



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, & Møller, 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; 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

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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°16'S, 149°06'E; Cockburn et al., 2008; Mulder, 1997) and Campbell Park ($N = 27$; 149°9'E, 35°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

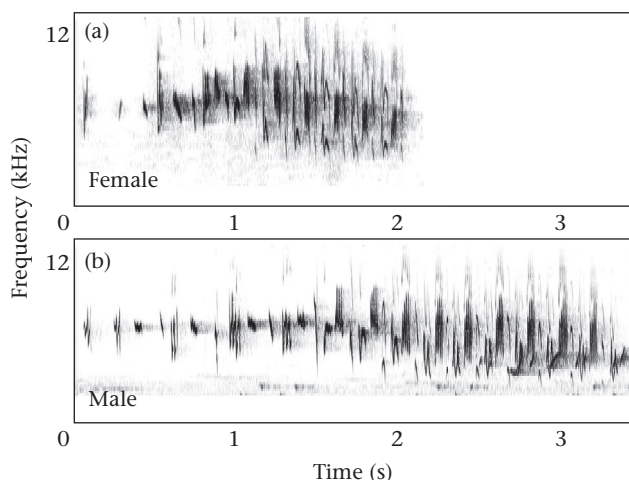


Figure 1. Spectrograms of typical (a) female and (b) male superb fairy-wren song (type 1 song, Langmore & Mulder, 1992).

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