The official journal of the **ISBE** International Society for Behavioral Ecology

Behavioral Ecology (2013), 24(6), 1279-1285. doi:10.1093/beheco/art062

Original Article

Flight calls signal group and individual identity but not kinship in a cooperatively breeding bird

Sara C. Keen,^a C. Daniel Meliza,^b and Dustin R. Rubenstein^a

^aDepartment of Ecology, Evolution and Environmental Biology, Columbia University, 1200 Amsterdam Avenue, New York, NY 10027, USA and ^bDepartment of Organismal Biology and Anatomy, University of Chicago, 1027 East 57th Street, Chicago, IL 60647, USA

Received 6 March 2013; revised 11 June 2013; accepted 12 June 2013; Advance Access publication 26 July 2013

In many complex societies, intricate communication and recognition systems may evolve to help support both direct and indirect benefits of group membership. In cooperatively breeding species where groups typically comprise relatives, both learned and innate vocal signals may serve as reliable cues for kin recognition. Here, we investigated vocal communication in the plural cooperatively breeding superb starling, *Lamprotornis superbus*, where flight calls—short, stereotyped vocalizations used when approaching conspecifics may communicate kin relationships, group membership, and/or individual identity. We found that flight calls were most similar within individual repertoires but were also more similar within groups than within the larger population. Although starlings responded differently to playback of calls from their own versus other neighboring and distant social groups, call similarity was uncorrelated with genetic relatedness. Additionally, immigrant females showed similar patterns to birds born in the study population. Together, these results suggest that flight calls are learned signals that reflect social association but may also carry a signal of individuality. Flight calls, therefore, provide a reliable recognition mechanism for groups and may also be used to recognize individuals. In complex societies comprising related and unrelated individuals, signaling individuality and group association, rather than kinship, may be a route to cooperation.

Key words: cooperative breeding, flight call, individual recognition, kin recognition, *Lamprotornis superbus*, vocal communication.

INTRODUCTION

Cooperative breeding societies, in which individuals care for others' offspring, have been observed in numerous vertebrate taxa (Emlen 1997; Clutton-Brock 2002; Griffin and West 2003), including nearly 10% of all avian species (Cockburn 2006). Kin selection theory, which predicts that individuals gain indirect fitness benefits by cooperating with close relatives (Hamilton 1964), is generally used to explain the evolution of cooperative breeding behavior in birds (reviewed in Cockburn 1998; Lehmann and Keller 2006). Cooperation requires mechanisms that allow individuals to recognize and interact preferentially with certain conspecifics (Hamilton 1964). In cooperatively breeding societies where individuals typically interact with relatives, mechanisms to distinguish kin from nonkin are necessary to gain indirect benefits (Cornwallis et al. 2009). In birds, vocalizations are frequently used in social communication. Differences in vocalizations can carry information about kinship (Payne et al. 1988; Price 1998; McDonald and Wright 2011), group membership (Tyack 2008), and individual identity (Stoddard 1996), which can be perceived and acted on by conspecifics (Bee and Gerhardt 2002; Sharp et al. 2005; Tibbetts and Dale 2007). The degree to which these sources of information are used in specific vocalizations depends not only on the context and function of the song or call (Marler 2004; Catchpole and Slater 2008), but, in cooperative breeders, also on the relative extent to which direct and indirect benefits drive social behavior (Cornwallis et al. 2009).

The role of vocal recognition in facilitating cooperative behavior has been demonstrated in relatively few avian species, particularly within species living in complex societies composed of a mix of kin and nonkin. Previous studies of vocal recognition in cooperative breeders have primarily focused on simple family groups with a socially dominant male and female, such as striped-back wrens (Price 1998) and splendid fairy-wrens (Payne et al. 1988). Fewer investigations have focused on more complex cooperatively breeding societies, like those of honeyeaters, which live in large, complex colonies, and use calls to assess

Address correspondence to S.C. Keen, who is now at Cornell Laboratory of Ornithology, Cornell University, Ithaca, NY 14850, USA. E-mail: sck74@cornell.edu.

[©] The Author 2013. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com

relatedness (bell miners, McDonald and Wright 2011) and discriminate among individuals (noisy miners, McDonald 2012). Among nonavian species that live in large social groups, vocal recognition of relatives and nonrelatives (e.g., African elephants, McComb et al. 2000; rhesus macaques, Rendall et al. 1996; vervet monkeys, Cheney and Seyfarth 1982) and of related and unrelated group members (e.g., spear-nosed bats, Boughman and Wilkinson 1998) has been observed. However, few previous studies have examined the use of vocal recognition in a complex cooperatively breeding species, where social groups consist of both related and unrelated individuals (but see McDonald and Wright 2011; McDonald 2012).

Here, we examine the recognition abilities of the superb starling (Lamprotornis superbus), a complex, plural cooperatively breeding bird that lives in large social groups containing multiple breeding pairs (Rubenstein 2007b). Within-group competition for breeding opportunities is intense in superb starlings, and nonbreeding helpers aid pairs at the nests of close relatives and occasionally at those of unrelated individuals (Rubenstein 2006). Despite the complex kin relationships in superb starling groups, the mechanism by which recognition occurs in this species is unknown. We focus on flight calls-short, stereotyped vocalizations used when approaching conspecifics-which could serve to signal kin relationships, group membership, and/or individual identity. To test these hypotheses, we measured call similarity within the repertoires of individuals, groups, and a large multigroup population and analyzed whether similarity differed among these categories and if it was correlated with genetic relatedness and/or geographic distance. We also tested whether calls from different groups were perceived differently in a playback experiment.

METHODS

Study population

We studied a marked population of 9 geographically isolated superb starling social groups at the Mpala Research Centre, Laikipia, Kenya (08.17°N, 378.52°E). Superb starlings exhibit male philopatry (and thus high relatedness among males), as most males remain in their natal groups to breed, whereas most females immigrate to new groups (Rubenstein 2007b). Breeding occurs during both the long rains from March to May and the short rains from October to November (Rubenstein 2007b, 2011). Each of the 9 social groups in this population was given a unique name: CF1, CF2, DRT1, DRT2, MRC1, MRCV, SRB1, SRB2, and WDB. The groups are located within 0.32–8.7 km (mean \pm SD = 4.4 \pm 2.8) of each other. Groups consist of up to 35 birds and included as many as 6 breeding pairs at any one time (Rubenstein 2007a). All individuals in the population are marked with a unique combination of colored leg bands and a numbered metal leg ring (Rubenstein 2007b). Blood samples have been collected from each marked individual to molecularly determine sex, parentage, and the genetic relationships among individuals (Rubenstein 2007a).

Relatedness analysis

We used Kingroup v2.0 (Konovalov and Heg 2008) to calculate pairwise relatedness values with likelihood ratio tests based on Queller and Goodnight's *r*, which estimates the probability of a pair of individuals being as closely related as known parent–offspring pairs or full siblings. Genetic data were collected for all individuals using 15 microsatellite markers (Rubenstein 2005) with methods described previously (Rubenstein 2007c). Briefly, genotyping was performed on 3130xl, 3130, and 3100 Genetic Analyzers (Life Technologies, Inc., Grand Island, NY), and all alleles were automatically scored and confirmed by eye using Geneious v6.1 (Biomatters, Auckland, New Zealand) (sensu Rubenstein 2007c). We used Cervus v3.0 (Kalinowski et al. 2007) to confirm that all loci were in Hardy–Weinberg equilibrium and that none of the loci had null alleles (sensu Rubenstein 2007c).

Acoustic recordings

When taking off or flying over conspecifics, superb starlings make loud flight calls consisting of a series of temporally discrete "motifs" that are tonal, harmonic, and rapidly modulated in frequency (Figure 1A). Superb starlings sometimes use the same motifs in other contexts, including songs and in short calls given from elevated perches (Pilowsky and Rubenstein 2013), so their function may be more general (Farnsworth 2005). Between May and July of 2008, 2009, and 2010, we recorded 365 call bouts during daylight hours from 109 banded adults (56 males and 53 females) using a PMD660 or PMD661 digital recorder (Marantz, Mahwah, NJ) and an ME66 or ME62 shotgun microphone (Sennheiser Electronic, Old Lyme, CT). All recordings were made during or immediately after the primary breeding season (Rubenstein 2011) and stored digitally at 44.1 or 48kHz in 16-bit WAV format. Files were time stamped by the recorder, and the caller identity (established by a second observer using a spotting scope) was noted vocally on the recording. Distance to the bird varied between 20 and 100 m. Between 5 and 21 birds (mean \pm SD = 13.8 \pm 5.0) were recorded from each social group. Call bouts were first divided into 2540 individual motifs (1-39 per bout; mean \pm SD = 6.98 \pm 4.27). Some motifs were excluded because of poor signal quality (N = 393) or because the focal singer could not be unambiguously identified (N = 211), resulting in a final data set comprising 1936 motifs from identified birds (1095 from males and 841 from females), with 239 ± 57 (mean \pm SD) motifs per group.

Call similarity analysis

To determine if variation in call structure reflects social structure, we compared the recorded motifs with each other using a pairwise similarity analysis. Because motifs were highly tonal, comprising a strong, temporally modulated fundamental frequency (F0) and several harmonics (Figure 1A–C), comparisons were made on the basis of the F0 contours. F0 contours were extracted from the motifs using a freely available software package called Chirp (Meliza et al. 2013; https://github.com/dmeliza/chirp), which uses harmonic template matching (Shapiro and Wang 2009) and Bayesian particle filtering to smoothly track F0 as a function of time. The F0 estimates were verified and refined by multiple observers who were blind to the source of the vocalization.

The F0 contours for each pair of motifs were compared using dynamic time warping (DTW; Vintsyuk 1971), an algorithm that measures the similarity of 2 time series while allowing them to compress and expand slightly in time to account for variations in production. Additional details on the signal processing methods are available in the Supplementary Materials. The similarity scores for each motif were then grouped by bird, and the highest score in each group (excluding the reference motif) was taken as the "best match score." This operation identifies the motif in each bird's repertoire most similar to the reference motif. An example of best match scores for an exemplar motif is shown in Figure 1D. By averaging best match scores across all the motifs in a bird's repertoire, an estimate of the similarity between 2 birds' vocal repertoires can be obtained.

We analyzed whether the distribution of best match scores was correlated with the social and genetic structure of the population using



Figure 1

Structure and similarity of superb starling flight calls. (A) Time-frequency spectrogram of a representative flight call bout. Darker shades indicate higher power, with the total dynamic range scaled to 50 dB. The bout consists of a series of temporally discrete motifs, which are marked by horizontal bars. (B) Detail of the last 3 motifs from (A), with overlaid F0 estimates (red line). Note the tonal, harmonic structure, and rapid modulations of F0. (C) Similar motifs from another starling in the same social group. (D) Ranked plot of highest similarity scores for each of the birds in the study to the reference motif (B, bottom). Similarity (arbitrary units) is measured using DTW of the F0 traces. Insets show F0 estimates for selected exemplars with high and low similarity. Color indicates whether the comparison motif is from the same bird, a bird in the same social group, or a bird in a different social group.

linear mixed-effects models (LMM) with the best match score as the dependent measure. Models included random intercepts for the reference motif to account for repeated measures. Random intercepts were also included for the social groups in the comparison (specifically, the pair of reference and target groups) to account for variation in the acoustics at different sites and for the year (the pair of reference and target) to account for variation across years due to differences in recording equipment, operator, and effects of weather conditions on acoustics. Social relationships were coded for each motif pair as a factor with 3 levels: "bird" for motif pairs from the same bird, "group" for motif pairs from different birds in the same group, and "none" for pairs from birds in different groups. The number of motifs tested for each comparison bird was also included as a covariate to account for the increased probability of finding a good match with larger numbers of comparisons. We tested the effects of geographic distance (measured in kilometers between the centers of territories) and genetic relatedness (r; see Relatedness analysis) by adding these variables, along with the interaction between relatedness and social relationship, as fixed effects. For these analyses, the within-bird motif pairs were excluded. Models were fit using lme4 (Bates et al. 2011), and the significance of the fixed effects was evaluated with multcomp (Hothorn et al. 2008); both are packages for R (R Development Core Team 2010).

Acoustic feature-based analysis

To determine which call characteristics could serve as recognition cues, we calculated 11 acoustic features for each motif from the fundamental frequency (F0) estimates: mean F0, mean F0 of each temporal quartile, duration, the number of times F0 crossed the mean, maximum temporal duration of increasing and decreasing F0, frequency modulation (the number of directional changes in F0), and the mean slope of F0 contours. Principal component analysis was used to determine which features accounted for the most variation in motifs (see Supplementary Materials). To determine if these features varied more among than within groups, we used one-way Kruskal–Wallis tests followed by Nemenyi post hoc tests.

Playback experiments

We conducted playback experiments in 2010 and 2012 in each social group (N = 9) using flight calls of within-group males, flight calls from extra-group males, and in 2012, within-group flight calls with manipulated pitch and duration. The stimuli consisted of complete bouts recorded between 2008 and 2010. In the manipulated calls, which were based on the same recordings as the within-group call treatments, the pitch and duration of each motif were altered (see Supplementary Materials).

Playbacks took place between 10:00-12:00 and 14:00-16:00. Flight calls were played using speakers (RadioShack No. 40-1409; 100-12 000 Hz frequency response) placed approximately 15 m from adult starlings foraging within territory boundaries. Each stimulus was presented 5 times, once per minute, with 5 min of silence before and after to act as controls. Observers remained hidden during all playbacks and recorded the following events during the control and playback periods: approaches within 5 m of a speaker, flight call bouts, songs, and alarm calls. Songs were distinguished from flight calls by their longer and more variable structure and >50 additional motifs (Pilowsky and Rubenstein 2013). The identities of the starlings present during playbacks were also recorded to obtain a count of individuals and to ensure that focal birds were not played their own calls. Observers were blind to the stimulus identities. The order of stimuli was randomized within each group, and a minimum of 1 day separated playbacks.

In the 2010 playback experiments, extra-group calls were taken from groups a few kilometers away from the focal group. In 2012, extra-group calls came from both distant and neighboring social groups. Because the birds were presumably familiar with calls from neighboring groups, this design allowed us to test whether birds could discriminate calls of their own group from other groups without the confound of familiarity.

We analyzed playback data first with a MANOVA for all the measured response variables, with time (i.e., before, during, and after playback), treatment (i.e., stimulus from the same group, a different group, or a manipulated call from the same group), and their interaction as independent variables. There was a significant effect of time period ($F_{10,230} = 3.36$; P = 0.0004) and the interaction of time period and treatment ($F_{20,468} = 2.08$; P = 0.004). We then analyzed each of the response variables separately with a univariate LMM. Fixed effects comprised treatment, time period, and their interaction, and for extra-group treatments, whether the call was from a neighboring or distant group. Social group and year were random effects. After it was determined that neighbor versus distant was not a significant effect (likelihood ratio test: $\chi_3^2 = 1.23$; P = 0.75), it was dropped from the model. We used planned contrasts to test for significant effects relative to the within-group stimulus and prestimulus condition. The number of occurrences of each of the recorded behaviors, normalized by the mean number of birds present in each time period, was used as the dependent measure in separate analyses. Data points with no birds present were dropped. There was no significant effect of time period or treatment on the mean number of birds.

RESULTS

Flight call similarity within social groups

Superb starling flight calls consisted of short bouts of repeated, temporally discrete motifs. Calls comprised multiple distinct motif types, which were often similar to motifs sung by other birds (see Figure 1B,C). Pairwise comparisons of flight call motifs using DTW of the fundamental frequency (F0) support this observation, identifying motifs from other starlings' repertoires with a high degree of similarity to many of the recorded motifs (e.g., Figure 1D). Although there were occasionally good matches with birds from other social groups, as in Figure 1D, similarity was on average higher between birds from the same social group than between birds from different social groups (LMM: $\chi = 4.73$, P < 0.0001; Figure 2). Best match scores were much higher within individual repertoires than they were within groups ($\chi = 51.03$, P < 0.0001) or throughout the population ($\chi = 21.58$, P < 0.0001), though this was not the case for every motif (e.g., Figure 1D).

Effects of geographic distance and genetic relatedness on call similarity

Greater call similarity within social groups could reflect genetic relatedness, a shared environment during vocal development, convergence of call structure from social familiarity, or some combination of the three. To distinguish among these possibilities, the call sharing analysis was repeated using only immigrant females who have dispersed from their natal territories, have immigrated into the study population, and are not closely related to most members of their adopted group (Rubenstein 2007b). Comparing only the calls of immigrant females to those of other immigrant females,



Figure 2

Call similarity versus social relationship. Mean \pm SE best match score (arbitrary units) is plotted against whether motifs were from the same bird, from different birds in the same social group, or from birds in different social groups (all comparisons, P < 0.05, LMM).

within-group similarity remained significantly greater than betweengroup similarity (Z = 3.10, P = 0.005). Furthermore, when genetic relatedness and geographic distance were included as covariates in the full analysis, there was no significant effect of relatedness on similarity (Figure 3A), either within groups (Z = -1.69, P = 0.37) or in the general population (Z = -1.76, P = 0.33). Call similarity decreased with geographic distance at a mean rate of -0.018 km⁻¹ (Z = -2.56, P = 0.039; Figure 3B), indicating that calls were more similar among nearby groups than among more distant ones. In this more complex analysis, calls were still significantly more similar within than between groups (Z = 3.06, P = 0.008).

Among-group variation in call features

Principal components analysis indicated that 5 of the 11 measured acoustic features accounted for 99% of the variance: motif duration, mean frequency crossing, maximum time of pitch increase and decrease, and frequency modulation (see Supplementary Materials and Table S1). These features all varied significantly among groups (Kruskal–Wallis: all $\chi_8^2 > 24.6$; all P < 0.01). Significant post hoc differences were observed for all 5 features between one or more pairs of groups (see Supplementary Materials and Figure S1). For all 5 of these motif features, the coefficient of variation (CV) within individuals was lower than the CV within groups, and both were lower than the CV for the larger population (see Supplementary Materials and Figure S2).

Response to same-group and extra-group calls

Starlings played flight calls on their home territories responded differently to calls from their own group than to calls from other groups. There were significantly more speaker approaches during playback of extra-group flight calls (LMM, planned contrast: Z = 3.14, P < 0.02; Figure 4) relative to the within-group stimulus and the prestimulus condition in both years. There was not a significant difference in responses to extra-group calls from neighboring versus more distant groups (LMM, likelihood ratio test: $\chi_3^2 = 1.23$; P = 0.75). Within-group calls in which the pitch and duration were manipulated did not result in more speaker approaches during playback experiments (LMM: Z = 1.09, P = 0.83). It is possible that the manipulations did not alter call features that serve as



Figure 3

Genetic and geographic factors affecting call similarity. (A) Mean \pm SE call similarity (arbitrary units) for each pair of birds from the same social group as a function of their genetic relatedness. Solid line indicates best linear fit, with standard error in light gray. The correlation is not significant. (B) Mean \pm SE call similarity for each pair of groups as a function of geographic distance between the geographic center of the groups' territories. Open squares indicate average similarity within each group. Within-bird comparisons are excluded. Solid line indicates best linear fit for the different-group pairs (P = 0.039).



Figure 4

Comparison of speaker approaches before, during, and after playback of flight calls from the same social group, manipulated calls from the same group, and calls from a different group. The rate of speaker approaches per bird was significantly higher during playback of extra-group calls (*P = 0.01).

group recognition cues or that they altered the calls to the point where they were no longer reliably recognized as conspecific. It is also possible that the speakers were not of high enough quality to transmit such subtle differences in call structure. Although birds showed a significant approach response, none of the other measured responses differed significantly for treatments of withingroup, extra-group, or manipulated calls.

DISCUSSION

Our results demonstrate that superb starlings' flight calls are more similar to the calls of other individuals in their social groups than to the calls of birds in other groups and that starlings respond differently to playback of calls from their own group versus calls from different groups. Surprisingly, genetic relatedness did not predict similarity in flight calls, and the flight calls of immigrant females, which entered the study population only after reaching maturity and are not closely related to other members of their adopted groups (Rubenstein 2007b), were as similar to the calls of other immigrant within-group females as they were to the calls of within-group males. Thus, the features of flight calls that are shared within groups are likely to reflect learning and imitation that continues into adulthood. Additionally, some degree of imitation appears to occur with neighboring groups, as evidenced by the negative correlation of call similarity with geographic distance between groups. The acoustic characteristics of flight call motifs that varied among groups were related to the duration and rate of frequency modulation, suggesting that starlings adjust the temporal parameters of their flight calls to more closely match their social group while maintaining the same overall structure of trills and hairpins. At the same time, the calls given by a single individual are more similar to each other than to the calls of other members of the group, indicating that starlings retain individually distinctive characteristics. Together, these findings suggest that flight calls are learned signals that encode information about both social group membership and possibly individual identity.

The behavioral experiments indicate that superb starlings discriminate between calls from their own group versus calls from other groups. The increased rate of speaker approaches to extragroup calls suggests an agonistic response to territorial intrusions, as has been shown for both cooperative and noncooperative species (Stoddard et al. 1990; Payne et al. 1991; Mennill and Ratcliffe 2004; Radford 2005; Bradley and Mennill 2009). Group recognition could in principle depend alone on memorization of the individually distinctive features of calls of other group members, but the high levels of motif similarity within groups suggest that shared vocal characteristics are likely to underlie this behavior. Additionally, because extra-group stimuli were from both neighboring and distant territories, it is unlikely that the response was predicated on unfamiliarity with extra-group stimuli, as focal birds may have previously heard both neighboring group and same-group calls. In the dry season, neighboring groups often form flocks around fruiting trees (e.g., Euclea divinorum), which are typically found in the low lying areas separating territories (Rubenstein DR, personal observations). This suggests that individuals from neighboring groups are likely to interact with each other. Thus, rather than making a binary distinction between familiar and unfamiliar calls, superb starlings may be able to distinguish the presence or absence of call features common to all group members. Vocal recognition of group members may help to reinforce boundaries between social groups and could be useful

in spatial coordination within groups (Mundinger 1970; Wilkinson and Boughman 1998; Hall and Peters 2008), as territories can be large (up to 1 km²) and birds may range widely in search of food during the nonbreeding season. Group recognition may also aid females in selecting males from other groups when seeking genetically different extrapair mates in order to increase the heterozygosity of their offspring (Rubenstein 2007a) or when joining a social group to breed on dispersing from their natal territory (Pollack L, Rubenstein DR, unpublished data).

In other cooperatively breeding species that exhibit variation in social group structure, both learned and innate vocal signals may serve as reliable cues for kin recognition, allowing helpers to preferentially help close relatives. The use of learned vocalizations has been demonstrated in facultative cooperative breeders, such as longtailed tits (Sharp et al. 2005), and in cooperative groups that contain a single breeding pair, such as striped-back wrens (Price 1998) and splendid fairy-wrens (Payne et al. 1988). Bell miners, which live in large coteries comprising kin and nonkin, use innate, familyspecific calls to recognize relatives (McDonald and Wright 2011). Here, we found no evidence that superb starling flight calls directly carry information about kinship. Rather, as suggested by the high levels of within-group motif similarity observed in philopatric males and females as well as immigrant females, individuals seem to modify their flight calls to match those of other group members, even as adults. Many songbirds, such as canaries (Nottebohm et al. 1986) and nightingales (Kiefer et al. 2006), are open-ended vocal learners and continue to modify their vocalizations throughout life. Moreover, many species may do so in a manner that causes convergence of vocalizations in social groups, as in the European starling (Eens et al. 1991) and other songbirds (Mammen and Nowicki 1981; Feekes 1982; Brown 1985; Brown and Farabaugh 1991), psittaformes (Wright 1996), bats (Boughman and Wilkinson 1998), and cetaceans (Smolker and Pepper 1999). We hypothesize that the predominance of social information over kin information in superb starling flight calls reflects the more complex cooperative society of this species. That is, superb starling helpers often help at multiple nests belonging to both related and unrelated individuals in their social group (Rubenstein 2006), rather than just at a single nest of a close relative, and genetic relationships among group members vary greatly in this species (Rubenstein 2007a).

Studies of social insects have suggested that individual recognition may be important in complex societies and that complex social behavior itself can lead to individual variability in identity traits (Tibbetts 2004). Instead of simply distinguishing kin from nonkin, superb starlings may need to individually recognize group mates to differentiate among individuals of varying degrees of genetic relatedness. Although flight calls showed increased similarity within social groups, individual calls were also highly distinct and thus may function in individual recognition. Here we cannot demonstrate "true" individual recognition, as this requires evidence of individual distinctiveness in calls, discrimination based on this distinctiveness, and association of calls with individualspecific information (Tibbetts and Dale 2007). However, having shown group and individual distinctiveness as well as group discrimination, we suspect that individual recognition occurs in this species. In social groups where most individuals of the philopatric sex are related and kin recognition is less advantageous, individual recognition may be favored as an alternative strategy, potentially facilitating cooperation for direct benefits and also permitting recognition of kin based on individual identity. The benefits of individuality may be counterbalanced by those selecting for similarity with other group members, a trade-off that could lead to the emergence of vocal behaviors that serve as both individual and group recognition cues. The use of learned calls that signal social identity, rather than learned or innate calls that signal kinship, distinguishes this species from other cooperative breeders and deserves further attention.

In summary, we propose that the need to signal group membership is a primary driver of variation in superb starling flight calls. Furthermore, although it is not certain that individual recognition occurs in this system, calls are more similar within versus between individuals' repertoires, providing a source of information that could be used to distinguish among individuals within these complex groups of kin and nonkin. Thus, signaling individuality and social association, rather than simply kinship, may be an important route to cooperation in socially complex animal societies.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco. oxfordjournals.org/

FUNDING

This work was supported by the National Science Foundation (IOS-1121435), the National Institutes of Health (F32 DC-008752), Columbia University, and Columbia University Earth Institute.

We thank W. Nderitu and G. Manyaas for help in the field and N. Bailey, M. Cohen, H. D'Angelo, and J. Hollarsmith for their help in analyzing acoustic recordings. 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.

Handling editor: Sarah Pryke

REFERENCES

- Bates D, Maechler M, Bolker BM. 2011. lme4: linear mixed-effects models using S4 classes. R package version 0.999375 [Internet] [cited 2013 July 10]. Available from: http://CRAN.R-project.org/package=lme4.
- Bee MA, Gerhardt HC. 2002. Individual voice recognition in a territorial frog (*Rana catesbeiana*). Proc R Soc Lond B. 269:1443–1448.
- Boughman JW, Wilkinson GS. 1998. Greater spear-nosed bats discriminate group mates by vocalizations. Anim Behav. 55:1717–1732.
- Bradley DW, Mennill DJ. 2009. Strong ungraded responses to playback of solos, duets and choruses in a cooperatively breeding Neotropical songbird. Anim Behav. 77:1321–1327.
- Brown ED. 1985. The role of song and vocal imitation among Common Crows (*C. brachyrhynchos*). Z Tierpsychol. 68:115–136.
- Brown ED, Farabaugh SM. 1991. Song sharing in a group-living songbird, the Australian magpie, *Gymnorhina tibicen*. Part III. Sex specificity and individual specificity of vocal parts in communal chorus and duet songs. Behaviour. 118:244–274.
- Catchpole CK, Slater PJB. 2008. Bird song: biological themes and variations. 2nd ed. Cambridge (MA): Cambridge University Press.
- Cheney DL, Seyfarth RM. 1982. Recognition of individuals within and between free-ranging groups of vervet monkeys. Am Zool. 22:519–529.
- Clutton-Brock TH. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. Science. 296:69–72.
- Cockburn A. 1998. Evolution of helping behaviour in cooperatively breeding birds. Annu Rev Ecol Syst. 29:141–177.
- Cockburn A. 2006. Prevalence of different modes of parental care in birds. Proc R Soc B. 273:1375–1383.
- Cornwallis CK, West SA, Griffin AS. 2009. Routes to indirect fitness in cooperatively breeding vertebrates: kin discrimination and limited dispersal. J Evol Biol. 22:2445–2457.

- Eens M, Pinxten R, Verheyen RF. 1991. Male song as a cue for mate choice in the European starling. Behaviour. 116:210–238.
- Emlen ST. 1997. Predicting family dynamics in social vertebrates. In: Krebs JR, Davies NB, editors. Behavioural ecology: an evolutionary approach. Oxford: Blackwell Scientific. p. 228–253.
- Farnsworth A. 2005. Flight calls and their value for future ornithological studies and conservation research. Auk. 3:733–746.
- Feekes F. 1982. Song mimesis within colonies of *Cacicus c. cela* (lcteidae, Aves). A colonial password? Z Tierpsychol. 58:119–152.
- Griffin AS, West SA. 2003. Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. Science. 302:634–636.
- Hall ML, Peters A. 2008. Coordination between the sexes for territorial defence in a duetting fairy-wren. Anim Behav. 76:65–73.
- Hamilton WD. 1964. The genetical evolution of social behaviour. II. J Theor Biol. 7:1–16.
- Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models. Biometrical J. 50:346–363.
- Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol. 16:1099–1106.
- Kiefer S, Spiess A, Kipper S, Mundry R, Sommer C, Hultsch H, Todt D. 2006. First-year common nightingales (*Luscinia megarhynchos*) have smaller song-type repertoire sizes than older males. Ethology. 112:1217–1224.
- Konovalov DA, Heg D. 2008. A maximum-likelihood relatedness estimator allowing for negative relatedness values. Mol Ecol Notes. 8:256–263.
- Lehmann L, Keller L. 2006. The evolution of cooperation and altruism: a general framework and a classification of models. J Evol Biol. 19:1365–1376.
- Mammen DL, Nowicki S. 1981. Individual differences and within-flock convergence in chickadee calls. Behav Ecol Sociobiol. 9:179–186.
- Marler P. 2004. Bird calls: their potential for behavioral neurobiology. Ann N Y Acad Sci. 1016:31–44.
- McComb K, Moss C, Sayialel S, Baker L. 2000. Unusually extensive networks of vocal recognition in African elephants. Anim Behav. 59:1103–1109.
- McDonald PG. 2012. Cooperative bird differentiates between the calls of different individuals, even when vocalizations were from completely unfamiliar individuals. Biol Lett. 8:365–368.
- McDonald PG, 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. Proc R Soc B. 278:3403–3411.
- Meliza CD, Keen SC, Rubenstein DR. 2013. Pitch- and spectralbased dynamic time warping methods for comparing field recordings of harmonic avian vocalizations. J Acoust Soc Am. doi: 10.1121/1.4812269.
- Mennill DJ, Ratcliffe LM. 2004. Do male black-capped chickadees eavesdrop on song contests? A multi-speaker playback experiment. Behaviour. 141:125–139.
- Mundinger PC. 1970. Vocal imitation and individual recognition of finch calls. Science. 168:480–482.
- Nottebohm F, Nottebohm ME, Crane L. 1986. Developmental and seasonal changes in canary song and their relation to changes in the anatomy of song-control nuclei. Behav Neural Biol. 46:445–471.
- Payne RB, Payne LL, Rowley I. 1988. Kin and social relationships in splendid fairy-wrens: recognition by song in a cooperative bird. Anim Behav. 36:1341–1351.
- Payne RB, Payne LL, Rowley I, Russell EM. 1991. Social recognition and response to song in cooperative red-winged fairy wrens. Auk. 108:811–819.

- Pilowsky JA, Rubenstein DR. 2013. Social context and the lack of sexual dimorphism in song in an avian cooperative breeder. Anim Behav. doi: 10.1016/j.anbehav.2013.01.012.
- Price JJ. 1998. Family- and sex-specific vocal traditions in a cooperatively breeding songbird. Proc R Soc B. 265:497–502.
- R Development Core Team. 2010. R: a language and environment for statistical computing, reference index version 2.2.1. Vienna (Austria): R Foundation for Statistical Computing.
- Radford AN. 2005. Group-specific vocal signatures and neighbour-stranger discrimination in the cooperatively breeding green woodhoopoe. Anim Behav. 70:1227–1234.
- Rendall D, Rodman PS, Emond RE. 1996. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. Anim Behav. 51:1007–1015.
- Rubenstein DR. 2005. Isolation and characterization of polymorphic microsatellite loci in the plural cooperatively breeding superb starling, *Lamprotornis superbus*. Mol Ecol Notes. 5:739–744.
- Rubenstein DR. 2006. The evolution of the social and mating systems of the plural cooperatively breeding superb starling, *Lamprotornis superbus* [PhD dissertation]. [Ithaca (NY)]: Cornell University.
- Rubenstein DR. 2007a. Female extrapair mate choice in a cooperative breeder: trading sex for help and increasing offspring heterozygosity. Proc R Soc B. 274:967–975.
- Rubenstein DR. 2007b. Territory quality drives intraspecific patterns in extrapair paternity. Behav Ecol. 18:1058–64.
- Rubenstein DR. 2007c. Temporal but not spatial environmental variation drives adaptive offspring sex allocation in a plural cooperative breeder. Am Nat. 170:155–165.
- Rubenstein DR. 2011. Spatiotemporal environmental variation, risk aversion and the evolution of cooperative breeding as a bet-hedging strategy. Proc Natl Acad Sci USA. 108:10816–10822.
- Shapiro AD, Wang C. 2009. A versatile pitch tracking algorithm: from human speech to killer whale vocalizations. J Acoust Soc Am. 126:451–459.
- Sharp SP, McGowan A, Wood MJ, Hatchwell BJ. 2005. Learned kin recognition cues in a social bird. Nature. 434:1127–1130.
- Smolker R, Pepper J. 1999. Whistle convergence among allied male bottlenose dolphins (Delphinidae, *Tursiops* sp.). Ethology. 105:595–617.
- Stoddard PK. 1996. Vocal recognition of neighbors by territorial passerines. In: Kroodsma DE, Miller EH, editors. Ecology and evolution of acoustic communication in birds. Ithaca (NY): Cornell University Press. p. 356–374.
- Stoddard PK, Beecher MD, Horning CL, Willis MS. 1990. Strong neighbor-stranger discrimination in song sparrows. Condor. 92:1051–1056.
- Tibbetts EA. 2004. Complex social behavior can select for variability in visual features: a case study in *Polistes* wasps. Proc R Soc B. 271:1955–1960.
- Tibbetts EA, Dale J. 2007. Individual recognition: it is good to be different. Trends Ecol Evol. 22:529–537.
- Tyack PL. 2008. Convergence of calls as animals form social bonds, active compensation for noisy communication channels, and the evolution of vocal learning in mammals. J Comp Psychol. 122:319–331.
- Vintsyuk TK. 1971. Element-wise recognition of continuous speech composed of words from a specified dictionary. J Cybern Syst Anal. 7:361–372.
- Wilkinson GS, Boughman JW. 1998. Social calls coordinate foraging in greater spear-nosed bats. Anim Behav. 55:337–350.
- Wright TF. 1996. Regional dialects in the contact call of a parrot. Proc R Soc B. 263:867–872.