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Animal behaviour

The fitness consequences of kin-biased dispersal in a cooperatively breeding bird

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Cooperative alliances among kin may not only lead to indirect fitness benefits for group-living species, but can also provide direct benefits through access to mates or higher social rank. However, the immigrant sex in most species loses any potential benefits of living with kin unless immigrants disperse together or recruit relatives into the group in subsequent years. To look for evidence of small subgroups of related immigrants within social groups (kin substructure), we used microsatellites to assess relatedness between immigrant females of the cooperatively breeding superb starling, *Lamprotornis superbus*. We determined how timing of immigration led to kin subgroup formation and if being part of one influenced female fitness. Although mean relatedness in groups was higher for males than females, 26% of immigrant females were part of a kin subgroup with a sister. These immigrant sibships formed through kin recruitment across years more often than through coalitions immigrating together in the same year. Furthermore, females were more likely to breed when part of a kin subgroup than when alone, suggesting that female siblings form alliances that may positively influence their fitness. Ultimately, kin substructure should be considered when determining the role of relatedness in the evolution of animal societies.

1. Introduction

Kin selection explains how altruism can evolve in animal societies through the sharing of genes among relatives [1]. Yet dispersal—often necessary to avoid inbreeding [2]—can reduce the role that kin selection plays in promoting cooperation by decreasing relatedness among group members [3]. In most vertebrate societies, dispersal is sex-biased [4]. Although this allows the philopatric sex to maintain high relatedness within the group, the dispersing sex typically loses the potential advantages of living with kin. However, if relatives disperse together [5–9], they may obtain the same benefits (e.g. inclusive fitness, increased social rank) as the philopatric sex.

Relatives emigrating together from their natal group—either seen dispersing in the same direction or identified genetically within a cohort of immigrants—have been documented in multiple cooperatively breeding birds [5–9]. Such ‘kin-biased dispersal’ can occur in two contexts: (i) co-dispersal of relatives at the same time (i.e. kin coalitions) [7–9] or (ii) an individual immigrates into a group that already contains a relative (i.e. kin recruitment) [6]. Kin-biased dispersal could influence the genetic structure of the dispersing sex through the formation of small subgroups of related immigrants (hereafter kin substructure). In cooperative societies, kin substructure could positively influence immigrant fitness if the presence of related social partners increases breeding opportunities or the likelihood of gaining indirect fitness from interacting with kin.

Here, we examine kin substructure and its fitness consequences in the plural cooperatively breeding superb starling, *Lamprotornis superbus*. As in most birds, females are the primary dispersing sex and males the philopatric sex [4].

Female–female competition for access to mates and/or breeding opportunities is thought to be common in superb starlings [10,11]. Using pairwise relatedness data generated from microsatellite markers [12], we searched for evidence of kin substructure among immigrant females of unknown origin in social groups. We then determined the fitness consequences of these immigrant sibships by examining the likelihood of (i) breeding based on seniority of arrival, and (ii) breeding and fledging offspring for females based on the presence or absence of sibling.

2. Material and methods

(a) Study system

We studied a population of superb starlings from 2001 to 2013 at the Mpala Research Centre, Kenya (0°170′ N, 37°520′ E). Birds defend year-round territories and breed biannually [12]. Group size of the nine marked social groups ranged from 18 to 43 individuals (mean ± s.d. = 25.8 ± 8.6; electronic supplementary material, table S1). Of the 830 marked birds in the population during the study (approx. 97% of the population), 183 were classified as immigrants. These include unbanded females captured after 2001, and females that bred. Females rarely breed in their natal group and those that did (1.5% of breeding pairs) were excluded from analyses. Breeding roles were determined using multiple 1–3 h focal observations at all active nests at different nest stages (i.e. building, incubation and hatchling) in all years [13].

(b) Relatedness

DNA was isolated from blood using DNeasy blood and tissue kits (Qiagen). Sex was determined using PCR primers [14] that have been confirmed previously in this species [10]. Individuals were genotyped on 3100, 3130 and 3i30xl genetic analysers (Life Technologies) using 15 microsatellite loci [10,12,13]. Alleles were scored using GENEIOUS v. 6.1 (Biomatters). Parentage was determined previously [15]. Pairwise relatedness values based on Queller and Goodnight's r [16] were calculated using KINGROUP v. 2 [17]. Separate yearly analyses from 2002 to 2012 were performed using all of the individuals in a social group in a given year. Mean r for each group was calculated for all males (mean ± s.d. = 0.12 ± 0.04), all females (mean ± s.d. = 0.07 ± 0.08), and both sexes combined (mean ± s.d. = 0.08 ± 0.05; electronic supplementary material, table S1). The mean ± s.d. mother–offspring r-value was 0.45 ± 0.13 ($n = 162$ pairs).

(c) Kinship reconstruction

We determined sibling-level relatedness (approx. $r = 0.5$) by using r-values above the upper 97.5th percentile confidence interval threshold of all immigrant female pairwise r-values within a group who overlapped in time (electronic supplementary material, table S1). To determine percentiles, we generated r-values for the entire population from 2001 to 2013, but then treated each group separately (electronic supplementary material, figure S1). It is unlikely that sibships formed purely by chance (see the electronic supplemental material for additional details).

(d) Fitness consequences

We determined the fitness consequences of being part of a sibship in three ways. First, we compared the breeding status of established (i.e. the female who first joined the group) and recruited (i.e. the female who immigrated at least one breeding season later) siblings to determine whether order of recruitment influenced a female's likelihood to breed. To address whether females were more likely to join a group with a sister who had already achieved dominance, we looked at the probability an established female bred before her sister immigrated. Next, we examined whether breeding females in sibships were more likely to breed (i.e. lay eggs) over the course of the study during the breeding seasons when their sister was present versus absent. By comparing the same females—either with or without their sister present—we were able to control for the effect of relative group size and territory quality on breeding opportunity. We also compared the absolute age of breeding females with and without siblings present. Finally, we looked at whether breeding females in sibships were more likely to fledge hatchlings during the breeding seasons when their sister was present versus absent. We considered all breeding seasons in which the female was present in the population, including those before, during, and after the time her sister was also present. We used Fisher's exact tests to compare categorical variables (i.e. sister present/absent, breed/not breed, fledge/not fledge) in each analysis, and all females were only considered once.

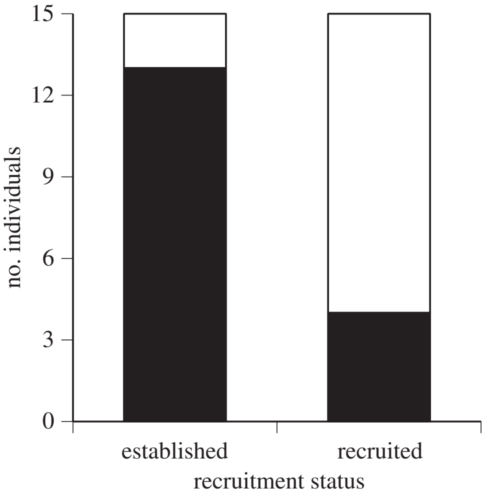

Figure 1. Breeding status of females in sibships formed through kin recruitment ($n = 15$). Established females were present in the group at least one breeding season before recruited females arrived. Females were categorized as those that attempted to breed (i.e. laid eggs in at least one season; black bars), or as those that did not attempt to breed (white bars).

3. Results

We found that 47 of 183 (26%) immigrant females were part of a sibship. These immigrant subgroups consisted of 22 pairs and one group of three females. The mean ± s.d. immigrant female sibling pairwise r-value was 0.52 ± 0.05 ($n = 24$ pairs; range = 0.41–0.72; electronic supplementary material, table S2). Each social group contained at least one kin subgroup. Of the 47 immigrant females identified as part of a sibship, 25 (53%) attempted to breed at least once. Of the 23 immigrant sibships, 15 (65%) formed through kin recruitment and seven (30%) through kin coalitions; one (5%) formed prior to the study. For those sibships formed through recruitment, the mean interval between immigration was 1.8 years (range = 0.5–5 years).

For subgroups formed through kin recruitment, established females were significantly more likely to be breeders than recruited females (Fisher's exact test, $p = 0.0025$; figure 1). There was no difference in the probability that a female recruited into a group with a sister that had or had not already bred (chi-squared test, $\chi^2_1 = 0.62$, $p = 0.44$), suggesting that relatives are not more likely to join a group where a sister had already achieved a dominant breeding position. Additionally, females in all sibships were more likely to attempt to breed when their sister was present than when they were alone (Fisher's exact test, $p = 0.0001$; figure 2). However, for those females in sibships

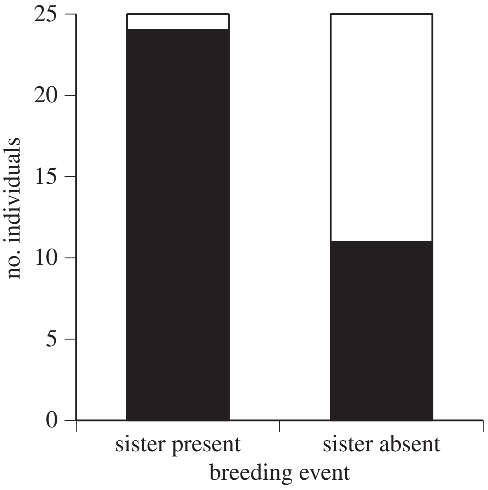

Figure 2. Breeding attempts by immigrant females in sibships when their sister was present and when their sister was absent ($n = 25$). Females were categorized as those that attempted to breed (i.e. laid eggs in at least one season; black bars), or as those that did not attempt to breed (white bars).

who attempted to breed, their broods were not more likely to fledge offspring when their sister was present than when they were alone (Fisher's exact test, $p = 0.72$; electronic supplementary material, figure S2). Importantly, the start and duration of the period within which a female overlapped with her sister did not appear to be related to age. That is, the absolute age of breeding females, approximated as the number of years since initial recruitment, did not differ between when siblings were present (mean ± s.d. = 2.63 ± 1.65) and when siblings were absent (mean ± s.d. = 3.35 ± 2.63; Mann–Whitney test, $U = 190$, d.f. = 36, $p = 0.31$), suggesting that age was not driving the difference in breeding status.

4. Discussion

Kin substructure was surprisingly common in superb starlings, as more than 25% of immigrant females overlapped for at least one breeding season with a sibling in their new social group, higher than expected by chance in this system (electronic supplementary material). Most of these immigrant sibships formed through kin recruitment, a phenomenon that has been observed in brown jay immigrants [6], but not described in other cooperatively breeding birds. Because kin recruitment is frequent, a kin-recognition mechanism other than spatial proximity is needed. Superb starlings encode group identity in their flight calls [18], a potential mechanism for kin recruitment in this and other species.

Immigrant females with sisters in their group were more likely to breed during seasons when their sister was present, indicating that female siblings form alliances that could impact social status and ultimately access to dominant breeding positions. Females may therefore benefit from a sister's presence because of improved access to breeding positions, and not necessarily owing to added care for offspring [8] (see the electronic supplementary material for more details). In sibships formed through kin recruitment, established females were more likely to become breeders than their recruited siblings. Although established females tended to be older than recruited females, the effect of relative age did not appear to influence the primary result of this study, namely that females were more likely to breed when part of a kin subgroup than when alone. While it is possible that older females were simply more likely to breed than younger females, we found no difference between the mean age of females whose sisters were present or absent. Together, these results suggest that age is unlikely to be driving the patterns in breeding status. Furthermore, our data do not support the hypothesis that recruited females are more likely to join a group where their sister has already achieved dominance. Despite the potential fitness benefits—particularly for established females—breeding females were not more likely to fledge offspring when a sister was present. This is not surprising, since most nest failure in superb starlings is the result of predation [19], not the lack of parental care. The most important predictor of high lifetime reproductive success in superb starlings is the number of times a female breeds [20], so simply being able to breed more often because kin are present may be vital to female fitness.

In summary, kin recruitment may be a common component of dispersal in cooperatively breeding species that is often ignored by researchers. The formation of kin substructure may be one way that immigrants in cooperatively breeding species can benefit from living with relatives. Whereas previous research on cooperatively breeding vertebrates has emphasized the role of kin selection in the philopatric sex [10], kin substructure in the dispersing sex should also be considered when examining the role of relatedness in the evolution of animal societies.

Ethics. This work was approved by the Columbia Institutional Animal Care and Use Committee (AC-AAAB1128).

Data accessibility. Data are available at doi:10.5061/dryad.426rq.

Authors' contributions. L.P. and D.R.R. designed the study, collected and analysed the data, and wrote the manuscript. L.P. assembled the long-term dataset.

Competing interests. The authors declare they have no competing interests.

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