



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

July A. Pilowsky\*, Dustin R. Rubenstein

Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, U.S.A.

### ARTICLE INFO

#### Article history:

Received 1 November 2012  
Initial acceptance 7 December 2012  
Final acceptance 4 January 2013  
Available online 28 February 2013  
MS. number: A12-00824

#### Keywords:

avian song  
communication  
cooperative breeding  
sexual dimorphism  
sexual selection  
social competition  
social rank  
social selection  
starling

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.

© 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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,

\* Correspondence: J. A. Pilowsky, Department of Ecology, Evolution and Environmental Biology, Columbia University, 1200 Amsterdam Avenue, New York, NY 10027, U.S.A.

E-mail address: [jap2178@caa.columbia.edu](mailto:jap2178@caa.columbia.edu) (J. A. Pilowsky).

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

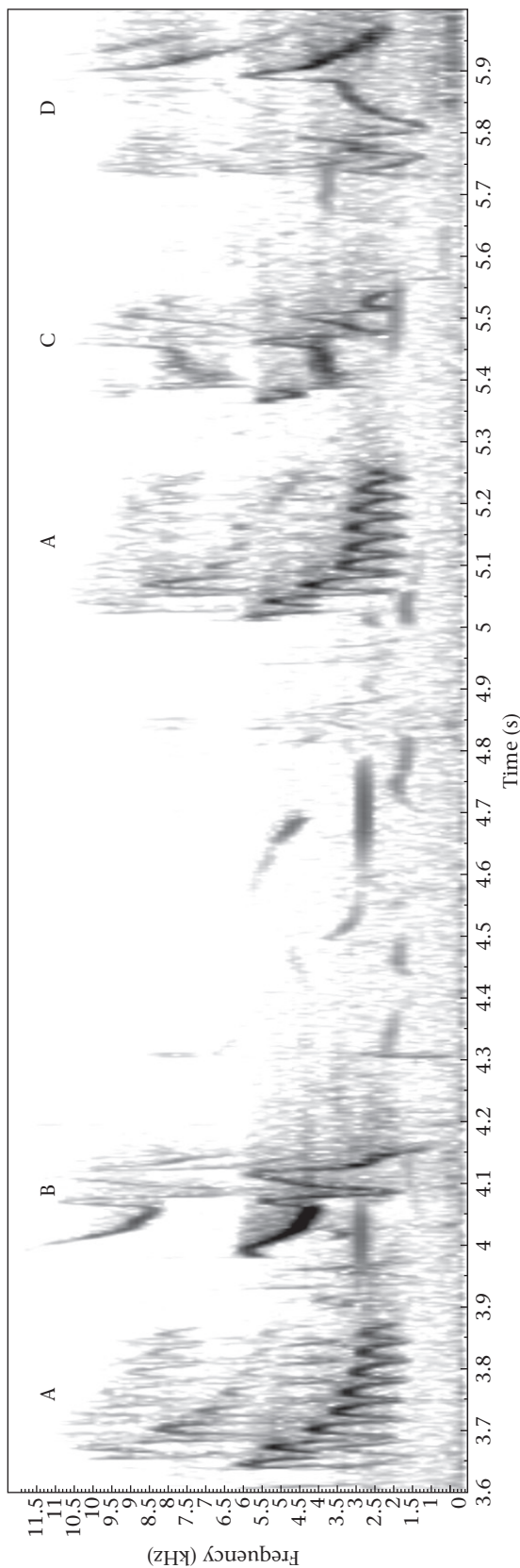
Superb starlings were studied at the Mpala Research Centre, Kenya (0°17'31"N, 36°53'52"E) between May and June 2011 at the end of the long rains breeding season. The population has been monitored continuously since 2001, and each bird is individually marked with a numbered leg ring and series of coloured 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  $8.8 \pm 0.2$  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



**Figure 1.** Sample sonagram of superb starling song from a male breeder demonstrating upper harmonic range and examples of four motif types. The background noise in the 2–6 kHz range from 3.9–4 s and 4.2–5 s is likely from a white-browed sparrow-weaver, *Plocepasser mahali*.

the flight calls of superb starlings from the same population (Keen 2011). Although flight calls are produced primarily by starlings when flying from one place to another, starlings have not been observed to sing while moving.

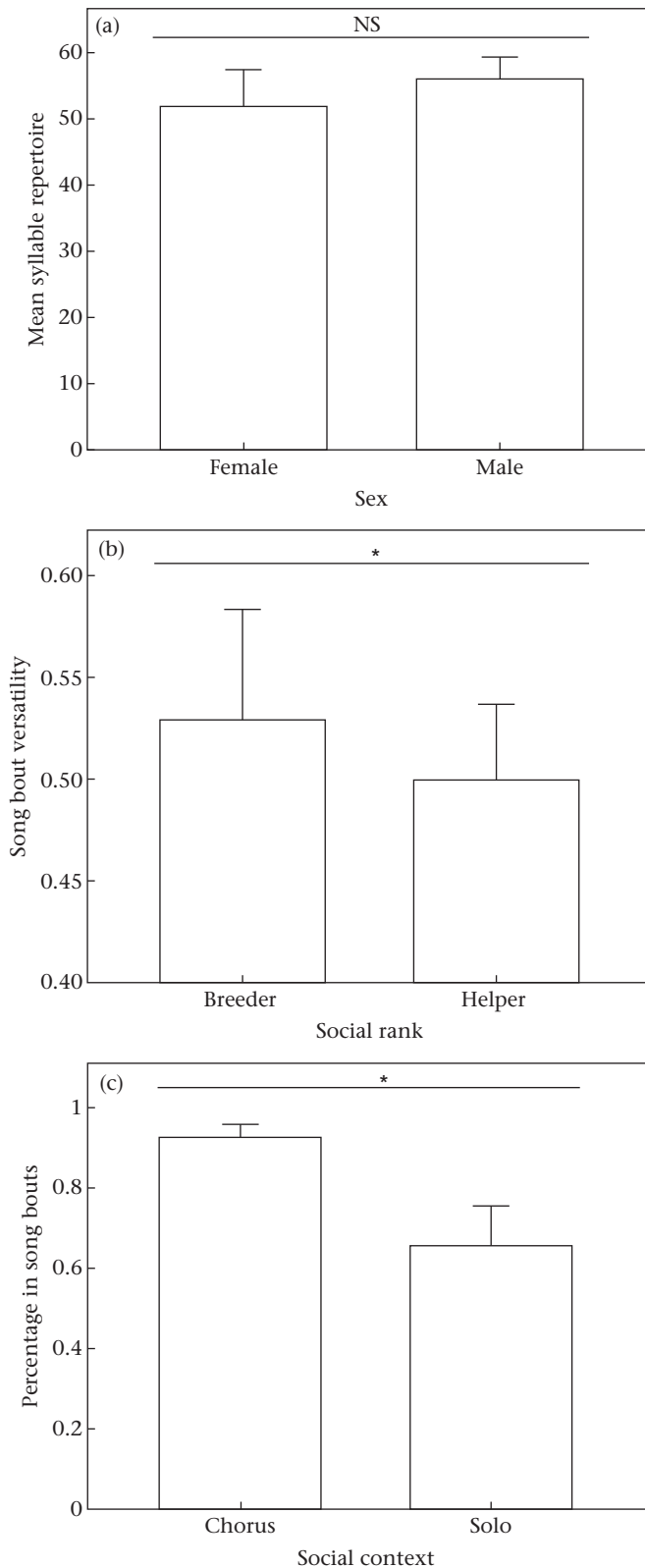
Songs were analysed (and recorded) blindly with respect to age, sex and social rank. We evaluated the pitch of songs using Chirp v.1.1.2 (C. D. Meliza, S. K. Chester & D. R. Rubenstein, unpublished data), a program that creates a contour of the tone of each motif, thus filtering out the effects of background noise. Each pitch contour was visually verified by J.A.P. to ensure that it correctly traced the motif; incorrect pitch contours were discarded prior to analysis. Chirp identified the mean, minimum and maximum frequency (in Hz) for each motif. For each individual, we then calculated a variety of song parameters including: (1) the number of motifs sung per second; (2) the ratio of flight call motifs to song-distinct motifs in each recording; (3) motif repertoire; and (4) motif sharing, as indicated by Dice's (1945) similarity index. We also measured several aspects of song structure, including: (1) the song bout length; (2) song bout versatility (i.e. the proportion of unique motifs per song bout); and (3) continuity (i.e. the percentage of song that could be classified into continuous song bouts; *sensu* Pavlova et al. 2005, 2010). The motif repertoire for each individual was based on the number of unique motifs identified within exactly 8 min of song. For eight individuals, all 8 min required for capturing the motif repertoire occurred in a single recording. The other 20 individuals' motif repertoires were analysed from a composite of up to seven recordings, totalling 8 min. There was no sampling effect on motif repertoire size, as the repertoires of birds with composite and continuous recordings were of similar size ( $t_{26} = 0.91$ ,  $P = 0.37$ ). Finally, other variables distinct from motif repertoire (e.g. flight call ratio and motifs sung per second) were calculated on a per-recording basis.

#### Statistical Analysis

Data were analysed using generalized linear mixed models (GLMM) in SPSS v.20 (IBM, Armonk, NY, U.S.A.). All tests were two tailed and used a threshold significance level of  $P < 0.05$ . Fixed effects in our models included sex, age, social context (i.e. alone versus in a group) and social rank (i.e. breeder versus helper). To account for repeated sampling of the same individuals and multiple individuals sampled from the same social groups, individual and social group were included as random effects in our models. The variables song bout length, continuity and flight call ratio were transformed to meet the assumptions of normality, using a log and two arcsine transformations, respectively. We used binary logistic regression models to determine whether birds of different sex, social rank and age sang in different social contexts. We used paired  $t$  tests to measure individual differences in song structure between different social contexts. We used the package *simba* in R v.2.15 (R Foundation for Statistical Computing, Vienna, Austria) to calculate Dice's similarity index between motif repertoires.

## RESULTS

We found that superb starlings in our long-term study population used 82 distinct motifs in their song. Male motif repertoire ranged from 47 to 64 motifs, and female motif repertoire ranged from 47 to 61 motifs. The mean individual repertoire size ( $56.1 \pm 1.6$  and  $54.7 \pm 1.9$  motifs for males and females, respectively) did not differ between sexes ( $F_{1,8.4} = 0.41$ ,  $P = 0.54$ ; Fig. 2a). Additionally, motif repertoire size did not vary with social rank ( $F_{1,8.8} = 0.006$ ,  $P = 0.94$ ) or age ( $F_{7,1.5} = 1.54$ ,  $P = 0.30$ ). The mean Dice's similarity index of motif repertoires, a measure of motif sharing, among all birds was  $s = 0.84 \pm 0.003$ , and did not differ between sexes ( $t_{375} = -0.45$ ,  $P = 0.67$ ).



**Figure 2.** (a) Mean  $\pm$  SE motif repertoire sizes of male and female superb starlings. Motif repertoire is the range of motifs that a bird is capable of producing. (b) Mean  $\pm$  SE song bout versatility (i.e. the proportion of unique motifs per song bout) of dominant breeder and subordinate helper superb starlings. (c) Mean  $\pm$  SE percentage of song sung in continuous bouts (i.e. greater than 5 s long with no gaps longer than 1.5 s) in superb starlings. \* $P < 0.01$ .

Similarly, the pitch of starling song, which ranged in frequency from 1548 to 4610 Hz (excluding harmonic frequencies), with a mean of  $3101 \pm 41$  Hz, also did not differ between sexes ( $F_{1,11.58} = 0.046$ ,  $P = 0.83$ ), or with social rank ( $F_{4,8.29} = 2.29$ ,  $P = 0.15$ ) or age ( $F_{9,8.04} = 0.91$ ,  $P = 0.56$ ). The ratio of flight calls to song motifs did not vary by sex ( $F_{1,1.27} = 0.62$ ,  $P = 0.7$ ), social rank ( $F_{1,0.61} = 0.27$ ,  $P = 0.7$ ), social context ( $F_{1,0.27} = 1.30$ ,  $P = 0.7$ ) or age ( $F_{7,2} = 2.33$ ,  $P = 0.33$ ).

Although there were no sex or rank differences in song parameters (i.e. motif repertoire size, motif sharing, pitch or ratio of flight calls to song motifs), social context and breeding role did influence song structure. We found that breeder song had higher song bout versatility than helper song ( $F_{1,10.57} = 6.11$ ,  $P = 0.032$ ; Fig. 2b). Additionally, when singing in a group, individuals produced song that was more continuous ( $F_{1,38.6} = 33.39$ ,  $P < 0.001$ ; Fig. 2c), with longer song bouts ( $F_{1,6.51} = 26.96$ ,  $P = 0.002$ ) than song produced when singing alone. Individuals for which both solo and group recordings were available sang more continuous songs (paired  $t$  test:  $t_{12} = -3.63$ ,  $P = 0.003$ ) with longer song bouts (paired  $t_{12} = -3.65$ ,  $P = 0.003$ ) when singing in a group.

## DISCUSSION

Superb starling song is highly complex, with a diverse repertoire of motif types. For all the structural components we measured, as well as song parameters such as pitch and the number of motifs sung per second, song was equally complex and completely indistinguishable between males and females. For example, both sexes had extensive repertoires and highly versatile song bouts, and motif sharing was very high within and between sexes, with no difference between same-sex and opposite-sex motif repertoire similarity. By contrast, the noncooperative European starling, *Sturnus vulgaris*, shows greater repertoire size in males than in females (Pavlova et al. 2005), despite some overlap in repertoire between the sexes. This is consistent with the broader pattern of more elaborate song in male birds, generally the more competitive sex (Searcy & Andersson 1986). In contrast to European starlings and many other passerine birds, both sexes in superb starlings appear to use and produce song that is similar in form.

Our results are consistent with the idea that traits used in intrasexual competition in cooperative breeders may be elaborated and of similar form or complexity in both sexes. If song mediates social competition in the superb starling, we would predict a difference between the vocalizations of socially dominant and socially subordinate individuals. Work in other species of songbirds has shown that song complexity can signal social dominance (Spencer et al. 2004) and that males with more versatile songs enjoy greater mating success (Lampe & Espmark 2002; Forstmeier & Leisler 2004). We found differences in the structure and versatility of the song in breeders and helpers. Socially dominant breeders produced more versatile song bouts than socially subordinate helpers. Since song is used during both the breeding and nonbreeding seasons in superb starlings, song may help mediate intrasexual competition for social rank in both sexes.

The difference in structure between solo and chorus song gives us insight into the function of superb starling song in different social contexts. Chorus song was more continuous, with the majority of song produced in long song bouts with fewer short 'bursts' of song interspersed, whereas solo song was divided into short song bouts with smaller, choppier units of song between them. Chorus song can serve a variety of functions in birds, such as joint territorial defence, promoting group cohesion and mediating social hierarchies (Bradley & Mennill 2009). Moreover, different functions of chorus song are associated with different behavioural profiles. Territorial chorus song is a highly coordinated display typically



performed at territorial borders, and often accompanied by other aggressive behaviours such as chasing and plumage displays (Reyer & Schimdl 1988; Seddon 2002; Mann et al. 2006). In superb starlings, however, group song is performed in the centre of the territory in an uncoordinated and seemingly chaotic fashion, with no accompanying displays or behaviours. This behavioural profile more closely matches group vocalizations associated with group cohesion, such as that of the cooperatively breeding Australian magpie, *Gymnorhina tibicen* (Brown et al. 1988). Solo song may serve a different role from chorus song (i.e. advertising to potential mates), although further work, particularly with experimental playbacks, is needed to establish its true function.

Female song has historically been understudied relative to male song (Garamszegi et al. 2007), partly because of Darwin's initial focus on male ornamentation in his work on sexual selection (Darwin 1871; Ah-King 2011; Rubenstein 2012a) and partly because of a bias towards studies in temperate regions where female song and year-round territoriality are less common than in the tropics (Price et al. 2009). We have shown that song in a tropical cooperative breeder can be similarly complex in males and females. In support of previous work on sexual dimorphism in African starlings (Rubenstein & Lovette 2009), our findings suggest that the evolution of mutual plumage ornamentation in cooperative breeders may be accompanied by mutual elaboration in song. Our work also shows that both males and females in cooperatively breeding species may use song to signal social dominance. This and other studies (e.g. Bradley & Mennill 2009; Illes & Yunes-Jimenez 2009) indicate that female song may be an important social signal in species where intra-sexual competition and intersexual selection are strong in both sexes.

## Acknowledgments

We thank Godfrey Manyas and Wilson Nderitu for their help in the field, as well as Sara Keen Chester and Dan Meliza for their help with analyses. Dan Meliza also provided us with recordings from 2008. We recognize Catherine Chen, Nathen Huang, Kerstin Nolan and Sonalee Rau for their assistance in evaluating pitch contours. We acknowledge the Kenyan National Council on Science and Technology, the National Museums of Kenya Ornithology Department and the Mpala Research Centre for enabling this work. J.A.P. was supported by Columbia University's Department of Ecology, Evolution and Environmental Biology. D.R.R. was supported by the National Science Foundation (IOS-1121435) and Columbia University.

## Supplementary Material

Supplementary material for this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2013.01.012>.

## References

- Ah-King, M. 2011. Female sexual selection in light of the Darwin–Bateman paradigm. *Behavioral Ecology*, **22**, 1142–1143.
- Amundsen, T. 2000. Why are female birds ornamented? *Trends in Ecology & Evolution*, **15**, 149–155.
- Andersson, M. B. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Arcese, P., Stoddard, P. K. & Hiebert, S. M. 1988. The form and function of song in female song sparrows. *Condor*, **90**, 44–50.
- Baptista, L. F., Trail, P. W., DeWolfe, B. B. & Morton, M. L. 1993. Singing and its functions in female white-crowned sparrows. *Animal Behaviour*, **46**, 511–524.
- Bradley, D. W. & Mennill, D. J. 2009. Strong ungraded responses to playback of solos, duets and choruses in a cooperatively breeding Neotropical songbird. *Animal Behaviour*, **77**, 1321–1327.
- Brown, E. D., Farabaugh, S. M. & Veltman, C. J. 1988. Song sharing in a group-living songbird, the Australian magpie, *Gymnorhina tibicen*. 1. Vocal sharing within and among social groups. *Behaviour*, **104**, 1–28.
- Clutton-Brock, T. 2007. Sexual selection in males and females. *Science*, **318**, 1882–1885.
- Clutton-Brock, T. & Parker, G. 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology*, **67**, 437–456.
- Clutton-Brock, T. H., Hodge, S. J., Spong, G., Russell, A. F., Jordan, N. R., Bennett, N. C., Sharpe, L. L. & Manser, M. B. 2006. Intrasexual competition and sexual selection in cooperative mammals. *Nature*, **444**, 1065–1068.
- Cooney, R. & Cockburn, A. 1995. Territorial defence is the major function of female song in the superb fairy-wren, *Malurus cyaneus*. *Animal Behaviour*, **49**, 1635–1647.
- Crook, J. H. 1972. Sexual selection, dimorphism, and social organization in the primates. In: *Sexual Selection and the Descent of Man 1871–1971* (Ed. by B. Campbell), pp. 231–281. Chicago: Aldine.
- Darwin, C. 1859. *On the Origin of Species*. London: J. Murray.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: J. Murray.
- Dice, L. R. 1945. Measures of the amount of ecologic association between species. *Ecology*, **26**, 297–302.
- Drea, C. M. 2005. Bateman revisited: the reproductive tactics of female primates. *Integrative and Comparative Biology*, **45**, 915–923.
- Forstmeier, W. & Leisler, B. 2004. Repertoire size, sexual selection, and offspring viability in the great reed warbler: changing patterns in space and time. *Behavioral Ecology*, **15**, 555–563.
- Garamszegi, L. Z., Pavlova, D. Z., Eens, M. & Møller, A. P. 2007. The evolution of song in female birds in Europe. *Behavioral Ecology*, **18**, 86–96.
- Geberzahn, N. & Gahr, M. 2011. Undirected (solitary) birdsong in female and male blue-capped cordon-bleus (*Uraeginthus cyanocephalus*) and its endocrine correlates. *PLoS One*, **6**.
- Hall, M. L. & Peters, A. 2008. Coordination between the sexes for territorial defence in a duetting fairy-wren. *Animal Behaviour*, **76**, 65–73.
- Hatchwell, B., Ross, D., Fowlie, M. & McGowan, A. 2001. Kin discrimination in cooperatively breeding long-tailed tits. *Proceedings of the Royal Society B*, **268**, 885–890.
- Hauber, M. E. & Lacey, E. A. 2005. Bateman's principle in cooperatively breeding vertebrates: the effects of non-breeding alloparents on variability in female and male reproductive success. *Integrative and Comparative Biology*, **45**, 903–914.
- Hobson, K. A. & Sealy, S. G. 1990. Female song in the yellow warbler. *Condor*, **92**, 259–261.
- Illes, A. E. & Yunes-Jimenez, L. 2009. A female songbird out-sings male conspecifics during simulated territorial intrusions. *Proceedings of the Royal Society B*, **276**, 981–986.
- Keen, S. 2011. Identifying pathways to cooperation: flight calls and kin recognition in superb starlings. Ph.D. thesis, Columbia University.
- Lampe, H. M. & Espmark, Y. O. 2002. Mate choice in pied flycatchers *Ficedula hypoleuca*: can females use song to find high-quality males and territories? *Ibis*, **145**, E24–E33.
- Langmore, N. E. 1998. Functions of duet and solo songs of female birds. *Trends in Ecology & Evolution*, **13**, 136–140.
- Langmore, N. E. & Davies, N. B. 1997. Female dunnocks use vocalizations to compete for males. *Animal Behaviour*, **53**, 881–890.
- Langmore, N. E., Davies, N. B., Hatchwell, B. J. & Hartley, I. R. 1996. Female song attracts males in the alpine accentor *Prunella collaris*. *Proceedings of the Royal Society B*, **263**, 141–146.
- Lyon, B. E. & Montgomerie, R. 2012. Sexual selection is a form of social selection. *Philosophical Transactions of the Royal Society B*, **367**, 2266–2273.
- McDonald, P. G. 2012. Cooperative bird differentiates between the calls of different individuals, even when vocalizations were from completely unfamiliar individuals. *Biology Letters*, **8**, 365–368.
- McDonald, P. G. & Wright, J. 2011. Bell miner provisioning calls are more similar among relatives and are used by helpers at the nest to bias their effort towards kin. *Proceedings of the Royal Society B*, **278**, 3403–3411.
- Mann, N. I., Dingess, K. A. & Slater, P. J. B. 2006. Antiphonal four-part synchronized chorusing in a Neotropical wren. *Biology Letters*, **2**, 1–4.
- Nolan, P. M. & Hill, G. E. 2004. Female choice for song characteristics in the house finch. *Animal Behaviour*, **67**, 403–410.
- Pavlova, D., Pinxten, R. & Eens, M. 2005. Female song in European starlings: sex differences, complexity, and composition. *Condor*, **107**, 559–569.
- Pavlova, D. Z., Pinxten, R. & Eens, M. 2010. Age-related changes of song traits in female European starlings (*Sturnus vulgaris*). *Animal Biology*, **60**, 43–59.
- Payne, R., Payne, L., Rowley, I. & Russell, E. 1991. Social recognition and response to song in cooperative red-winged fairy-wrens. *Auk*, **108**, 811–819.
- Payne, R., Payne, L. & Rowley, I. 1988. Kin and social relationships in splendid fairy-wrens: recognition by song in a cooperative bird. *Animal Behaviour*, **36**, 1341–1351.
- Price, J. J., Lanyon, S. M. & Omland, K. E. 2009. Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. *Proceedings of the Royal Society B*, **276**, 1971–1980.
- Price, J. J. 1998. Family- and sex-specific vocal traditions in a cooperatively breeding songbird. *Proceedings of the Royal Society B*, **265**, 497–502.
- Price, J. J. 2004. Recognition of family-specific calls in stripe-backed wrens. *Animal Behaviour*, **57**, 483–492.

- Reyer, H. U. & Schmidl, D.** 1988. Helpers have little to laugh about: group structure and vocalization in the laughing kookaburra *Dacelo novaeguineae*. *Emu*, **88**, 150–160.
- Rubenstein, D. R.** 2006. The evolution of the social and mating systems of the plural cooperatively breeding superb starling, *Lamprotornis superbus*. Ph.D. thesis, Cornell University.
- Rubenstein, D. R.** 2007a. Stress hormones and sociality: integrating social and environmental stressors. *Proceedings of the Royal Society B*, **274**, 967–975.
- Rubenstein, D. R.** 2007b. Temporal but not spatial environmental variation drives adaptive offspring sex allocation in a plural cooperative breeder. *American Naturalist*, **170**, 155–165.
- Rubenstein, D. R.** 2012a. Sexual and social competition: broadening perspectives by defining females roles. *Philosophical Transactions of the Royal Society B*, **367**, 2248–2252.
- Rubenstein, D. R.** 2012b. Family feuds: social competition and sexual conflict in complex societies. *Philosophical Transactions of the Royal Society B*, **367**, 2304–2313.
- Rubenstein, D. R. & Lovette, I. J.** 2009. Reproductive skew and selection on female ornamentation in social species. *Nature*, **462**, 786–790.
- Searcy, W. A. & Andersson, M.** 1986. Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics*, **17**, 507–533.
- Seddon, N.** 2002. The structure, context and possible functions of solos, duets and choruses in the subdesert mesite (*Monias benschi*). *Behaviour*, **139**, 645–676.
- Sethi, V. K., Bhatt, D. & Kumar, A.** 2012. Structure and context of female song in a tropical bird, the pied bush chat. *Current Science*, **103**, 827–832.
- Sharp, S. P., McGowan, A., Wood, M. J. & Hatchwell, B. J.** 2005. Learned kin recognition cues in a social bird. *Nature*, **434**, 1127–1130.
- de Silva, H. G., Marantz, C. A. & Pérez-Villafañá, M.** 2004. Song in female *Hylorchilus* wrens. *Wilson Bulletin*, **116**, 186–188.
- Soma, M. & Garamszegi, L. Z.** 2011. Rethinking birdsong evolution: meta-analysis of the relationship between song complexity and reproductive success. *Behavioral Ecology*, **22**, 363–371.
- Spencer, K. A., Buchanan, K. L., Goldsmith, A. R. & Catchpole, C. K.** 2004. Developmental stress, social rank and song complexity in the European starling (*Sturnus vulgaris*). *Proceedings of the Royal Society B*, **271**, S121–S123.
- Tobias, J. A., Gamarra-Toledo, V., García-Olachea, D., Pulgarín, P. C. & Seddon, N.** 2011. Year-round resource defence and the evolution of male and female song in suboscine birds: social armaments are mutual ornaments. *Journal of Evolutionary Biology*, **24**, 2118–2138.
- Tobias, J. A., Montgomerie, R. & Lyon, B. E.** 2012. The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Philosophical Transactions of the Royal Society B*, **367**, 2274–2293.
- West-Eberhard, M. J.** 1975. The evolution of social behavior by kin selection. *Quarterly Review of Biology*, **50**, 1–33.
- West-Eberhard, M. J.** 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology*, **58**, 155–183.