeated measures analysis of song patterns focusing
85 on the pre-breeding ($N=15$) and nest-building periods ($N=5$). This study found that
86 females sang more during the breeding season than over-winter, suggesting a
87 breeding function. Females also showed a stronger response to foreign females than
88 neighbors, suggesting a territorial defence function. However, this study did not
89 examine song rates once breeding had begun and did not quantify how the breeding
90 male responded to unfamiliar female playback within the territory.

91

92 Here, we build on this study by examining spontaneous song rates in both sexes
93 across the breeding season in a larger sample ($N=75$ of each sex). We also quantify
94 song rates in both sexes in response to unfamiliar female song playback, simulating
95 a potential female competitor (for the female), or potential mate (for the male). The
96 hypotheses for female song generate contrasting predictions. First, if female song is
97 used to attract a mate, song rates should be highest when unpaired, while if song is
98 used to advertise fertility, then song rates should be highest when females are
99 breeding but before they have completed egg laying. Further, unfamiliar female song
100 will have no effect on female song rates, but may affect male song rates. Second, if
101 females use song to coordinate care with social partners, song rates should be high
102 when there are young, but we would not expect a change in song rates in response
103 to unfamiliar playback from either sex. Finally, if females use song primarily to
104 communicate territory ownership with other females, or to defend social partners
105 or territories, we predict that females will respond robustly to the simulated
106 competitor (unfamiliar female song), while males may show no behavioural
107 changes. Further, if females defend territories in a manner similar to males, we
108 might observe that song rates attenuate across date (Catchpole & Slater, 1995).
109 However, because fairy-wrens nest multiply and resources may become scarcer as
110 the season progresses, territory defense throughout the breeding season may be
111 essential. If so, we may observe that song rates are sustained or increase across the
112 breeding season. We also examined the relationships in song rates within pairs, to
113 determine if there is an association between female and male song rates, which may
114 reflect coordinated resource defense. 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 2012-13 breeding season (Aug-Jan). 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 pre-breeding (more than 10 days before laying the first egg of the season, $N=37$), breeding but currently without young (within 10 days of laying, nesting 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 6km apart in Canberra, south-eastern 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).

138

139 **Song recording and playback construction**

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

150

151 Each playback consisted of 2 unique songs taken from a single bout of song from the
152 same female. Playbacks began with 60s of silence followed by the first song,
153 repeated 3 times and with 20s of silence between each song bout; this was followed
154 with 45s of silence and then 3 repeats of the 2nd song, again with 20s between song
155 bouts. This pattern was then repeated (1st song x 3, 2nd song x 3, silence, 1st song x 3,
156 2nd song x 3). Each playback was 400s long with slight variation due to the length of
157 selected songs (mean \pm SE, 402.4 ± 5.8). The silence to song ratio, and the length of
158 the playback are consistent with observed natural variation in female song (Cooney
159 & Cockburn, 1995). To minimize pseudoreplication we created 36 playback tapes
160 (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 3 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 and Langmore, in review). Focal females were identified randomly, thus the observer was initially blind to breeding stage (though behaviour occasionally revealed stage), and female age during the trial. While an equal sample per breeding stage was the goal, due to predation and random selection of females, this was not achieved (pre-breeding, $N=37$; 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: pre-playback (spontaneous song rates) and response (song rates in response to playback stimuli). During the pre-playback period, each focal female was observed passively for 10min 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 5m of the female in the immediate area she was observed in, with preference given to areas with good visibility. In the center of this area we placed an Apple iPod (Apple, Cupertino, CA) 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 multiple males (subordinates) and identity of the singer could not be determined; there were no differences in female song rates for trials where males were excluded (t -ratio = 1.0, $P = 0.3$). In order 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.

Ethical Note

This study required non-manipulative and manipulative behavioural observations. Manipulations were song playbacks, restricted to 7mins, 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 under 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 model, with Poisson distribution and log link, provided the same qualitative results (Table S1). 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 (pre-breeding, 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. In order to maximize our power to detect potential relationships, we choose to simplify the full model using stepwise backward procedures to remove non-significant 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 Development 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's rho, and analysed the spontaneous and response song rates separately.

To estimate repeatability we used the analysis of variance approach recommended by Lessels 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 & 2). These differences were driven by a significant interaction between sex and the context of the songs (Figure 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 (Figure 3, 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 & 2). Female and male song rates

were strongly correlated (Figure 3, Spontaneous, $\rho = 0.4$, $P = 0.001$; Response, $\rho = 0.6$, $P < 0.0001$).

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

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, though 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 (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 extra-pair 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 extra-group 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, though 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 though 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 example, female black-headed grosbeaks (*Pheucticus melanocephalus*) sing to elicit begging from fledglings (Ritchinson, 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-wren. 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 data 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 pre-breeding 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 pre-breeding 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 into 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 (*Anthornis melanura*) also found that female song rates increased as the breeding season progressed (Brunton et al., 2008), while in stripe-headed sparrows (*Aimophila r. ruficauda*), date was unrelated to female response song rates (Illes & Yunes-Jimenez, 2009). In captive European starlings (*Sturnus vulgaris*), females occupying nest-

boxes 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 where 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 bellbirds (Brunton et al., 2008), dusky antbirds (*Cercomacra tyrannina*) (Morton & Derrickson, 1996), subdesert mesites (*Monias benshi*) (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 (*Aimophila r. ruficauda*) 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 suggests that female song is most important for female-female competition (Illes, 2014).

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 bi-parental 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; extra-pair 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 neighboring females; the male moved between the two territories and the spontaneous song rates for those females were 0.9 and 1.1 songs per minute when they were unaccompanied by the male, roughly 5x the mean spontaneous song rate reported here (Langmore unpublished data). 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 enhancing lifespan (A. F. Russell, Langmore, Cockburn, Astheimer, & Kilner, 2007). Subordinates are also associated with an increase in the proportion of extra-pair 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 finch suggests that in males, individual differences in song rates are likely 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).

435

436 **CONCLUSIONS**

437 Taken together, these results suggest that though female song may serve multiple
438 functions, as is commonly reported in males, it appears that in superb fairy-wrens
439 the primary function is defence of reproductive resources from same-sex
440 competitors. However, it is difficult to disentangle the relative importance of
441 competition over social partners versus territories as drivers of female song. This
442 entanglement suggests that differentiating between the different resources
443 important for female reproductive success may be logistically very difficult (Cain &
444 Rosvall, 2014; Clutton-Brock, 2009; LeBas, 2006; Tobias et al., 2012). As a
445 consequence, an examination of the functional consequences of song rates is
446 essential to developing a deeper understanding of the mechanisms favoring the
447 evolution and maintenance of female song (Cain & Rosvall, 2014; Odom et al., 2014),
448 and would shed light on other key questions, such as why many northern-temperate
449 species have apparently lost female song while it persists in many tropical and
450 southern species (Garamszegi et al., 2006; Odom et al., 2014; Price, 2009; Price et al.,
451 2009).

452

453

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TABLES

Table 1: Song rates before and in response to playback of unfamiliar female song.

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

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

Table 2: Results of LMM examining potential factors related to song rates of female and male superb fairy-wren.

	Est. coefficient	SE	<i>F</i>	<i>P</i> Value
Minimum adequate model				
Intercept	-0.6	-	-	-
Female ¹	0.04	0.06	1.9	0.17
Day of Trial	0.003	0.001	4.7	0.03
Response to playback ²	0.2	0.06	1.8	0.18
Female x Response	-0.2	0.09	5.6	0.02
Excluded variables				
Age ³	-0.03	0.06		0.6
Breeding Status				0.5
Trial number	0.002	0.002		0.9
Relative to first year x Female	-0.04	0.12		0.7
Group breeding ⁴	0.06	0.07		0.4
Subordinates x Female	0.01	0.1		0.5
Female x Day of trial	0.0002	0.004		0.95
Female x Breeding status				0.5

¹ Relative to male song rate, ² Relative to spontaneous song rates, ³ Relative to first year, ⁴ Relative to pair breeding. For excluded variables we report estimates and *P* values from the step prior to exclusion from the final model.

FIGURES CAPTIONS

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

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.

Figure 3. (a) Scatterplot of song rates according to the day of trial and sex, females are denoted with open circles and dashed line, males denoted with solid circles and the solid line. (b) Correlation between female and male song rates within pairs, spontaneous song rates are denoted with open squares and dashed line, response song rates are denoted with solid diamonds and solid line.

APPENDIX

Song rate was analysed in the main manuscript 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 S1: Results of GLMM examining potential factors related to song rates of female and male superb fairy-wren. (Poisson distribution).

Final model	Est. coefficient	SE	Wald's t	P Value
Minimum adequate model				
Intercept	-3.3	-	-	-
Female ¹	0.13	0.16	0.8	0.40
Day of Trial	0.0064	0.0038	1.7	0.096
Response to playback ²	0.47	0.15	3.2	0.0017
Female x Response	0.64	0.24	-2.7	0.0076
Excluded variables				
Age (older than first year) ³	0.034	0.18		0.85
Breeding Status				0.5
Trial number	-0.013	0.19		0.95
Old x Female	-0.20	0.36		0.98
Group breeding ⁴	0.22	0.17		0.20
Subordinates x Female	0.079	0.34		0.82
Female x day of trial	0.004	0.011		0.69
Female x Breeding status				0.5

659 ¹ Relative to male song rate, ² Relative to spontaneous song rates, ³ Relative to
660 first year, ⁴ Relative to pair breeding. For excluded variables we report
661 estimates and *P* values from the step prior to exclusion from the final model.