Received: 14 July 2023 | Accepted: 16 July 2024

DOI: 10.1111/1365-2656.14162

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Intraspecific Variation in Evolution and Ecology

Intraspecific variation in group structure arises due to environmentally-mediated directional dispersal in a cooperative breeder

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Funding information
American Ornithological Society; Sigma Xi; Columbia University; NSF Division of Integrative Organismal Systems, Grant/Award Number: IOS-1257530 and IOS-1656098; Department of Ornithology, American Museum of Natural History

Handling Editor: Marlène Gamelon

Abstract

1. Many cooperatively breeding species live in groups with complex structure—large group sizes, low and variable kin structure, and multiple breeding pairs. Since these mixed-kin groups typically form because of immigration of unrelated individuals of both sexes in addition to limited offspring dispersal, differences in patterns of dispersal can generate variation in group structure, even within the same species or population.
2. Here, we examine how environmentally mediated dispersal patterns influence variation in group structure in the plural breeding superb starling (*Lamprotornis superbus*), an avian cooperative breeder that inhabits a spatiotemporally variable savanna environment and forms mixed-kin groups with variable group sizes and more than one breeding pair per group.
3. Using 4068 genome-wide polymorphic loci and fine-scale, remotely sensed ecological data from 22 groups sampled across a nearly 200 km^2 environmental gradient in central Kenya, we find evidence of not only frequent and long-distance dispersal in both sexes (low isolation-by-distance and weak genetic structure), but also directional dispersal from small groups in lower quality habitat with low normalised difference vegetation index (NDVI) to large groups in higher quality habitat with high NDVI.
4. Additionally, we find stronger genetic structure among groups in lower quality habitat, and higher genetic diversity and lower relatedness of groups in higher quality habitat. Previous work using long-term data from groups in the same population has shown that groups with lower relatedness are larger and have more breeding pairs.
5. Long-distance, directional dispersal to maximise individual fitness can thus lead to smaller and simpler kin-based social groups in lower quality habitat, but larger and more complex mixed-kin groups in higher quality habitat.
6. Such intraspecific, within-population variation in group structure, including variation in kin structure of social groups, could have profound implications for the relative importance of the evolutionary mechanisms (i.e. direct vs. indirect fitness benefits) underlying the formation of cooperative societies.

KEYWORDS
cooperative breeding, dispersal, environmental gradient, gene flow, group structure, kin structure, population structure, superb starling

1 | INTRODUCTION

In cooperatively breeding species, individuals form social groups and jointly care for young (Brown, 1978). Across cooperative breeders, the structure of these groups varies in complexity from small kin-based groups with a single breeding pair to large groups with low and variable kin structure and multiple breeders (Brown, 1978; Lukas & Clutton-Brock, 2020; Pereira et al., 2023; Riehl, 2013). This interspecific variation in the group structure can have significant implications on the costs and benefits of group living and thus on how cooperative breeding societies form and are maintained over time. In general, small, kin-based groups result in higher indirect fitness benefits of helping close relatives and are formed primarily by offspring delaying or foregoing dispersal (Burland et al., 2002; Clutton-Brock & Manser, 2016; Nelson-Flower et al., 2018). Conversely, mixed-kin groups with low and variable kin structure can be formed by immigration of both sexes in addition to limited dispersal of offspring and result primarily in direct fitness benefits of group living such as increased survival and/or reproduction (Heg et al., 2005; Shah & Rubenstein, 2023). Thus, dispersal is a key demographic process determining the complexity of group structure. Differences in the underlying fitness benefits of group living can therefore manifest as variation in dispersal patterns, generating considerable variation in group structure even within the same species (Komdeur, 1992; Schradin & Pillay, 2005; Stacey & Bock, 1978) or population (Smith & Dobson, 2022; von Schantz, 1984).

Dispersal patterns are often determined by social and ecological factors such as group size and habitat quality which may covary. Most theoretical work assumes (Shen et al., 2014, 2017), and some empirical studies have shown (Ridley, 2016), that larger groups in higher quality habitat are more likely to resist potential immigrants. Moreover, immigrants might have better access to breeding opportunities in, and thus prefer to join, smaller groups (Bateman et al., 2012; Bergmüller et al., 2005; Nelson-Flower et al., 2018). However, empirical studies have largely been limited to cooperative breeders that only form small, kin-based groups with breeding opportunities monopolised by one pair (singular breeding) (Bateman et al., 2012; Bergmüller et al., 2005; Nelson-Flower et al., 2018; Ridley, 2016). In more complex cooperative breeders with larger groups, mixed kinship, and multiple breeding pairs (plural breeding), the potential fitness payoffs for immigrants may instead be greater in larger groups where survival and reproductive success are higher (Shah & Rubenstein, 2023). Larger groups in such species may thus be primarily maintained by direct benefits of group living, whereas smaller groups may be governed mostly by indirect, kin-selection benefits (Clutton-Brock, 2002; García-Ruiz et al., 2022), with directional dispersal from small groups in low-quality habitat to large groups in high-quality habitat. Variation in the cost-benefits of group living can thus create an intraspecific pattern of increasing complexity of group structure with increasing habitat quality. Examining how dispersal patterns between groups and their structure vary across a heterogeneous landscape is the first step towards a better understanding of intraspecific variation in cooperative societies.

Superb starlings (*Lamprotornis superbus*) are avian plural cooperative breeders that form large, complex groups with mixed kinship containing multiple breeding pairs that are aided by non-breeding helpers in offspring provisioning and nest defence (mean (±SD) group size: 23 ± 11 individuals) (Rubenstein, 2016). They inhabit semi-arid savanna habitat with high spatiotemporal variation in rainfall, which governs key demographic processes including dispersal (Shah & Rubenstein, 2022, 2023). Groups defend year-round territories centred around glades (Rubenstein, 2007b), open areas embedded within semi-arid bushland that were created by high nitrogen and phosphorus input from traditional livestock corrals (Augustine, 2003). Glades are discrete patches of suitable breeding and foraging habitat that host a unique, nutrient-rich grass community and a high density of insect prey critical for feeding starling chicks (Rubenstein, 2007b) (Figure S1). Ultimately, coarse-grained spatial variation in rainfall interacts with finer-scale variation in glade characteristics (e.g. age, size and duration of the original livestock corral) to determine the quality of superb starling habitat (Rubenstein, 2007b). Immigration decisions in superb starlings are at least partly influenced by this spatial variation in habitat quality. Even though smaller groups in lower quality habitat stand to benefit more from immigration and appear to provide greater joining incentives, dispersers prefer to join larger groups found in higher quality habitat where they stand to gain higher survival and reproductive benefits (Text S1; Shah & Rubenstein, 2023). Yet, how far birds disperse, how variation in habitat quality determines dispersal patterns, and how intergroup dispersal patterns impact intraspecific variation in group structure are not yet known.

Here, we employed a landscape genetic approach to infer patterns of dispersal and gene flow among superb starling groups spanning an environmental gradient in central Kenya. Since our study population is spatially structured (i.e. groups occupy discrete habitat patches with varying inter-group geographic distances), we first examined patterns of isolation-by-distance (IBD) to account for the effect of geographic distance on gene flow and the resulting population genetic structure. IBD predicts that geographically closer individuals will be more genetically similar due to short dispersal distances or high retention of individuals in their natal groups (Wright, 1943). We predicted that males, who are more likely to remain in their natal group (~70%) than females (~50%) (Shah & Rubenstein, 2022), would show a higher degree of IBD than females. However, despite male philopatry, a high proportion of both sexes disperse (~30% of males and ~50% of females) away from their natal

group (Shah & Rubenstein, 2022). Accordingly, we also predicted that dispersal between groups would be more frequent, and dispersal distances longer (i.e. far enough from their natal group so as to not create a pattern of IBD), for both sexes than has been found in other cooperatively breeding bird species of similar size but with simpler group structure (Aguillon et al., 2017; Harrison et al., 2014; Leedale et al., 2018; Nelson-Flower et al., 2012; Painter et al., 2000). High rates of dispersal and subsequent gene flow, between groups would also result in low genetic differentiation (global F_{ST}) among groups (Malécot, 1948; Wright, 1946).

To understand how fine-scale environmental variation influences patterns of dispersal between groups, we next quantified how among- and within-group genetic structure varies with habitat quality. Since we know that larger groups, which are found in higher quality habitat, experience higher immigration of both sexes (Text S1; Shah & Rubenstein, 2023), we predicted that genetic differentiation among groups would reflect a pattern of gene flow from low- to high-quality habitat. Specifically, we predicted that (1) genetic structure among groups (i.e. global F_{ST}) would be stronger across groups in low-quality habitat than those in high-quality habitat, (2) genetic differentiation between groups (i.e. pairwise F_{ST}) would be stronger between two groups found in low-quality habitat than between either two groups found in high-quality habitat or one group found in low- and the other in high-quality habitat, (3) genetic diversity of groups would increase with habitat quality and (4) kin structure within groups would decrease with increasing habitat quality. Ultimately, identifying patterns of dispersal between groups is fundamental to understanding what generates variation in the structure of cooperatively breeding groups and how this variation influences the evolution of complex societies.

2 | MATERIALS AND METHODS

2.1 | Data collection

2.1.1 | Genetic samples

We sampled 6–19 individuals (mean ± SD = 11 ± 4 individuals; total $N = 235$, $N_{males} = 123$, $N_{females} = 112$) from 22 superb starling groups across an environmental gradient spanning approximately 200 km^2 (from 0°16′50.991″ N, 36°50′22.2″ E (southwest corner) to 0°31′2.5752″ N, 36°55′27.876″ E (northeast corner) at the Mpala Research Centre [MRC], Kenya, Figure 1; Table S1). Groups not part of a long-term study were identified via surveys in 2018 of the entire 48,000-acre property. To find groups, we slowly drove along roads as well as checked known glades twice over a period of 28 days (March 25 to April 21, 2018) (Figure 1c). We located birds via both sight and sound, and always confirmed their presence visually. We typically watched the birds for as long as they were within sight, often finding active nests, which confirmed the presence of a territory. We targeted groups for sampling at locations where we reliably found superb starlings again during our second survey (22 out of 77 [28.57%] locations), thus confirming that the area was part of a group's territory. Ultimately, we successfully sampled >5 individuals at 14 of the 22 [63.64%] newly identified groups (Figure 1c, blue), which, coupled with eight groups part of a long-term study (Rubenstein, 2016) (Figure 1c, orange), resulted in a total of 22 groups in our analysis. The two farthest groups were 26.13 km apart, the two closest groups were 0.34 km apart, and the mean (±SD) distance between neighbouring groups was 1.68 km (±0.91 km). Territories of 5 of 22 groups overlapped with human settlements and cattle ranching activities (Figure 1c, triangles), which likely affects demographic processes in this species (Shah & Rubenstein, 2023).

Birds were captured using baited pull-string traps or mist-nets (Rubenstein, 2007a). All birds were fitted with a numbered metal leg ring and a combination of coloured leg bands that was unique to the individual, if part of the long-term study population, or to the group, if not (Rubenstein, 2007a). We collected blood from the brachial vein and stored it in 2% SDS Queens lysis buffer (Seutin et al., 1991). Individuals from groups not part of the long-term study were sampled in 2018 and 2019 during the non-breeding season. Birds from the long-term study population were primarily sampled during the non-breeding season if sampled as adults and during the breeding season if sampled as hatchlings. Although samples from the long-term study population were collected between 2002 and 2018, all individuals included were last seen between 2015 and 2019. Moreover, truncating the dataset to only include individuals seen between 2018 and 2019 did not change our results (Text S2). We aimed to catch at least 10 individuals per group. In smaller groups, birds became increasingly trap shy after about seven individuals were captured, and often not many unbanded group members remained, so we abandoned trapping effort in the interest of time after multiple days passed without successful capture of unbanded individuals. All samples from groups not part of the long-term study population were collected within an average of 16 days (range: 1–42 days; two groups were sampled in both 2018 and 2019 within <5 days each time). Group composition, which is stable within—and changes by an average of 2.40 (±2.40 SD) individuals between—breeding seasons, was determined both by location and association of the adults at roosts and while foraging (S.S.S., pers. obs.).

Birds were categorised as adults ($N = 220$) or subadults ($N = 15$) using eye colour (sensu Guindre-Parker & Rubenstein, 2020). Superb starlings are thought to either disperse or forego dispersal when they are about 1 year old (Shah & Rubenstein, 2022) but can retain 'subadult' eye colour up to 2 years of age (Guindre-Parker & Rubenstein, 2020). Thus, we included subadults in our analyses since they were likely new immigrants into the group or natal individuals that were unlikely to disperse in the future. DNA was extracted from the blood samples using a DNeasy Tissue Kit (QIAGEN). We used standard PCR primers (Griffiths et al., 1998) that have been previously validated in superb starlings to determine sex (Rubenstein, 2007a). All research was approved by the Institutional Animal Care and Use Committee at Columbia University (IACUC protocol # AC-AAAW6451), as well as the Kenyan National Commission for Science, Technology and Innovation, the Kenyan National

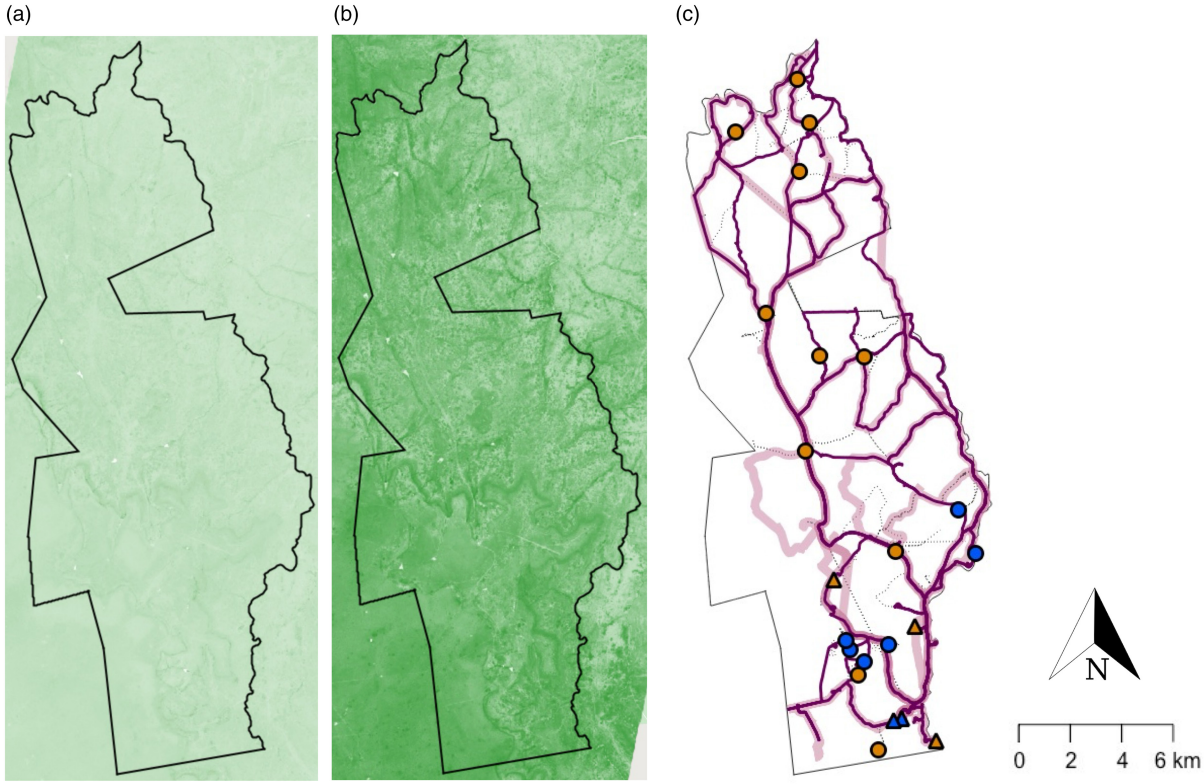

FIGURE 1 Map of the study area, including seasonal patterns of normalised difference vegetation index (NDVI) and sampling sites. Our study area spanned approximately 200 km^2 across an environmental gradient at Mpala Research Centre (solid black line = boundary). The area is (a) driest in February and (b) wettest in May as indicated by NDVI measured at a 5 m resolution (green) in 2018. (c) We sampled 22 social groups across the gradient, including groups monitored (orange) and not monitored (blue) as part of a long-term study. Some groups were found near human settlements (triangles = near humans, circles = not near humans). Groups were identified via two surveys (light purple, thick line = first survey; dark purple, thin line = second survey) along roads (dotted lines underlying survey tracks).

Environmental Management Authority, the Kenya Wildlife Service, the Kenyan Wildlife Research and Training Institute, and the MRC.

2.1.2 | Genetic sequencing

We used double-digest restriction-site associated DNA sequencing (ddRAD Seq) to identify single nucleotide polymorphisms (SNPs) across the genome of all individuals following established protocols (Thrasher et al., 2018). Specifically, 20–500 ng of DNA was digested with restriction enzymes SbfI-HF and MspI (New England Biolabs [NEB]) and ligated to one of 20 unique P1 adapters and a P2 adapter (P2-MspI) using T4 DNA ligase (NEB) in a single reaction at 37°C for 30 min, 20°C for 60 min, and hold at 4°C. Individual reactions were pooled in index groups of 20, with each sample identified with a unique P1 adapter, and purified using 1.5× volume homemade solid-phase reversible immobilisation (SPRI) beads made with Sera-Mag SpeedBead Carboxylate-Modified Magnetic Particles (Cytiva) (Rohland & Reich, 2012). Index groups were then size selected between 400 and 700 bp using the BluePippin (Sage Science) by the Cornell University Biotechnology Resource Center (BRC). This adapter ligated DNA was enriched by 11 cycles of polymerase chain reaction with a universal i5 primer and a unique indexed i7 primer for each index group using Phusion DNA polymerase (NEB) at (1) 98°C for 30 s; (2) 11 cycles of 98°C for 5 s, 60°C for 25 s, and 72°C for 10 s; (3) 72°C for 5 min; and (4) hold at 10°C. Reactions were again cleaned using 0.7× volume of SPRI beads and the index groups pooled in equimolar ratios to create a single sequencing library run on one lane of Ilumnia NextSeq500 (150 bp paired end) at BRC. Sequencing was performed with a ~20% PhiX spike-in to introduce diversity into the library.

We trimmed all reads to 147 bp using FASTX Trimmer (FASTX-Toolkit), filtered the reads using FASTQ Quality Filter, and demultiplexed the reads using the *process_radtags* program from STACKS v2.3d (Catchen et al., 2013). We concatenated the forward and reverse reads for each sample using the protocol described by Rochette and Catchen (2017), and then aligned the reads to the superb starling reference genome (Rubenstein et al., 2021) using Bowtie 2 (Langmead & Salzberg, 2012). SNPs were called using the *refmap.pl* program from STACKS (Catchen et al., 2013). We used the *populations* program from STACKS to export SNPs and population summary statistics. We restricted our analysis to a single SNP from each RAD locus to filter out tightly linked loci and required that a locus be present in at least two-thirds of all groups (14 out of 22) and in at least 70% of all individuals. We required a minimum minor allele frequency of 5% (Linck & Battey, 2019) and maximum observed heterozygosity of 80% (Hohenlohe et al., 2011) for a nucleotide site

at a locus to be processed. Our final dataset comprised 4068 polymorphic loci (8136 SNPs) at a mean (±SD) coverage depth of 21.9*x* (±6.3*x*; range: 1.4*x*–40.3*x*).

To estimate genetic differentiation, we calculated global F_{ST} among groups using the 'wc' function in the R package *hierfstat* (Goudet, 2005), and pairwise F_{ST} between groups as well as the inbreeding coefficient (F_{IS}), nucleotide diversity (pi), and gene diversity (H_e) per group using the 'fstats' flag in the *populations* program in STACKS (Table S1). To quantify within-group kin structure, we calculated the average relatedness coefficients (Queller & Goodnight, 1989; range: ≤0 = unrelated to 1 = self or identical twins) across all individuals sampled from a group (mean ± SD = 11 ± 4 individuals per group) as well as separately for the two sexes (mean ± SD = 6 ± 2 males, 5 ± 3 females per group) using the R package *related* (Pew et al., 2015).

2.1.3 | Habitat quality

To quantify habitat quality across the study area, we computed normalised difference vegetation index (NDVI) in Google Earth Engine using PlanetScope 4-band multispectral, orthorectified imagery at 5 m resolution (Planet Team, 2017). NDVI, a measure of chlorophyll level calculated by comparing the relative amounts of reflected near-infrared and visible red light (Tucker, 1979), is an accurate measure of rainfall (Goheen et al., 2013) and resource availability in glades (Castillo Vardaro et al., 2021). We estimated territory boundaries with a 300 m radius buffer around the trapping and nest (when available) locations for each group (Table S1). For each month in 2018, we calculated the mean NDVI across all pixels within each territory (Table S2). We then calculated the mean and coefficient of variation (CV) of NDVI of these 12 monthly values for each territory to estimate habitat quality (mean NDVI: range = 0.31 to 0.42, mean ± SD = 0.36 ± 0.03; CV of NDVI: range = 0.21 to 0.41, mean ± SD = 0.31 ± 0.04). Varying buffer radius size yielded highly correlated values of mean and CV of NDVI (Table S3). Central Kenya experiences two rainy seasons per year (March–August and October–November), which were reflected in the monthly NDVI values (Figure S2C). Mean NDVI was statistically significantly (hereafter, 'significant' or 'significantly') lower for northern sites ($t = -5.83$, df = 20, $p < 0.001$, 95% CI = −0.43 to −0.20; Figure S2A), consistent with the rainfall gradient (Goheen et al., 2013). CV of NDVI did not show a linear relationship with latitude ($t = 0.18$, df = 20, $p = 0.86$, 95% CI = −0.07 to 0.40; Figure S2B).

2.2 | Data analysis

2.2.1 | IBD, dispersal distance and global genetic structure

To examine patterns of IBD, we calculated the correlation between geographic and genetic distances (Mantel's *r*) for both sexes using the 'mantel' function in the R package *ecodist* (Goslee & Urban, 2007) with 10,000 permutations to assess significance ($N_{males} = 123$; $N_{females} = 112$). To examine IBD on a finer geographical scale and estimate dispersal distances, we used mantel correlograms generated using the 'mantel.correlog' function from the R package *vegan* (Oksanen et al., 2022) to compare pairwise geographic and genetic distances within 14 distinct distance classes each 1.87 km wide (determined by Sturges' rule, Sturges, 1926 to ensure even sampling). *p*-Values were corrected for multiple testing using Holm's method (Holm, 1979). We also examined whether mean pairwise relatedness (Queller & Goodnight, 1989) for all individuals within the same distance classes was higher than expected by chance (sensu Leedale et al., 2018). We randomly assigned pairwise relatedness values to individual pairs (1000 iterations) and calculated 95% confidence intervals. If the mean relatedness was higher than the upper 95% confidence limit, we deemed it as significantly higher than expected by chance. Finally, we used global F_{ST} (see above) to estimate genetic structure across the study population and assessed its significance using the Goudet's *G*-statistic Monte Carlo test with 1000 permutations implemented with the 'gstat.randtest' function in the R package *adegenet* (Jombart, 2008). Since this function does not work with missing data, we used a trimmed dataset of 1653 polymorphic loci which excluded loci with more than 2% missing data. Trimming the dataset did not affect the global F_{ST} value.

2.2.2 | Fine-scale environmental variation and gene flow

To identify dispersal patterns driven by individual-level benefits of group living, we examined variation in between- and within-group genetic structure in relation to habitat quality. First, we calculated global F_{ST} across groups broadly categorised as occupying low- or high- quality habitat based on the average mean NDVI across all groups (0.36; $N_{low} = 12$, $N_{high} = 10$). For all other analyses we used continuous values of mean NDVI. Next, we ran a partial Mantel test using the 'mantel' function in the R package *ecodist* to estimate the correlation between pairwise F_{ST} between two groups and their habitat quality while accounting for their geographic distance. For a pairwise value of habitat quality, we used the mean of the mean NDVI of the two groups such that pairwise NDVI was higher when both groups occupied higher quality habitat than a pair in which one group occupied a lower and the other a higher quality habitat. Pairwise NDVI was lowest when both groups occupied lower quality habitat. Third, we fit separate linear models with two measures of genetic diversity—nucleotide diversity (pi) and gene diversity (H_e)—as the dependent variables and mean and CV of NDVI, and proximity to permanent human settlement (yes/no) as the fixed effects ($N = 22$). Finally, we fit three linear models with average relatedness among all within-group individuals, males only and females only as the dependent variables, and mean and CV of NDVI and proximity to permanent human settlement (yes/no) as the fixed

effects ($N = 22$). An interaction term for mean and CV of NDVI was also included, but later removed if not statistically significant. Since the mean and CV of NDVI were not correlated (Pearson's $r = 0.04$), we were able to independently examine the effects of the average resource availability and the degree of variation in resource availability across a year. Linear models were fit using the R package *lme4* (Bates et al., 2015) and model fit checked using the 'check_model' function in the R package *performance* (Lüdecke et al., 2021). Continuous fixed effects were standardised using *z*-scores (Schielzeth, 2010). All statistical analysis was conducted using R v3.6.3 (R Core Team, 2019).

3 | RESULTS

3.1 | IBD, dispersal distance and global genetic structure

As we predicted, superb starling males showed significant IBD (Mantel's $r = 0.16$, $p = 0.001$, 95% CI = 0.13 to 0.18) but females did not (Mantel's $r = 0.05$, $p = 0.17$, 95% CI = 0.02 to 0.13). However, on a finer geographical scale, both sexes only showed a significant positive autocorrelation between genetic and geographical distance in the first distance class (0–1.87 km), which was driven entirely by intragroup kin structure (Figure 2a; Table S4). Similarly, mean pairwise relatedness did not show a pattern of gradual decrease with increasing distance as expected in a population with short dispersal distances (Figure 2b; Table S4). Instead of significantly higher relatedness than expected by chance at shorter distances, superb starlings belonging to different groups in our study population showed higher than expected relatedness only at distances greater than 9.33 km apart, though mean relatedness in females was marginally higher than expected by chance in neighbouring groups (Figure 2b; Table S4). Altogether, these results suggest that neither sex experiences limited dispersal and that both sexes can disperse up to at least 9.33 km away from their natal group. Our findings are consistent with anecdotal evidence of dispersed colour-banded individuals from our long-term study population near MRC being sighted as far as in a village 19 km away (Rubenstein and Watetu, unpublished data). Further, these large dispersal distances explain our finding of weak, non-significant genetic structure in our study population (global $F_{ST} = 0.04$, $p = 0.22$). All groups also showed levels of heterozygosity higher than or equal to that expected under Hardy–Weinberg equilibrium, and none of the groups showed significant levels of inbreeding ($F_{IS} \leq 0$ for all groups, Table S1).

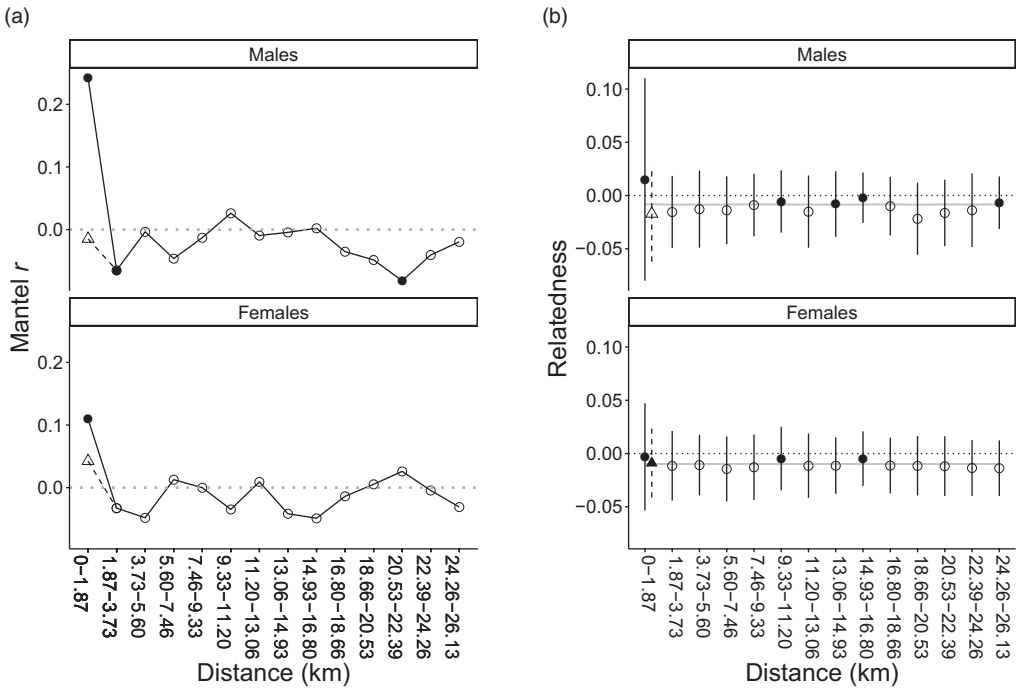

FIGURE 2 Relationship between genetic and geographical distance for both sexes. Symbols (circles = including, triangles = excluding intragroup pairs) indicate (a) Mantel's *r* values, and (b) mean (±SD) relatedness. Neither males ($N = 123$) nor females ($N = 112$) showed strong evidence of isolation by distance. Neither sex exhibited positive autocorrelation (filled symbol = significant, empty symbol = non-significant autocorrelation) in genetic and geographical distance beyond the first distance class (0–1.87 km). Similarly, neither sex showed a pattern of significantly higher mean relatedness than expected by chance (grey lines) at short distances, with a gradual decrease at longer distances. Higher relatedness than expected by chance at longer distances instead suggest that both sexes disperse at least as far as 9.33 km away. Positive autocorrelation and significantly higher relatedness at <1.87 km are driven by within-group kin structure, not short-distance dispersal, as indicated by the non-significance of Mantel's *r* values and mean pairwise relatedness values after intragroup pairs were excluded (triangles, dashed lines), though pairwise relatedness remained marginally higher than expected by chance in females (Table S4).

3.2 | Fine-scale environmental variation and gene flow

Consistent with our prediction, multiple lines of evidence suggest directional dispersal of superb starlings from groups in lower to groups in higher quality habitat. First, genetic structure across groups was slightly higher for those occupying lower quality habitat ($F_{ST}=0.06$) than higher quality habitat ($F_{ST}=0.03$). Second, we found significant negative autocorrelation between pairwise F_{ST} and pairwise habitat quality while accounting for geographical distance between groups (Mantel's $r=-0.53$, $p=0.001$, 95% CI $=-0.65$ to -0.46). Pairs in which both groups occupied lower quality habitat were more genetically differentiated than pairs in which one group occupied higher and the other lower quality habitat and pairs in which both groups occupied higher quality habitat. Third, both measures of genetic diversity—nucleotide diversity (pi) and gene diversity (H_e)—of groups increased with an increase in mean NDVI (pi: $t=3.37$, $p=0.003$; H_e: $t=3.92$, $p<0.001$). Nucleotide diversity also showed a negative relationship with CV of NDVI ($t=-2.13$, $p=0.04$), while gene diversity showed a similar, marginally significant trend ($t=-1.91$, $p=0.07$), together indicating that genetic diversity of groups is also higher when habitat quality is more consistent across the year (Table S5; Figure S4). However, this result should be interpreted with caution, as the relationship with CV of NDVI was not significant when using truncated datasets including only individuals last seen in 2018–2019 (Table S9) or excluding two groups with the most extreme CV values (Table S11). Fourth, we found a significant effect of the interaction between the mean and CV of NDVI on within-group kin structure when including all individuals ($t=-2.36$, $p=0.03$) or only males ($t=-2.63$, $p=0.02$), but not when including only females (Table S6). Genetic relatedness decreased with an increase in mean NDVI, and the slope of this relationship was steeper among groups with higher variability in NDVI values across the year (i.e. higher CV) than among groups with less variable intra-annual NDVI (Figure 3). Excluding two groups with the two most extreme values of CV of NDVI did not qualitatively change the results (Table S12). Thus, groups in the highest quality habitat (high mean and low CV of NDVI) had the lowest average relatedness, and this pattern was driven by relatedness among males in the group, not females (Table S6; Figure 3). Groups whose territories overlapped with permanent human settlement also had significantly higher group and male-only relatedness (Table S6).

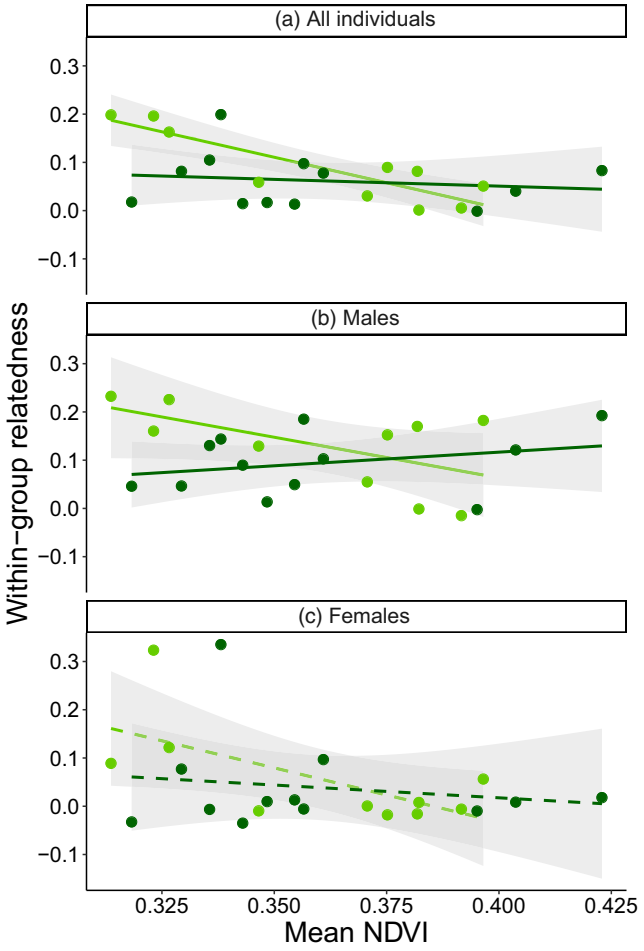

FIGURE 3 Within-group kin structure of superb starlings varies with habitat quality. (a) Groups ($N=22$, circles) experiencing higher mean normalised difference vegetation index (NDVI) showed lower within-group kin structure, and this relationship was stronger among groups with high intra-annual variation in habitat quality ($t=-2.36$, $p=0.03$) (light green = higher than, dark green = lower than mean coefficient of variation (CV); while CV of NDVI is shown as a categorical variable here, it was included in the model as a continuous variable). (b) Results were consistent for kin structure of only males ($t=-2.63$, $p=0.02$), however (c) female kin structure did not vary significantly with habitat quality (mean NDVI: $t=-1.62$, $p=0.12$; CV of NDVI: $t=1.05$, $p=0.31$). Model estimates (solid line = significant, dashed line = non-significant effect) are bounded by 95% confidence intervals (shaded areas).

4 | DISCUSSION

In cooperatively breeding species, the complexity of group structure is largely driven by variation in dispersal patterns, with more complex groups comprising a high proportion of immigrants of both sexes that leads to larger group sizes, low and variable kinship, and multiple breeding pairs (Brown, 1978; Lukas & Clutton-Brock, 2020; Pereira et al., 2023; Riehl, 2013). Here, we present genetic evidence of directional dispersal and gene flow from groups in lower to higher quality habitat, generating intraspecific variation in group structure within the same population of an avian cooperative breeder. Our results provide insight into how ecological and demographic processes can impact the mechanisms (direct vs. indirect fitness benefits) underlying the formation of cooperative societies (García-Ruiz et al., 2022; Shah & Rubenstein, 2023).

Superb starlings form large, mixed-kin groups that comprise a high proportion of immigrants of both sexes (Shah & Rubenstein, 2022), indicating high rates of dispersal connecting these discrete groups. Indeed, we found that even though males, the more philopatric and less dispersive sex, show a degree of IBD, this is driven entirely by within-group relatedness from individuals delaying or foregoing

dispersal from their natal group, not short-distance dispersal. Both sexes show genetic signatures of dispersal up to at least 9 km away from their natal territory. Since the average distance to the closest territory in our study population is just 1.68 km, instead of dispersing to neighbouring groups superb starlings seem to travel farther in search of groups where they can maximise their survival and reproductive fitness (Shah & Rubenstein, 2022).

Weak genetic structure across all groups in our study population and negative inbreeding coefficient values indicate higher dispersal and gene flow between superb starling groups than has been found in other avian cooperative breeders of similar size (Aguillon et al., 2017; Harrison et al., 2014; Leedale et al., 2018; Painter et al., 2000). This difference may be explained by two factors. First, previous studies have focused primarily on species forming small, kin-based social groups with only one breeding pair (i.e. singular breeders) (Double et al., 2005; Fitzpatrick & Bowman, 2016; Leedale et al., 2018; Nelson-Flower et al., 2012; Temple et al., 2006). This simpler group structure, where most or all non-breeders are offspring of the breeding pair from previous broods, limits dispersal and generates stronger genetic structure (Wright, 1946). Moreover, since dispersers typically fill a breeding vacancy, short-distance dispersal may be beneficial due to continued environmental familiarity (Fitzpatrick & Bowman, 2016; Nelson-Flower et al., 2012) or the option to revert to helping kin (i.e. redirected helping) (Emlen & Wrege, 1992; Leedale et al., 2018). However, since superb starlings typically disperse as non-breeders (Shah & Rubenstein, 2023), access to resources for longer-term fitness may instead be key (Shah & Rubenstein, 2022; Shen et al., 2017), driving long-distance dispersal. Second, since species forming small, kin-based cooperative groups typically live in contiguous habitat, prospecting and dispersal through multiple intervening territories may prove costly due to aggression from conspecifics (Daniels & Walters, 2000; Kingma et al., 2016). In contrast, superb starling territories are separated by a kilometre or more of habitat matrix that is unsuitable for breeding but may be easily traversed for dispersal into more distant groups (Rubenstein, 2016). Similarly, while cooperative mammals societies also predominantly exhibit short dispersal distances in at least one sex (e.g. Guschanski et al., 2008; Holekamp et al., 2012; Nichols et al., 2012; Spong et al., 2002; Tensen et al., 2016), recent studies have found longer dispersal distances in some species (e.g. Firman et al., 2019), though the underlying life history traits remain unexamined.

Although dispersal does not appear to be limited by geographic distance within our study population, fine-scale variation in genetic structure in relation to habitat quality suggests that it is governed by local environmental conditions. Directional dispersal from lower to higher quality habitat is indicated by greater genetic differentiation between groups in lower quality habitat than between groups in which one or both groups occupied higher quality habitat, and lower kin structure within groups in higher quality habitat. These results are consistent with previous work using 15 years of long-term data showing that larger groups, found in higher quality habitat, experience higher immigration (Text S1; Shah & Rubenstein, 2023). Altogether, these findings suggest that group structure becomes more complex as local environmental quality increases because of higher immigration rates. Within a population where harsh and unpredictable environmental conditions overall impact resource availability and nestling survival (Rubenstein, 2007a; Shah & Rubenstein, 2022), this dispersal pattern is likely driven by individual-level benefits of living in larger groups, as has been suggested previously (Shah & Rubenstein, 2022). While theoretical work has shown that the relative importance of direct and indirect benefits in the evolution of cooperative breeding societies can depend on the ecological environment (García-Ruiz et al., 2022), our results suggest a possible mechanism by highlighting how dispersal patterns governed by individual-level fitness outcomes can create the link between the ecological environment and type of benefits by generating intraspecific variation in complexity of group structure. Interestingly, spotted hyenas (*Crocuta crocuta*)—another plural cooperative breeder with a more extensive range in sub-Saharan Africa—show a similar pattern of more complex group structure with larger group sizes in regions with higher prey availability (Holekamp et al., 2012), and the striped mouse (*Rhabdomys pumilio*)—a rodent found in southern Africa—exhibits social plasticity, forming groups where resource availability is higher (Schradin & Pillay, 2005). Future work should examine whether environment variability across East Africa (Guindre-Parker & Rubenstein, 2021) generates similar intraspecific variation in group structure of superb starlings across their range and whether any such variation is consistent with local adaptation (Schradin & Pillay, 2005; Stacey & Bock, 1978).

When partitioned by sex, the kin structure of males—but not females—showed a similar relationship with mean and variance in resource availability. In superb starlings, males are the less dispersive sex and are able to attain breeding positions within their natal groups if they forego dispersal; females never breed in their natal groups (Rubenstein, 2016). A male's likelihood of dispersing is tied to interannual variation in rainfall, with males more likely to disperse if born following a period of higher rainfall during the dry season preceding their breeding season of birth (Shah & Rubenstein, 2022). Across the environmental gradient in our study area, rainfall is higher in the south (Goheen et al., 2013). Thus, our results, coupled with insight from previous studies (Shah & Rubenstein, 2022, 2023), suggest that northern groups, occupying lower quality habitat, may experience both higher retention of natal males as well as lower immigration of non-natal males, generating the significant male kin structure that we observed. In contrast, preferential immigration by males into more southern groups on higher quality habitat likely dilutes their kin structure. Since females never breed in their natal group, even if their dispersal followed a similar pattern, groups in low quality habitat would not exhibit a build-up of female kin structure. Conversely, female dispersal direction may be governed by different, or additional, factors than habitat quality. Further, our results suggest that superb starling males born in groups whose territories overlap human settlements are either more likely to survive or forego dispersal at a higher rate. Understanding how food subsidies, which disrupt seasonal patterns of resource availability, impact

demographic rates of superb starling groups and consequently their group structure, merits further study since superb starlings associate with human settlements throughout their range. Overall, groups within our population fall along a gradient from more kin-based and likely smaller groups with fewer breeding pairs in the north to groups with lower kin structure and presumably larger group sizes with more breeding pairs in the south.

In summary, we have shown that superb starlings of both sexes, which are known to disperse frequently (Shah & Rubenstein, 2022), move across long distances, and that, at least for males, dispersal is directional with respect to fine-scale environmental conditions. Directional dispersal from lower to higher quality habitat likely shapes intraspecific variation in the complexity of group structure within our study population. Although previous studies of cooperative breeders have examined interspecific variation in group structure (Lin et al., 2019) and even intraspecific variation in the structure of groups found in different, geographically isolated populations of the same species (Komdeur, 1992; Stacey & Bock, 1978), to our knowledge, ours is the first study in a cooperative breeder to examine finer-scale variation of structure among groups within the same population occurring along an ecological gradient of habitat quality. Our results suggest that determining how fine-scale environmental conditions and demographic processes like dispersal influence the structure of groups within the same species—and even the same population—can shed new light on how and why cooperative societies arise and are maintained, particularly in the relative roles that direct benefits versus kinship play in the evolution and maintenance of complex animal societies (García-Ruiz et al., 2022; Shah & Rubenstein, 2023).

AUTHOR CONTRIBUTIONS

Shailee S. Shah and Dustin R. Rubenstein conceived the ideas and designed methodology; Shailee S. Shah and Dustin R. Rubenstein collected the data; Shailee S. Shah and Dustin R. Rubenstein analysed the data; Shailee S. Shah and Dustin R. Rubenstein led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank W. N. Watetu and P. Kiplangat for guidance and assistance in the field, as well as past field assistants and students who collected the long-term data; J. Solomon, B. Butcher, I. Lovette, and the Fuller Evolutionary Biology Program at the Cornell Lab of Ornithology for guidance and resources towards genetic sequencing and bioinformatics; E. Carlen, M. Combs, N. Fusco, J. Munshi-South, and M. Uriarte for guidance on data analysis; and F. Romero, S. Siller, and anonymous reviewers for feedback that improved this manuscript. All research was approved by the Institutional Animal Care and Use Committee at Columbia University (IACUC protocol #AC-AAAW6451), and the Kenyan National Commission for Science, Technology and Innovation, the Kenyan National Environmental Management Authority, the Kenya Wildlife Service, the Kenya Wildlife Research and Training Institute, and the Mpala Research Centre. This research was funded by Sigma Xi, the American Ornithological Society, the American Museum of Natural History, Columbia University's Department of Ecology, Evolution, and Environmental Biology, and the US National Science Foundation (IOS-1257530, IOS-1656098).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.hqbzkh1kr (Shah & Rubenstein, 2024).

STATEMENT ON INCLUSION

We hired local field assistants and managers to help with data and sample collection. Field assistants were trained in avian field ecology methods. A version of this manuscript was shared with the relevant institutions and government organisations, samples collected for this study are archived at National Museums of Kenya, and all data will be shared with the broader public via appropriate databases as described above.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Satellite imagery showing a glade at Mpala Research Center.

Figure S2. Territory quality across the environmental gradient.

Figure S3. Correlation between two measures of habitat quality for superb starlings.

Figure S4. Genetic diversity of superb starling groups varies habitat quality.

Figure S5. Within-group relatedness variation with territory quality.

Table S1. Sample sizes, location, and metrics of genetic structure of the social groups in our study population.

Table S2. Satellite imagery used to calculate territory quality.

Table S3. Correlation between (A) mean and (B) coefficient of variation of normalised difference vegetation index calculated within circular buffers of varying radii around the territory centers of superb starling social groups ($N = 22$).

Table S4. Results of Mantel correlograms and mean pairwise relatedness examining the relationship between genetic and geographic distances for both sexes.

Table S5. Results of linear models examining variation in genetic diversity in relation to habitat quality.

Table S6. Results of linear models examining variation in within-group kin structure of all individuals and both sexes separately with habitat quality.

Table S7. Sample sizes, location, and metrics of genetic structure of the social groups in our study population, with a truncated dataset from the long-term study population including only individuals last seen between 2018 and 2019.

Table S8. Results of Mantel correlograms and mean pairwise relatedness examining the relationship between genetic and geographic distances for both sexes with a truncated dataset from the long-term study population including only individuals last seen between 2018 and 2019.

Table S9. Results of linear models examining variation in genetic diversity in relation to habitat quality, with data from the long-term study population truncated to include only individuals last seen between 2018 and 2019 ($N = 21$ groups).

Table S10. Results of linear models examining variation in within-group kin structure of all individuals and both sexes separately with habitat quality, with data from the long-term study population truncated to include only individuals last seen between 2018 and 2019 ($N = 21$ groups).

Table S11. Results of linear models examining variation in genetic diversity in relation to habitat quality, with data from the long-term study population truncated to exclude two groups with values of coefficient of variation of normalised difference vegetation index at the extremes of the range ($N = 20$ groups).

Table S12. Results of linear models examining variation in within-group kin structure of all individuals and both sexes separately with habitat quality, with data from the long-term study population truncated to exclude two groups with values of coefficient of variation of normalised difference vegetation index at the extremes of the range ($N = 20$ groups).

Text S1. Group size and habitat quality.

Text S2. Isolation-by-distance, dispersal distance, global genetic structure, and fine scale environmental variation and gene flow with truncated dataset from the long-term study population.

How to cite this article: Shah, S. S., & Rubenstein, D. R. (2024). Intraspecific variation in group structure arises due to environmentally-mediated directional dispersal in a cooperative breeder. *Journal of Animal Ecology*, *00*, 1–12. https://doi.org/10.1111/1365-2656.14162