



Social context and the lack of sexual dimorphism in song in an avian cooperative breeder

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Elaborate male traits are typically used to attract mates and to compete with other males for mating opportunities. However, similarly ornate secondary sexual characteristics are also found in females in many species and may be used in competition in both sexual and nonsexual contexts. Trait elaboration in females may be particularly important in cooperatively breeding species where reproduction is monopolized by a few individuals in a group and where both sexes must compete for these limited mating opportunities. Previous work in African starlings has shown that females in cooperatively breeding species are larger and more ornamented than those in noncooperative species, resulting in reduced plumage and size dimorphism. To further examine patterns of sexual dimorphism in signalling traits and to better understand their role in mediating social competition, we investigated the form and function of song in cooperatively breeding superb starlings, *Lamprotornis superbus*. In addition to comparing song between sexes, we contrasted song in dominant breeders and subordinate helpers of both sexes and examined its use in various social contexts. We found that song was indistinguishable between males and females, with both sexes showing similar complexity, pitch, versatility and structure. However, the song of breeders was more versatile than that of helpers. Moreover, song structure differed when birds sang in chorus from when they sang alone. These findings suggest that, like male song, female song may be used in social competition, and that song may be an important signal in both sexes in species where intrasexual competition is high in males and females.

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In most animals, males tend to have more elaborate traits than females (Andersson 1994). Darwin (1859) was the first to note that these elaborate traits (e.g. ornaments and armaments) were typically used in competition and mate attraction. He coined the term 'sexual selection' to describe the process that could lead to the evolution of such complex male traits. However, elaborate traits are not just limited to males, as females in many species also produce ornaments and armaments (Amundsen 2000; Rubenstein 2012a; Tobias et al. 2012). Moreover, elaborate animal traits used in competitive interactions can be used in both sexual contexts, as Darwin pointed out, as well as in nonsexual contexts (Crook 1972; West-Eberhard 1975, 1983; Lyon & Montgomerie 2012; Tobias et al. 2012). Evidence from a variety of taxa suggests that females may use these social signals primarily in competition for ecological resources, rather than just in competition for mates (West-Eberhard 1975, 1983; Tobias et al. 2012).

Most of what we know about trait evolution in animals comes from considering traditional polygamous or monogamous mating systems (Drea 2005). In such systems, one sex typically competes more intensively for access to mates or resources than the other, resulting in trait elaboration in the more competitive sex (Clutton-Brock & Parker 1992). However, when competition for mates or resources is intense in both sexes, males and females are each expected to evolve elaborate traits (West-Eberhard 1983; Clutton-Brock 2007). In cooperatively breeding social systems, where reproductive skew is high in both sexes and few individuals of each sex monopolize reproduction (Hauber & Lacey 2005), traits used in intrasexual competition are predicted to be under strong selection in both males and females (Clutton-Brock et al. 2006; Rubenstein & Lovette 2009). Thus, in cooperatively breeding species, both males and females would be expected to have elaborate secondary sexual characteristics used in intraspecific competition for mates, resources or social rank (Rubenstein 2012b).

In many species of birds, song is a sexually dimorphic trait used primarily by males to compete with other males or to attract females (Searcy & Andersson 1986). Song can serve as an honest signal of male quality (Nolan & Hill 2004), and in many species,

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males with extraordinary vocal performances (e.g. complex or higher-pitched songs) often attract more mates (Soma & Garamszegi 2011). Although males produce more complex song than females in most avian species (Baptista et al. 1993; Geberzahn & Gahr 2011; Sethi et al. 2012), analysis of female song structure in a variety of oscine songbirds has revealed considerable complexity (de Silva et al. 2004; Pavlova et al. 2010). In some cooperatively breeding species, female song may be as frequent as male song (Illes & Yunes-Jimenez 2009). Singing to establish territorial boundaries is typically associated with males (Searcy & Andersson 1986), but when competition for nesting sites is high, females may also sing (Arcese et al. 1988; Hobson & Sealy 1990; Langmore 1998). Territorial female song is more common in tropical species, where territory and other ecological resources are scarce and competition for these resources can be intense (Cooney & Cockburn 1995; de Silva et al. 2004; Hall & Peters 2008; Illes & Yunes-Jimenez 2009; Tobias et al. 2011). Females also use song to compete with other females, both directly and indirectly, for male parental care (Langmore et al. 1996; Langmore & Davies 1997). Thus, although females sing less frequently than males in most avian species, when they do, they use song in a variety of social and competitive contexts.

Although most studies of vocal communication in cooperative breeders have focused on the role of vocalizations in kin recognition (Payne et al. 1988, 1991; Price 1998, 2004; Hatchwell et al. 2001; Sharp et al. 2005; McDonald & Wright 2011; McDonald 2012), a few studies have examined their role in social interactions such as territorial defence (Cooney & Cockburn 1995; Hall & Peters 2008). Social interactions among same-sex group members may be especially intense in cooperative breeders and result in strong selection on traits used in signalling (Rubenstein 2012b). Because complex traits used in female–female competition are generally elaborated in cooperatively breeding species (Rubenstein & Lovette 2009), female song in cooperative breeders may also be complicated and used frequently in a variety of competitive contexts.

Here we examine the form and function of song in the superb starling, *Lamprolornis superbus*, a cooperative breeder commonly found in the savannas of East Africa. Both sexes sing in superb starlings, and they do so year-round at the same time of the day, suggesting that song may function in more than just a sexual context in this species. Superb starlings are plural cooperative breeders with up to six breeding pairs per group (Rubenstein 2007a, b). They live in some of the most complex social groups of any cooperatively breeding bird, as helpers can help at multiple nests simultaneously, and breeders occasionally help at the nest of other breeders in the group (Rubenstein 2006). Superb starlings use flight calls, which are simpler and shorter vocalizations than songs, for group, kin and individual recognition (S. K. Chester, C. D. Meliza & D. R. Rubenstein, unpublished data), but the function of the more complex songs remains unknown. Previous comparative work in African starlings has shown that dimorphism in plumage and body size is reduced in cooperative species and driven primarily by increased trait elaboration in females (Rubenstein & Lovette 2009). Thus, since female morphological traits are elaborated and more similar to male traits in cooperatively breeding starlings, we hypothesized that song would be equally complex in both male and female superb starlings, and that it would be used in the same contexts by both sexes. We analysed song in both sexes recorded after the primary breeding season, and we examined the function of song in different social contexts. Ultimately, this work will provide important insights into the role of song in a tropical cooperative breeder where both sexes compete intensively for reproductive opportunities.

METHODS

Vocal Data Collection

Superb starlings were studied at the Mpala Research Centre, Kenya (0°17'31"N, 36°53'52"E) between May and June 2011 at the end of the long rains breeding season. The population has been monitored continuously since 2001, and each bird is individually marked with a numbered leg ring and series of coloured leg bands. Song, which we define as a vocalization lasting more than 5 s, was recorded daily for 5 weeks from perched birds from 0900 to 1700 hours. Superb starlings only sing when perched, and when singing, birds performed no other behaviours except for occasional preening. Songs were recorded from five marked social groups: 16 individuals from MRC1 (eight males, eight females), seven from SRB1 (three males, four females), two from SRB2 (two males), two from DRT1 (two males), and one from MRCV (one male). Recordings were made by a single person (J.A.P.), while a second observer identified each individual using a spotting scope. All work was approved by Columbia University's Institutional Animal Care and Use Committee (AC-AAAB1128).

Digital recordings in the form of monoaural uncompressed WAV files (16 bit, 44 kHz) were made using a Sennheiser ME66 directional microphone and a Marantz PMD661 portable field recorder. To determine the amount of song to record for each individual to accurately assess its complete repertoire, we created cumulative motif repertoire curves from previously made recordings. After plotting the cumulative number of unique motifs against time until it reached an asymptote, we visually determined that 8 min of song per individual captured the majority of its song repertoire (see [Supplementary Material](#)). The mean \pm SE recording length for birds in our samples was 8.8 ± 0.2 min. Although two females had slightly less than 8 min of song recorded (5 min each), we included them in our analysis because of a small female sample size. Excluding these females did not change our results.

For each recording, we noted whether the focal individual was singing alone or in a group chorus with other birds from its social group. Of the 71 recordings, 39 recordings from 16 individuals were of birds singing alone and 32 recordings from 25 individuals were of birds singing in a group. If song from other birds in a chorus overlapped with the song of the focal individual and obscured the recording, these recordings were excluded from our analysis. In total, we recorded 271 min of song from 26 individuals in 2011 and included 14 min of recordings from two individuals recorded in 2008 ($N = 16$ males and 12 females). Ages of the recorded birds ranged from 1 to 10 years. Social rank was determined by categorizing birds as recent breeders or helpers (sensu Rubenstein 2007a). Birds were identified as breeders if they bred in 2010 or 2011, and they were identified as helpers if they brought food to nests during those years but were not the social parents of those nests. Breeders are socially dominant to helpers in this species (Rubenstein 2007a).

Song Analysis

We generated spectrograms of the songs with a Hann evaluation window, a bandwidth of 248 Hz, frequency resolution of 172 Hz and temporal resolution of 2.90 ms using RavenPro v.1.2 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.). We annotated the spectrograms by song bout and motif type based on a classification system of 82 unique motifs (sensu Keen 2011). We define a motif as a continuous unit of sound within a song divided by gaps of silence from other such units (Fig. 1). We define a song bout as a unit of song at least 5 s in length with no gaps longer than 1.5 s (sensu Pavlova et al. 2005). We created the classification system as an extension of an existing set of motifs that have been identified in

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