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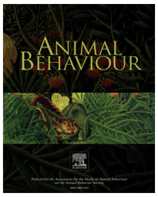

Female splendid and variegated fairy-wrens display different strategies during territory defence

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Contrary to the traditional view that territory defence is a male behaviour, there is now evidence that female birds actively engage in territory defence, either alone or with their mate. In males, song sharing between neighbours has been shown to facilitate territory defence, but little is known about the importance of song sharing for such behaviour in females. Here, I examined sex roles and song element sharing in two related species: the splendid fairy-wren, *Malurus splendens*, and the variegated fairy-wren, *Malurus lamberti*. I first described song structure and song element sharing between partners and neighbours in both male and female songs. I then simulated conspecific intrusions by broadcasting a female or a male song within a pair's territory. Both splendid and variegated fairy-wren females sang songs as complex as their male counterparts and responded to playback of simulated conspecific intrusions. Song element sharing with neighbours was common in both species, but only splendid fairy-wren females shared more elements with their mate than with other recorded males on average. Females in each species engaged in different strategies when responding to territory intruders: female splendid fairy-wrens competed with female intruders, while variegated fairy-wren females coordinated their defence with their mates and exhibited cooperative defence behaviours toward male intruders. I discuss the ideas that variation in levels of extrapair paternity and/or female competition may drive the evolution of different female strategies when responding to territory intruders.

Female territory defence in birds is an understudied behaviour. This is partly because many studies have focused on the northern hemisphere, where females supposedly rarely sing and males are believed to be the sole defenders of the territory (Catchpole & Slater, 2008). There is now increasing evidence that many females do sing (reviewed in Odom, Hall, Riebel, Omland, & Langmore, 2014; see also Kleindorfer, Evans, & Mahr, 2016) and also engage actively in territory defence, either alone or with their mate (e.g. Cooney & Cockburn, 1995; Hall & Peters, 2008; Illes & Yunes-Jimenez, 2009; Kleindorfer et al., 2013; Langmore, 1998). In superb fairy-wrens, *Malurus cyaneus*, for example, females often have to defend the territory alone while their mates are absent seeking extrapair copulations (Cooney & Cockburn, 1995; see also Cain, Cockburn, & Langmore, 2015). Similarly, a study in stripe-headed sparrows, *Peucaea ruficauda*, showed that females were the leading sex for territory defence in this species because females almost always sang before their mates during simulated territory intrusions, initiated more singing bouts and exhibited stronger responses than males (Illes & Yunes-Jimenez, 2009). However, many questions remain to fully understand sex roles and the evolution of female territory defence, such as why some females only respond to particular intruders (e.g. same-sex intruders) while others prefer to join their partners in cooperative defence.

Territory defence is a costly behaviour (Mares, Young, & Clutton-Brock, 2012). Individuals should therefore vary the intensity of their defence behaviours according to the potential threat that the intruder represents, such as its condition, degree of familiarity or the outcomes of past interactions (Marler & Slabbekoorn, 2004; Temeles, 1994). In many songbird species, resident males use characteristics of their opponent's songs to discriminate between intruders and adjust their behaviour accordingly (e.g. Kleindorfer et al., 2013; Stoddard, Beecher, Horning, & Willis, 1990; Wilson & Mennill, 2010). As such, song sharing (where resident males share song types or element repertoires with their neighbours) has been shown to regulate potential escalations during these agonistic encounters and thus facilitate territory tenure and defence (Beecher & Campbell, 2005; Beecher, Campbell, & Nordby, 2000; Burt, Campbell, & Beecher, 2001; Wilson, Towner, & Vehrencamp, 2000). Specifically, resident males responded less aggressively

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towards intruders singing unshared songs while intruders with shared songs were perceived as a higher threat (see Beecher & Campbell, 2005; Burt et al., 2001). Although some studies have investigated song sharing in females (e.g. Hall, 2006; Hall, Rittenbach, & Vehrencamp, 2015; Hile, Burley, Coopersmith, Foster, & Striedter, 2005; Marshall-Ball & Slater, 2008; Rogers, 2004), most of our knowledge on the importance of song sharing for territory defence is restricted to male–male interactions. If song sharing between neighbours improves the efficiency of territory defence in males, and females actively engage in such activity, it would seem advantageous for females to also share song types or element repertoires with their neighbours to better coordinate territory defence.

Here, I investigated sex roles and the importance of song sharing for territory defence in two related species (Driskell et al., 2011): the splendid fairy-wren, *Malurus splendens*, and the variegated fairy-wren, *Malurus lamberti*. Fairy-wren species are ideal for answering these questions because both sexes sing (e.g. Cain et al., 2015; Cooney & Cockburn, 1995; Greig & Pruett-Jones, 2008; Kleindorfer et al., 2013) and females are known to engage in territory defence (Cain et al., 2015; Cooney & Cockburn, 1995; Dowling & Webster, 2016; Hall & Peters, 2008; Kleindorfer et al., 2013). Individuals live in the same territory all year long in large family groups (Rowley & Russell, 1997) and as such the territory provides the necessary resources for both survival and reproduction, therefore making territory defence an important behaviour for the fitness of all members of the group. In this study, I first described song structure, song elements and song sharing in both male and female songs with a focus on element sharing between partners and with neighbours. I then simulated conspecific intrusions by broadcasting a female or a male chatter song within a mated pair's territory and by observing the responses of both males and females. I specifically asked the following questions. (1) Did the sex of the intruder impact which sex responded first? (2) Were male and female responses correlated? (3) Did the degree of element sharing between partners influence the intensity of their response to the intruders? (4) Did element sharing with intruders influence the responses of resident males and females? Following results from previous studies showing that territorial birds responded less aggressively to unshared songs (see Beecher & Campbell, 2005; Burt et al., 2001), I predicted that (1) pairs that shared more elements with each other would show a stronger response to intruders and (2) territory defence should be stronger to intruders that shared more elements with the pair.

METHODS

Field Site and Study Species

All recordings and experiments were done at Gluepot Reserve (140°14′E, 33°45′S), 64 km north of Waikerie and the Murray River (South Australia) between August and September 2012. The habitat mainly consisted of open Mallee and Casuarina woodland. Group size ranged from two to four birds. Most groups' breeding status was monitored every week from early August until the end of November (Criddle, 2015; Kleindorfer & Colombelli-Négrel, 2012). Not all monitored birds were colour banded but groups were considered to be distinct and independent if they were at least 500 m–1 km apart (see also Greig, Spendel, & Brandley, 2010; total study site = 338 km^2). I was therefore confident in the identity of 23 different splendid groups and 20 different variegated groups. When more than one male was present in the group, the first male that moulted into full nuptial plumage was considered as the dominant male and any other male in eclipsed plumage as a helper (more than one male was present in four of 23 (17%) monitored groups for the splendid fairy-wrens and in eight of 20 (40%) monitored groups for the variegated fairy-wrens).

Song Recordings and Analysis

Overall, the chatter song of 30 splendid fairy-wrens (17 males and 13 females) and 17 variegated fairy-wrens (10 males and seven females) were recorded. I limited my study to ‘chatter songs’ (also referred to as ‘type I songs’), which are sung year-round by both sexes in territory encounters (Cooney & Cockburn, 1995; Greig & Pruett-Jones, 2008; Kleindorfer et al., 2013), because ‘trill songs’ (or ‘type II songs’) are only sung by males and almost exclusively in contexts of mate attraction or in the presence of predators (Greig & Pruett-Jones, 2009; Greig & Webster, 2014; Langmore & Mulder, 1992; Zelano, Tarvin, & Pruett-Jones, 2001). I also chose to concentrate on element sharing because a previous study on splendid fairy-wrens showed that individuals rarely sang the same song but instead used a combination of the same elements to create new songs (Greig & Pruett-Jones, 2008).

All birds were recorded at a distance of about 5 m on the same day as the playback experiment (see below) prior to the experiment. A Telinga parabolic microphone (Telinga Microphones, Tobo, Sweden) connected to a portable Sound Devices 722 digital audio recorder (Sound Devices LLC, Reedsburg, WI, U.S.A) was used to record songs as wave files at 48 kHz sampling rate, 24-bit depth. The audio files were then visualized on an Apple MacPro using Amadeus Pro 1.5 (Hairersoft Inc., Kenilworth, U.K.) and analysed with Raven Pro1.4 (Bioacoustics Research Program, 2011). Spectrograms of audio recordings were created using the Hann algorithm (DFT = 512 samples; frequency resolution = 124 Hz; time resolution = 11.6 ms; frame overlap = 50%). For each song, the following were measured: (1) the duration (s); (2) the minimum and maximum frequency (Hz); (3) the frequency bandwidth (Hz); (4) the total number of elements and syllables per song; (5) the number of element categories and the number of different syllables per song; (6) the element rate (the total number of elements divided by the song duration); (7) the element and syllable versatilities (the number of element categories or syllable types in each song divided by the total number of elements or syllables, respectively; see also Briefer, Osiejuk, Rybak, & Aubin, 2010); and (8) the observed element repertoire size (the total number of element categories recorded for a given individual) (see Fig. 1).

Element and Syllable Classification

Elements were defined as a single continuous trace on a spectrogram that did not overlap with other traces (Dalziell & Cockburn, 2008; Kroodsma, 2005; Marler & Slabbekoorn, 2004). Element categories were identified by visual inspection according to their overall appearance on the basis of structural similarities and frequency and temporal modulations, following previously described methods for fairy-wren songs (see Colombelli-Négrel, Robertson, & Kleindorfer, 2011; Dalziell & Cockburn, 2008; Greig & Pruett-Jones, 2008; Kleindorfer et al., 2013; Langmore & Mulder, 1992). This manual method was chosen because visual categorization of song types or elements is a task for which humans are believed to perform better than automated methods (Keen, Ross, Griffiths, Lanzone, & Farnsworth, 2014; Von Ahn, 2009). Three judges independently compared the spectrograms and classified the elements into a set of categories. The final categories were created if at least two out of three judges agreed on the classification. Some of the element categories had previously been identified in other studies. Therefore, in these cases, the previously used category names for these elements were retained. Syllables were defined as the same