Group augmentation underlies the evolution of complex sociality in the face of environmental instability

Shailee S. Shah[a,1,2] and Dustin R. Rubenstein[a,b]

Although kin selection is assumed to underlie the evolution of sociality, many vertebrates—including nearly half of all cooperatively breeding birds—form groups that also include unrelated individuals. Theory predicts that despite reducing kin structure, immigration of unrelated individuals into groups can provide direct, group augmentation benefits, particularly when offspring recruitment is insufficient for group persistence. Using population dynamic modeling and analysis of long-term data, we provide clear empirical evidence of group augmentation benefits favoring the evolution and maintenance of complex societies with low kin structure and multiple reproductives. We show that in the superb starling (*Lamprotornis superbus*)—a plural cooperative breeder that forms large groups with multiple breeding pairs, and related and unrelated nonbreeders of both sexes—offspring recruitment alone cannot prevent group extinction, especially in smaller groups. Further, smaller groups, which stand to benefit more from immigration, exhibit lower reproductive skew for immigrants, suggesting that reproductive opportunities as joining incentives lead to plural breeding. Yet, despite a greater likelihood of becoming a breeder in smaller groups, immigrants are more likely to join larger groups where they experience increased survivorship and greater reproductive success as breeders. Moreover, immigrants form additional breeding pairs, increasing future offspring recruitment into the group and guarding against complete reproductive failure in the face of environmental instability and high nest predation. Thus, plural breeding likely evolves because the benefits of group augmentation by immigrants generate a positive feedback loop that maintains societies with low and mixed kinship, large group sizes, and multiple reproductives.

social evolution | cooperative breeding | plural breeding | group augmentation | direct benefits

Recent genetic advances have revealed previously hidden complexities of group structure in cooperatively breeding societies (1, 2), in which more than two individuals care for the young (3). For example, although most avian cooperative breeders were historically thought to form social groups primarily with closely related individuals (4), more recent work suggests that nearly half of all cooperatively breeding birds actually form groups comprising a high proportion of unrelated individuals (1). In contrast to societies with simpler group structure—those that typically comprise small, nuclear families with one breeding pair and one or more helpers that are offspring from previous broods (4)—these mixed-kin societies form via immigration of unrelated individuals of both sexes in addition to the retention of offspring born into the group (1, 5). Moreover, immigrants often acquire breeding opportunities alongside natal individuals, resulting in plural breeding societies characterized by not only multiple breeding pairs, but also large groups and low but mixed kinship (6, 7). Such plural breeding societies are thought to be evolutionarily distinct from singular breeding societies with one breeding pair and high kinship, representing alternative evolutionary outcomes (6, 8, 9) in response to distinct selection pressures (10) and genetic architectures (11, 12). Because of the increased reproductive opportunities for subordinates and the mixed kinship within plural breeding groups, reproductive conflict and social instability are predicted to be higher than those in singular breeding groups (13), as has been demonstrated in a variety of taxa (14–16). Nonetheless, large cooperative societies with multiple reproductives and low but mixed kinship are found in taxa ranging from insects (17, 18) to fishes (19), birds (20), mammals (21), and even crustaceans (22). With a reduced potential for indirect benefits (i.e., fitness gained by positively influencing the reproduction of relatives) due to low kin structure within these groups, the formation of such demographically and socially complex societies is thought to be primarily governed by direct benefits (23, 24).

Complex group structure may arise as a by-product of demographic processes that influence the long-term persistence of animal societies, particularly in the face of environmental challenges (25–27). Obligate cooperative breeders, for example, commonly exhibit high rates of group extinction due to inverse density dependence (i.e., Allee effect)

Significance

Complex cooperative animal societies—those with large group sizes, low kin structure, and multiple breeding pairs—occur commonly in harsh and unpredictable environments. Yet, how or why such social complexity arises remains unclear. Using population dynamics models and analysis of long-term data from the superb starling, an avian cooperative breeder inhabiting a fluctuating environment on the African savanna, we provide clear empirical evidence that immigration and breeding by unrelated individuals in a social group confer direct, group augmentation benefits, leading to the rise of complex societies. Immigrants are vital to group persistence because they boost current group size and future reproductive success of the group. Ultimately, the mutual benefits of living in larger groups can maintain complex cooperative animal societies.

[1]Present address: Department of Biology, University of Rochester, Rochester, NY 14627.

[2]To whom correspondence may be addressed. Email: shailee.shah@columbia.edu.

at small group sizes (28). Below a threshold group size, there are too few individuals within a social group to successfully recruit offspring, and those group members are also less likely to survive (29, 30), resulting in the group spiraling toward extinction (31–33). The risk of group extinction is especially high in species where group members cooperate to increase both reproductive success and survival (i.e., group augmentation) (31), as well as in harsh and unpredictable environments that negatively impact population growth (34). By affecting demographic processes that alter the group's social structure (e.g., offspring recruitment and emigration), even one low quality year can lead to population crashes in obligate cooperatively breeding species (32, 34). Admitting immigrants into a social group can therefore generate direct, group augmentation benefits at the group level by buffering against environmental stochasticity and decreasing risk of group extinction, particularly when recruitment of offspring is lower than necessary to achieve and maintain optimal group sizes (35, 36).

Despite the potential group-level benefits of increasing group size, insider–outsider conflict theory predicts that existing group members (insiders) may exhibit resistance toward potential immigrants (outsiders) if they stand to incur personal fitness costs (e.g., reduced access to resources or breeding opportunities) from admitting immigrants (37). In cooperatively breeding mongoose species, for example, dominant females are more likely to evict subordinate females in larger social groups to reduce reproductive conflict (38, 39), despite the group-level benefits of living in larger groups (40–42). When immigration can generate substantial group- and individual-level group augmentation benefits, however, insider–outsider conflict may be low (36). In addition to protection from group extinction due to reproductive failure, group augmentation by immigration may also improve individual survival likelihoods of group members (43). Groups facing high predation pressure and/or low offspring recruitment may thus be more accepting of unrelated immigrants (44). Further, if the demand for immigrants exceeds their availability, groups may even compete for outsiders in a biological market (45). In such cases, dominant breeders may concede breeding opportunities to immigrants as joining incentives (46, 47) or exert incomplete control over reproduction (48–50), effectively giving rise to plural breeding. Plural breeding may then be maintained by a positive feedback loop of group augmentation benefits if having additional breeding pairs further increases group productivity (13). Biological market theory also predicts that when immigrants are rare relative to the demand for additional group members, they can afford to be choosy and preferentially join groups that maximize their own individual fitness (45). Consequently, while all groups may permit or even favor immigration, social and ecological factors (e.g., group size, kinship, and resource availability) that affect individual fitness outcomes may govern immigration rates and determine group social structure and persistence over time.

While theoretical work suggests that plural breeding societies with large groups, multiple breeding pairs, and low but mixed kinship can form and remain stable due to group augmentation benefits despite the potential for high insider–outsider conflict (23, 24, 51), empirical evidence is limited (35). Understanding how and why such plural breeding societies form and persist requires studying a species that shows variation not only in group structure, but also in the types of fitness benefits achieved by grouping. Superb starlings (*Lamprotornis superbus*) live in large but variable social groups (mean group size ranged from 13 to 41 individuals across nine groups during our study period) that contain multiple breeding pairs (up to eight breeding pairs per group) and a combination of related and unrelated nonbreeding individuals that may act as alloparents (mean ± SD coefficient of relatedness = 0.07 ± 0.07 for

nine groups during our study period) (52). In superb starlings, group size, kin structure, and the number of breeding pairs per group covary such that larger groups have lower kin structure and more breeding pairs (*SI Appendix*, Fig. S1). Individuals of both sexes may either forego dispersal (residents) or immigrate from other social groups (immigrants) (53). Residents and immigrants are thus defined here based on the group that they were born into. Since immigrants are unrelated to resident individuals of the group they join, conflict between residents and immigrants may persist throughout their lifetimes. Although resident female superb starlings never breed in their natal groups, both resident and immigrant males can acquire breeding status within a social group during the same breeding season (52). Within our study population, all breeding females and more than half of all breeding males are immigrants (53). Individuals of both sexes and immigration statuses may, however, remain as nonbreeders throughout their lifetimes, never gaining any direct fitness (52). Importantly, immigrant males commonly acquire breeding opportunities within their new social groups despite the presence of reproductively capable resident males and unrelated potential mates (52). In addition to the potential inclusive fitness benefits of helping relatives raise their offspring, superb starlings also receive group- and individual-level group augmentation benefits. That is, living in a larger social group increases an individual's survival likelihood (43) and decreases reproductive variance within the group (54), likely due to larger predator mobbing and alloparenting groups (43, 54), and higher resource availability in territories occupied by larger groups (55). Superb starlings inhabit the East African savanna, where unpredictable variation in rainfall from year-to-year creates a temporally variable environment (25) that affects demographic processes such as dispersal (53), offspring recruitment (54), and the adoption of different breeding roles (56, 57). In general, conditions for the starlings are typically harsh, as low rainfall is the norm in most years and food resources are scarce throughout much of the year (52). Further, superb starlings face high rates of nest failure (>70% of all nests and >90% of all offspring), primarily due to predation, a largely stochastic process (52) that typically results in complete reproductive failure in a given breeding season (54) (*SI Appendix*, Fig. S2).

Here, we combine population dynamic modeling with empirical analysis of longitudinal, individual-level data from a long-term study of superb starlings to examine the formation and maintenance of plural breeding, mixed-kin societies. Specifically, we explore the patterns and fitness consequences of immigration at both the individual and group level to understand how immigrants contribute to group augmentation both directly and indirectly, thus influencing the long-term persistence of societies in the face of environmental stochasticity. First, we simulate group dynamics using models of population growth parameterized with data from our long-term study to investigate how both immigration and offspring recruitment contribute to group persistence over time via group augmentation directly (i.e., the addition of adult individuals to the group). We further investigate whether immigration can compensate for low offspring recruitment to counter erosion of group size. Because superb starlings have low offspring recruitment (52), we predict that immigration is necessary to prevent groups from going extinct, and that smaller groups will be more likely to go extinct unless they have higher rates of immigration than larger groups. Although we used our long-term data from starlings as a starting point to parametrize the model, we also vary the demographic rates to make the model generalizable to other social species.

Next, we use long-term empirical data to investigate how immigration results in plural breeding via the sharing of reproductive opportunities. Further, we examine whether immigrants also provide indirect group augmentation benefits by assuming breeding

positions and increasing future offspring recruitment into the group. We predict that if immigrants provide direct group augmentation benefits, conflict over group membership between existing group members and potential immigrants may be low such that immigrants can acquire breeding opportunities in groups of all sizes, resulting in plural breeding. However, reproductive opportunities should be more likely shared equitably in smaller groups, which are more susceptible to extinction and thus more likely to benefit from immigration. More equitable sharing of reproductive opportunities (i.e., lower reproductive skew) should lead to more immigration into smaller groups, as well as higher fitness benefits to birds joining such groups. Alternatively, due to lower survival (43) and more variable reproductive success (54), immigrants may instead have lower fitness in smaller groups. Finally, we examine the indirect group augmentation benefits of immigration, predicting that groups with at least one immigrant male breeding will contain more breeding pairs, despite the presence of reproductively capable but nonbreeding resident males. More breeding pairs will, in turn, increase group reproductive output further. Ultimately, we investigate whether, in a temporally variable and unpredictable environment that generates high annual variation in fecundity, direct and indirect group augmentation benefits associated with immigration can give rise to and help maintain plural breeding by favoring both individual- and group-level fitness.

Results

Models of Group Population Dynamics. We began by building a discrete time population growth model with group size at time t + 1 (N_{t+1}) as a function of five demographic processes—immigration (of males and females), disappearance (of males and females), and offspring recruitment—parameterized with longitudinal data from nine superb starling social groups collected over 15 y (Eq. **1**, *SI Appendix*, Table S1 and Fig. S3). We grouped dispersal and mortality under one demographic process, "disappearance," since our model did not incorporate an age-structured population, and both dispersal and mortality lead to the same net result: loss of group members. Although 30 to 50% of offspring emigrate to nonnatal groups (53), this loss of group members is captured within "disappearance." Offspring recruitment here is defined as the recruitment of fledglings into the social group.

After 100 iterations of the model, only 18% of the simulated group trajectories resulted in group extinction (i.e., group size = 0) (Fig. 1*B*), a result comparable to our long-term data in which two of nine (22%) social groups went locally extinct over the 15-y period. However, when immigration was set to zero, group extinction increased more than threefold (61% of group trajectories went to extinction), indicating that immigration contributes to group persistence over time by bolstering group size (Fig. 1*A*). Without immigration (male: mean ± SD = 0.29 ± 0.71; female: mean ± SD = 0.58 ± 1.03 immigrants per group per year), offspring production and recruitment alone (mean ± SD = 1.35 ± 2.33 offspring from 11.17 ± 10.59 eggs per group per year; *SI Appendix*, Fig. S2) is insufficient for persistence of groups, which quickly spiral toward extinction. Note again that while the rate of offspring recruitment is higher than immigration, 30 to 50% of offspring emigrate out of their natal groups at around 1 y of age (53). Thus, on average, group size only increases by 0.68 to 0.95 individuals per year due to offspring recruitment, which is comparable to total immigration (i.e., 0.29 + 0.58 = 0.87 immigrants per year). Setting offspring recruitment to zero generated a similar result (51% of group trajectories went to extinction, *SI Appendix*, Fig. S4*A*). Further, the percentage of group trajectories resulting in extinction fell below 10% only when both offspring recruitment and immigration rates were inflated by 1.5× or 2× (*SI Appendix*, Fig. S5 and Table S2). Finally, when the rate of disappearance for both sexes was reduced by half, none of the group trajectories resulted in group extinction (*SI Appendix*, Fig. S4*B*). Together, these results suggest that both offspring recruitment and immigration are necessary for the persistence of superb starling groups in the face of mortality and dispersal that lead to, on average, the loss of individuals from the group that is almost equivalent to the number of individuals added by offspring recruitment and immigration combined (males: mean ± SD = 0.87 ± 1.23; females: mean ± SD = 1.47 ± 1.18 lost from the group). Moreover, we found that, similar to other obligate cooperative breeders (31), superb starling social groups exhibit inverse density dependence at low group sizes, such that per capita growth rate [i.e., the rate at which group size changes per individual or ($N_{t+1} - N_t)/N_t$] declines at low group sizes (*SI Appendix*, Table S3 and Fig. S6). Thus, immigration is necessary to keep groups above a minimum group size threshold, at which point extinction is likely to occur.
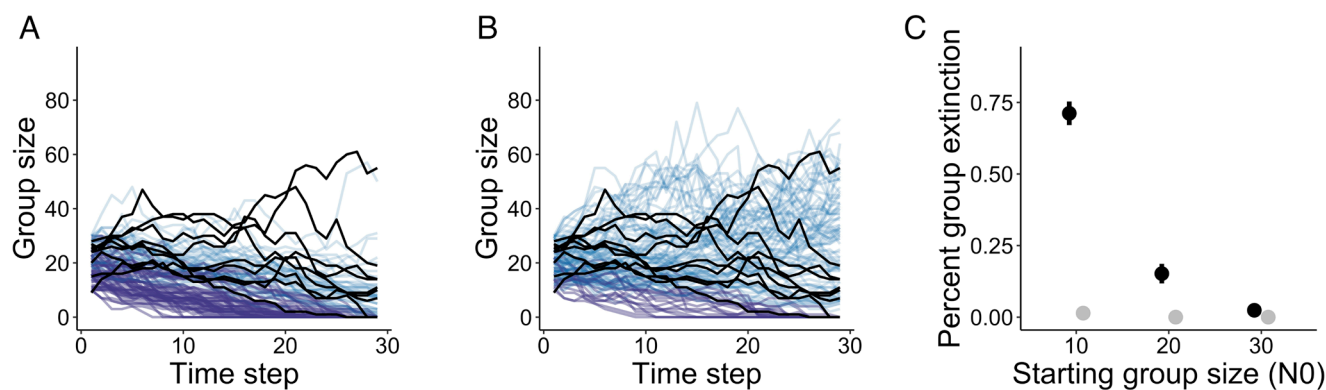

Fig. 1. Simulations of discrete time population growth models show the effects of immigration and starting group size on the extinction risk of superb starling social groups. (*A*) The results of 100 simulations of a discrete time population growth model (purple = simulation trajectories that resulted in group extinction, blue = simulation trajectories that did not lead to group extinction) overlaid with longitudinal data from nine social groups (black). With immigration set to zero, over half of all iterations (61%) resulted in group extinction in 29 time-steps. However, (*B*) with immigration, only 18% of the iterations resulted in group extinction over the same time period. Thus, immigration increases the persistence of superb starling social groups. (*C*) Larger groups are more stable over time. With a larger starting group size (x axis), the percentage of groups going extinct over 29 time-steps (y axis) decreased (Z = −21.93, P < 0.001) (black points). However, when the relationship between immigration and group size was reversed artificially, the percentage of groups going extinct approaches or falls to zero (N₀10: mean ± SD = 1 ± 0.5%; N₀20: 0 ± 0%; N₀30: 0 ± 0% of iterations resulting in group extinction) and does not vary with variation in starting group size (gray points), indicating that in this scenario, immigration compensates for lower offspring recruitment in smaller groups (*SI Appendix*).

Next, to determine whether small groups are more likely to go extinct than large groups, or are instead buffered against extinction by immigration, we ran simulations that varied in starting group size (N_0 = 10, 20, or 30 individuals), but that fell within the range of natural group size variation within our study population (mean ± SD = 23 ± 11 individuals). We found that groups were more likely to go extinct when starting with a smaller group size (Z = –21.93, P < 0.001; Fig. 1C). However, when the relationship between immigration and group size was artificially reversed to simulate a scenario of higher immigration rates into smaller groups, the likelihood of group extinction decreased dramatically, regardless of the starting group size ($N_0$10: mean ± SD = 1 ± 0.5%; $N_0$20: 0 ± 0%; $N_0$30: 0 ± 0% of iterations resulting in group extinction) (Fig. 1C). Decreased group extinction risk in smaller groups in this artificial scenario is due to immigration compensating for low offspring recruitment rates, which is not the case in reality (*SI Appendix*, Fig. S7). Using empirical data from our long-term study to estimate a threshold group size below which offspring recruitment is unsuccessful, we found that groups with fewer than seven individuals never successfully fledged offspring (Fig. 2) and almost never exhibited per capita increases in group size (*SI Appendix*, Fig. S6). However, we note that the sample size of groups with fewer than seven individuals is quite low. Over 15 y, 3 out of 9 groups fell below this threshold, but only in 11 out of 255 [4%] group breeding years, with 2 of those 3 groups eventually going extinct. Groups that shrunk below the threshold group size had significantly lower offspring recruitment in the preceding years, but a similar number of immigrants, than groups that remained above the threshold group size (*SI Appendix, Table S4*). Thus, offspring recruitment is also necessary for keeping groups above a minimum group size threshold, indicating that both demographic processes are critical for preventing groups from going extinct. Together, our population dynamic models suggest that immigration is vital for the long-term persistence of superb starling groups, particularly for small groups with lower offspring recruitment.

Individual- and Group-Level Benefits Driving Immigration and Plural Breeding. Next, we tested three key predictions regarding the role of reproductive sharing in determining the group augmentation benefit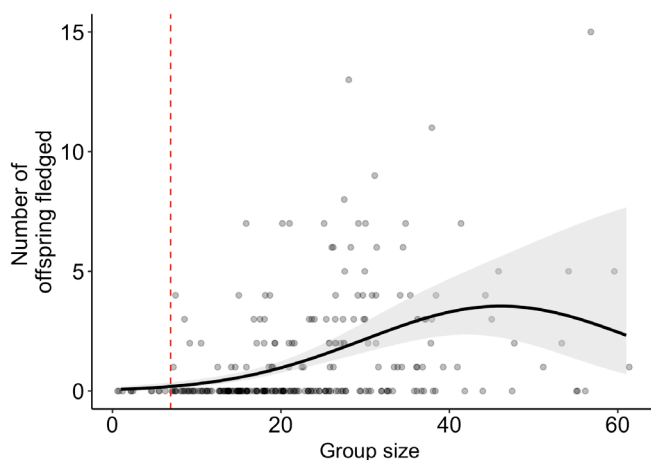s of immigration and the rise and maintenance of plural breeding in superb starling groups using the long-term empirical data. First, our simulations suggest that smaller groups stand to benefit more from immigration than larger groups since they experience lower offspring recruitment, though all groups may permit immigrants to join due to the survival (43) and reproductive (54) benefits associated with being in a larger group. Therefore, we predicted that offspring recruitment would increase with group size and that immigrants would be more likely to acquire breeding positions in smaller groups (i.e., small groups exhibit lower reproductive skew), due to the mutual fitness benefits of enhancing group size. As predicted, offspring recruitment increased with group size, though only up to a point, after which it declined at larger group sizes (group size: Z = 4.51, P < 0.001, 95% CI = 0.57 to 1.37, group size^2: Z = –1.94, P = 0.05, 95% CI = –0.39 to –0.01; *SI Appendix*, Table S5 and Fig. 2). Although this suggests that reproductive success of groups declines beyond an optimal group size, fewer samples at large group sizes limit this interpretation.

For both sexes, reproductive opportunities were more equitably distributed among group members (i.e., reproductive skew was lower) in smaller groups, but again only up to a point. And while a quadratic term for group size led to a better model fit (*Methods*), the small sample size at large group sizes again limits our interpretation. In fact, for reproductive skew, this effect was driven by only 4% of the data where group size was greater than two SDs above the mean group size (*SI Appendix*, Table S6). For males, reproductive skew was lower in smaller groups, both among all males (resident and immigrant) (group size: t = 1.43, P = 0.15, 95% CI = –0.01 to 0.04; group size^2: t = –2.00, P = 0.04, 95% CI = –0.03 to –0.00; *SI Appendix*, Table S5 and Fig. 3A) and immigrant males only (group size: t = 5.65, P < 0.001, 95% CI = 0.21 to 0.43; group size^2: t = –4.92, P < 0.001, 95% CI = –0.18 to –0.08; *SI Appendix*, Table S5 and Fig. 3A). However, the effect size was much smaller when all males were considered than when only immigrant males were included (*SI Appendix*, Table S5 and Fig. 3A), suggesting that while reproductive opportunities may be only marginally more equitably shared among all males in smaller groups, a larger share of the reproduction is monopolized by immigrant males in particular in smaller groups. Reproductive skew among immigrant females showed a similar relationship with group size (group size: t = 2.59, P = 0.01, 95% CI = 0.02 to 0.14, group size^2: Z = –2.79, P = 0.005, 95% CI = –0.06 to –0.01; *SI Appendix*, Table S5 and Fig. 3A).

Second, we predicted that immigrants should be more likely to join smaller groups, where they have a higher likelihood of acquiring breeding positions. However, despite the potentially higher fitness payoff for both immigrants and existing group members in smaller groups, we found that immigrants of both sexes were actually more likely to join larger groups, not smaller ones (males: Z = 2.08, P = 0.04, 95% CI = –0.01 to 0.83, females: Z = 2.83, P = 0.005, 95% CI = 0.19 to 0.80; *SI Appendix*, Table S5 and Fig. 3B). Although larger groups did not significantly improve the likelihood of achieving reproductive success per individual nesting attempt (i.e., fledging one or more offspring) for immigrants (males: Z = 0.06, P = 0.95, 95% CI = –0.50 to 0.52; females: Z = 0.63, P = 0.53, 95% CI = –0.17 to 0.32) or residents (males: Z = 0.32, P = 0.26, 95% CI = –0.33 to 0.92; females: since resident females do not acquire breeding positions in their natal groups, we cannot perform similar analyses), we found that individual immigrant breeders in larger groups were able to nest more often than immigrant breeders in smaller groups when controlling for the length of the breeding season (males: Z = 2.10, P = 0.04, 95% CI = 0.01 to 0.23, females: Z = 2.89, P = 0.004, 95% CI = 0.03 to 0.15; *SI Appendix*, Table S5 and Fig. 3C), which

Fig. 2. Inverse density dependence, or Allee effects, in superb starling social groups. Smaller groups fledged fewer offspring in a breeding season than larger groups (N = 255, group size: Z = 4.51, P < 0.001; group size^2: Z = –1.94, P = 0.05), and those below the group size threshold of seven individuals (dotted red line) never fledged any offspring. Points indicate raw data slightly jittered horizontally to improve visual discrimination. Solid line indicates model fit bounded by 95% CIs in light gray.
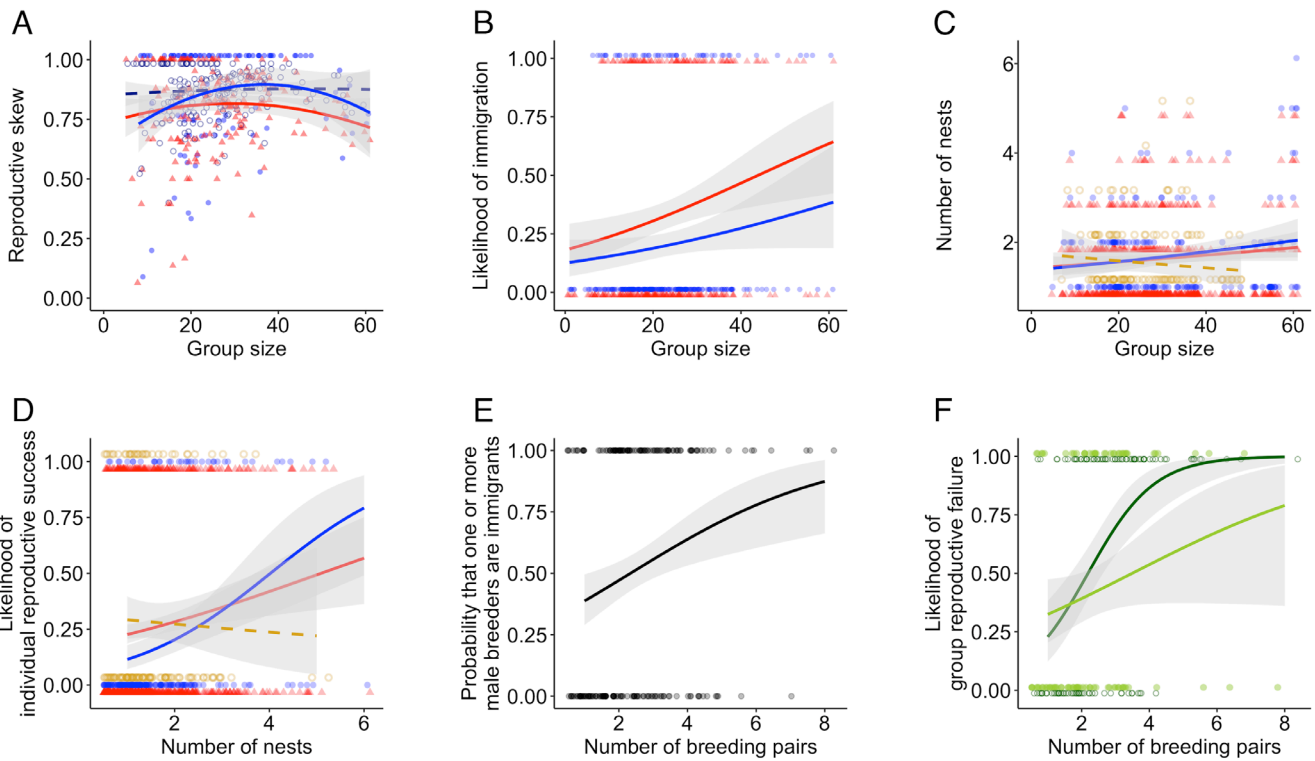
Fig. 3. Reproductive skew, likelihood of immigration, reproductive fitness outcomes, and group augmentation benefits of immigrants in superb starling social groups. (*A*) The sharing of reproductive opportunities was more equitable for both sexes (all males = black, open circles, dashed line; immigrant males only = blue, closed circles, solid line; immigrant females = red, closed triangles, solid line) in smaller groups and in very large groups (*SI Appendix*). Moreover, in males, the effect size was larger for immigrants only than that for all males. However, (*B*) immigrants of both sexes were more likely to join larger groups where they were able to (*C*) nest more times per breeding season and thus (*D*) accrue higher reproductive success. In contrast, resident males (orange, open circles, dashed lines) did not nest more times per breeding season in larger groups, and the number of nesting attempts did not affect their likelihood of reproductive success in a breeding season, suggesting that they employ an alternative reproductive strategy and are thus likely not negatively impacted by immigrant males breeding within the same social group. Additionally, (*E*) with more breeding pairs in a group, the likelihood of at least one breeding male being an immigrant increased, despite the presence of more than enough reproductively capable resident males (*SI Appendix*). (*F*) While fewer breeding pairs were enough to ensure reproductive success for the group as a whole in benign environmental conditions (dark green, open circles = higher than mean rainfall), more breeding pairs were needed to collectively insure the group against complete reproductive failure in harsh environmental conditions (light green, closed circles = lower than mean rainfall). Points indicate raw data slightly jittered horizontally to improve visual discrimination. Lines indicate model fits surrounded by 95% CIs in light gray.

consequently increased their individual likelihood of achieving reproductive success in a given breeding season (males: Z = 3.56, P < 0.001, 95% CI = 0.41 to 1.65, females: Z = 2.81, P = 0.005, 95% CI = 0.08 to 0.51; *SI Appendix*, Table S5 and Fig. 3*D*). This suggests that nest failure is largely stochastic due to predation pressure, and that immigrant breeders can only maximize reproductive success by increasing the number of nesting attempts, as has been shown previously for this species (58). Interestingly, for resident males, we did not find the same patterns of more nesting attempts in larger groups (Z = −0.38, P = 0.70, 95% CI = −0.16 to 0.11; *SI Appendix*, Table S5 and Fig. 3*D*), nor increased likelihood of achieving reproductive success with more nesting attempts (Z = −0.17, P = 0.86, 95% CI = −0.64 to 0.39; *SI Appendix*, Table S5 and Fig. 3*D*). These results suggest that resident males use a different reproductive strategy to maximize their fitness, as has been found previously in this species (53), and that, subsequently, they may not be negatively affected by immigrant males breeding within the same social group. Finally, the operational sex ratio (i.e., an estimate of the potential mate competition calculated as the number of males divided by the sum of the number of males and immigrant females in the group) and the total group reproductive success in the previous breeding season (i.e., the number of offspring fledged) had no impact on the likelihood of an individual immigrating into a group (*SI Appendix*, Table S5). Thus, even though immigrants are more likely to breed in smaller groups, their likelihood of breeding successfully is higher in larger groups.

This, in addition to the already-known positive impact of group size on survival of group members from a previous study of this species (43), contributes to higher fitness of immigrants in larger groups.

Third, we predicted that immigration will not only lead to an increase in group size that generates direct group augmentation benefits (37), but that male immigration specifically will also increase the number of breeders in a group, ultimately leading to additional, indirect group augmentation benefits by increasing the group's total future reproductive output. Indeed, we found that groups with more breeding pairs had a higher likelihood of one or more of the breeding males being an immigrant (Z = 2.82, P = 0.005, 95% CI = 0.29 to 1.38; *SI Appendix*, Table S5 and Fig. 3*E*), almost always despite the presence of more than enough reproductively capable resident males (and available, unrelated mates) in the group that did not attempt to breed [in 194 out of 199 (97%) instances, *SI Appendix*, Fig. S8]. Moreover, groups with more breeding pairs were significantly more likely to fledge offspring (*SI Appendix*, Table S5 and Fig. 3*F*). We note that in 100% of instances when only resident males bred (N = 96), the number of reproductively capable resident males in the group was higher than the number of breeding pairs (*SI Appendix*, Fig. S8). This suggests that factors other than competition with immigrant males are preventing resident males from acquiring breeding positions. Although only a few breeding pairs were necessary to ensure some reproductive success for the group as a whole in benign years

with high rainfall, more breeding pairs were needed to increase the group's collective insurance against complete reproductive failure in harsh years with low rainfall (breeding pairs × rainfall: Z = 3.40, P = 0.001, 95% CI = 0.36 to 1.40; *SI Appendix*, Table S5 and Fig. 3*F*), a finding consistent with ideas about sociality and bet-hedging in this (54) and other avian species (59).

Taken together, our empirical results suggest that a positive feedback loop of both direct and indirect group augmentation benefits generated by immigration helps maintain complex group social structure in superb starling societies via selection for larger group sizes. In other words, immigrants prefer to join larger groups, presumably because of the potential individual fitness benefits [both survival (43) and reproduction], which in turn increases group size and the number of breeding pairs in a group. As group size and the number of breeding pairs in a group increase, group productivity and offspring recruitment is enhanced, leading to further increases in group size and persistence, all despite a decrease in kin structure and in the face of environmental stochasticity that impacts both reproductive success and group demography (Fig. 4).

Discussion

Cooperatively breeding species exhibit tremendous variation in social organization, including in group size, kin structure, and the number of reproductives in a social group, three demographic traits of the group that are often linked in social species (6, 7). Variation in group structure arises due to the interplay of two demographic processes that lead to the addition of new group members—recruitment of offspring and immigration of unrelated individuals (35)—in conjunction with the loss of group members via dispersal or mortality. Recruitment only of offspring typically results in the formation of societies with relatively simple group structure characterized by small, nuclear families (i.e., high genetic relatedness) with a single breeding pair (60). A combination of offspring and immigrant recruitment (of both sexes), on the other hand, typically results in the formation of societies with complex group structure characterized by large, mixed-kin (or even nonkin) groups with multiple breeding pairs (1, 2, 60). In contrast to singular breeding societies that have high kin structure and likely evolve due to the indirect fitness benefits of helping relatives gained by offspring that delay dispersal (61, 62), plural breeding societies have low kin structure and, as theoretical work suggests, are instead likely to have evolved as a result of direct fitness benefits (23, 24). These direct fitness benefits must, in part, be derived from unrelated immigrants joining and acquiring breeding positions in social groups alongside natal individuals. Using empirical data, we demonstrate that direct benefits derived from group augmentation acting at both the individual and group level can lead to the formation and maintenance of cooperative societies with large group sizes, multiple breeding pairs, and low kin structure due to the inverse density dependence that is inherent in nearly all cooperatively breeding societies (28). Moreover, we show that the importance of these direct benefits is exacerbated by living in a harsh and unpredictable environment, suggesting that cooperation in the form of plural breeding may be an adaptation to ecological uncertainty.

Theoretical work suggests that when fitness benefits on both the individual and group level increase with group size, but offspring recruitment is insufficient to achieve and maintain optimal group sizes, immigration of unrelated individuals should be adaptive despite the accompanying reduction in group kin structure (23, 24, 51). Like other obligate cooperative breeders (30), superb starlings, which form large social groups with low and variable kin structure and multiple breeding pairs, are unable to successfully fledge offspring below a threshold group size (of approximately seven individuals in this species). Even in groups above the threshold group size, offspring recruitment is almost always low such that >70% of nests fail and >90% of offspring fail to fledge (52), and of those that do fledge, about 30% of males and 50% of female offspring emigrate to other social groups at around 1 y of age (53). By simulating population dynamics using models parameterized with long-term empirical data from nine social groups of superb starlings studied continuously over a 15-y period, and then
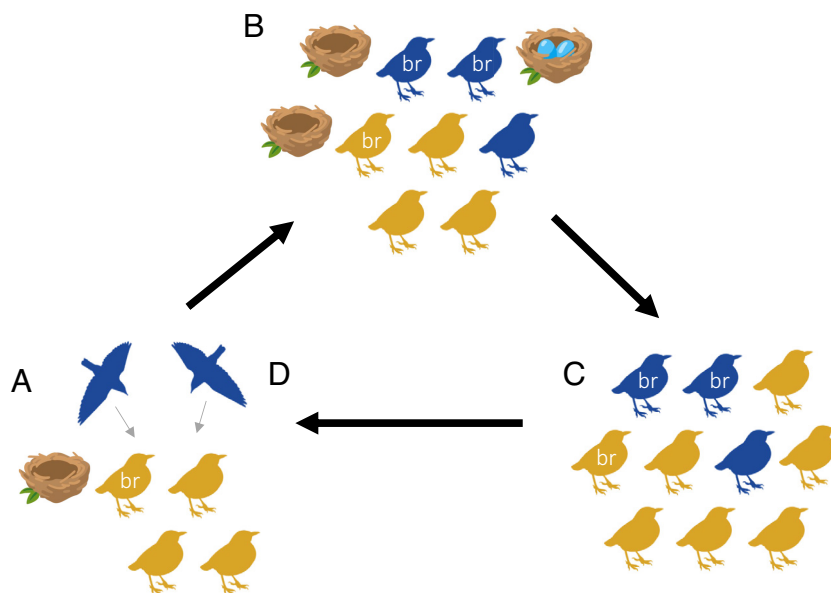

Fig. 4. Conceptual framework of direct and indirect group augmentation benefits driving formation and maintenance of social groups with complex group structure in superb starlings. (*A*) Immigrants (blue) directly augment the size of a group by increasing the number of group members. (*B*) Some of the immigrant males acquire breeding positions in the group alongside residents (yellow), increasing the number of breeding pairs (indicated as "br") and consequently the likelihood of reproductive success for the group as a whole, which (*C*) indirectly augments the size of the group by increasing the number of future group members. (*D*) Larger groups attract more immigrants, creating a positive feedback loop that maintains immigration and plural breeding, despite the accompanying decline in group kin structure, in superb starling societies.

by varying these demographic rates to test the generality of the model, we show that group augmentation via offspring recruitment alone is insufficient—and immigration is essential—to maintaining group persistence over time (a group-level benefit). In fact, neither offspring recruitment nor immigration alone bolsters group size to the extent necessary to combat the stochastic effects of temporal environmental variability that lead to group extinction. However, contrary to our expectation, immigration does not appear to compensate for reduced mean and increased variance in offspring recruitment in smaller groups. Smaller groups are thus more likely to go extinct, a pattern similar to that found in some singular breeding societies (33, 63). Increased risk of group extinction for smaller superb starling groups is likely due to preferred immigration of dispersing individuals into larger groups, driven by individual-level fitness benefits [e.g., higher survival (43)], such that, on the group level, smaller social groups do not experience substantial group augmentation from the recruitment of immigrants.

To maximize their individual-level fitness, immigrants should prefer to join groups where they can optimize survival and reproduction. While previous work has shown that individual superb starlings in larger groups have higher survival likelihoods (43) and that both residents and immigrants have equivalent survival likelihoods, at least in males (53), immigrants might have lower reproductive success in larger groups due to increased competition for breeding positions. In contrast, smaller groups in which immigration can protect against imminent group extinction might be more permissive to immigrants joining and acquiring breeding positions. Consistent with this prediction, we found that for both sexes, reproductive opportunities are more equitably shared among group members in smaller groups. For males in particular, our results suggest that in smaller groups, reproductive opportunities are more likely to be conceded to, or monopolized by, immigrant males. Yet, despite this apparent fitness benefit of joining smaller groups, we found that both sexes actually preferred to immigrate into larger groups, where immigrant breeders can nest more often in a breeding season and therefore substantially increase their likelihood of fledging offspring. Although nestling starvation occurs in this system, nest failure is largely the result of predation, a top-down, stochastic process that accounts for >90% of all nest failures (52). Thus, reproductive success in a breeding season overwhelmingly depends on the number of nesting attempts, as indicated by our results here as well as from previous studies of lifetime reproductive success in this species (53, 58). Although we do not yet know why larger group sizes facilitate more nesting attempts per breeding season for immigrant breeders, load-lightening effects found in previous studies of this species may play a role (64). Alternatively, larger groups are known to be found in territories with higher resource availability, which may support more nesting attempts per breeding season (55). Interestingly, we found that resident males did not show the same pattern of more nesting attempts per breeding season in larger groups nor an increased likelihood of reproductive success with more nesting attempts. As has been suggested previously for superb starlings (53), this may be because resident males adopt a different reproductive strategy than immigrant males and may have more related helpers in the social group that could increase their likelihood of reproductive success even in smaller groups. Conversely, immigrant males may be more successful in reproductive competition against resident males in larger groups, though equivalent direct lifetime fitness of resident and immigrant males in our study population suggests otherwise (53). While further investigation of the cause of this pattern is beyond the scope of this study, nevertheless it suggests that resident male breeders (i.e., group insiders) may not be

negatively affected by immigrant males (i.e., group outsiders) breeding within the social group, resulting in low insider–outsider conflict (37). Overall, our models of group dynamics suggest that small groups can theoretically be rescued from extinction by group augmentation via immigration, and our empirical results suggest that smaller groups present more breeding opportunities that should attract more immigrants than larger groups. However, this may rarely happen due to the individual fitness benefits pursued by immigrants and their apparent preference to join larger groups, condemning smaller groups to a higher risk of extinction (65, 66) as has been shown in other cooperatively breeding societies governed by group augmentation benefits (33, 67).

Finally, we found that male immigration and group augmentation benefits govern not just the formation of cooperative societies with complex group social structure, but also their maintenance over time. Specifically, groups with more breeding pairs are more likely to fledge offspring, especially in harsh years with low rainfall, and in order to have more breeding pairs, groups must allow immigrant males to breed alongside resident males. This result is somewhat surprising because in 97% of instances, groups had reproductively capable resident males who could have instead bred with unrelated immigrant females. Nonetheless, in a harsh and unpredictable environment characterized by high among-year variability in rainfall, food availability, and predation pressure (all of which contribute to high nest failure), additional breeding pairs increase the likelihood of successful offspring recruitment by simply increasing the number of breeding attempts for the group as a whole. A similar effect was observed in the plural breeding Mexican jay (*Aphelocoma wollweberi*) (68). Moreover, immigrants that do not breed likely still contribute to future group augmentation by providing alloparental care to offspring in the group (64, 69). On the whole, the increased offspring recruitment as a result of immigration leads to further group augmentation, creating a positive feedback loop that reinforces the adaptive value of plural breeding in superb starling societies despite the accompanying decrease in kin structure (13). While few, if any, other studies on birds have examined the group augmentation benefits of plural breeding, plural breeding avian species tend to inhabit harsh, unpredictable environments worldwide (52, 70–73), suggesting that plural breeding is likely to be adaptive for cooperatively breeding species in the face of ecological uncertainty.

By decreasing the likelihood of complete reproductive failure for the group in harsh years, plural breeding may serve as a conservative, within-generation bet-hedging strategy for resident males in unpredictable environments to reduce fecundity variance (54) and guard against group extinction (74). Even though sharing reproductive opportunities with unrelated immigrants may reduce their own fitness in benign years and reduce the potential indirect fitness benefits of helping related group members, the decreased likelihood of complete reproductive failure in harsh years would increase the longer-term fitness for all group members, many of whom happen to be relatives (75, 76). In other words, we hypothesize that group augmentation benefits likely outweigh any potential kin-selected benefits in plural breeding systems, particularly when they occur in fluctuating environments or where fecundity variance is high. Further, the reduction in fitness benefits for residents in benign years may be minimal. That is, despite the clutch size of superb starlings ranging from three to four eggs (52), the mean number of offspring fledged from a successful nest is only two (*SI Appendix*, Table S7). Similar to mammals where plural breeding is more common in species where females give birth to a single offspring (monotocy) as opposed to a litter (polytocy), a phenomenon that leads to decreased competition for resources between different females for their offspring (21), the nearly 50%

reduction in offspring number in superb starlings may greatly reduce resource competition between breeders, further facilitating plural breeding (77). Moreover, while most East African savanna resident avian species breed in the long rainy season, superb starlings and other plural cooperatively breeding avian species such as vulturine guineafowl (*Acryllium vulturinum*) (78) and gray-capped social weavers (*Pseduonigrita arnaudi*) (79) are known to also breed in the short rainy season at our study site, effectively doubling their reproductive effort each year. Large group sizes and plural breeding may thus enable breeding during the short rainy season when invertebrate prey is scarcer (80), further increasing the likelihood of reproductive success and guarding against group extinction. Plural breeding may thus be generally more prevalent in cooperative societies with high fecundity variance and overall low annual and lifetime reproductive success, both traits characteristic of species living in harsh and unpredictable environments globally.

Reproductive success is typically low and more variable in unpredictable environments where climatic uncertainty generates fecundity variance (54). Our results suggest that in such environments, the reproductive sharing characteristic of plural breeding (in vertebrates) and polygyny (in invertebrates) may be a more successful strategy for the formation of large, cooperative societies than complete reproductive monopolization as in singular breeding (in vertebrates) and monogyny (in invertebrates) (6, 70). The effect of environmental quality, including predation pressure, on social complexity has been demonstrated in social vertebrates such as fish (81), birds (82), and primates (83, 84), but its impact on plural breeding in particular is not well studied. In addition, a relationship between polygyny and environmental quality has been shown in eusocial insects between colonies of harvester ants (*Pogonomyrmex californicus*) (85) and between species in the wasp genus *Polistes* (86). Polygyny in both *P. californicus* and *Polistes spp.* leads to increased colony size, conferring group augmentation benefits such as increased foraging activity (85, 87) and survival (86, 87). Thus, group augmentation benefits may also drive the evolution of reproductive sharing in invertebrate societies with complex social structure, particularly those living in unpredictable environments where, like vertebrates, such species are most common (87).

In summary, group augmentation and plural breeding in superb starlings is partly driven by immigration of unrelated individuals from other social groups. Our study provides a clear empirical demonstration that immigration can play a vital role in group augmentation of cooperative societies where offspring recruitment is inadequate for long-term group persistence, as has been suggested by previous theoretical and conceptual work (23, 35). We show that animal social behavior is at least partly influenced by the demography of the group, such that reproductive decisions are informed by the need to maintain large group sizes that foster the persistence of groups in the face of environmental instability. Such need-based group size adjustments have previously been demonstrated in cooperatively breeding fish where group augmentation benefits similarly drive the formation of mixed-kin groups in an environment with high predation pressure (44, 88), but not in terrestrial species where climatic variability influences fitness. Interestingly, however, two other cooperatively breeding bird species living in harsh environments have been observed actively "kidnapping" unrelated young from other groups to augment group size and mitigate the risk of group extinction (89, 90), indicating that species may have different solutions to the same demographic and environmental challenges. By adjusting their reproductive strategies to alter group demography, social animals may therefore maximize fitness directly via group augmentation to ensure the persistence of their long-term associations in the face of environmental uncertainty. Our work shows that group

augmentation and other forms of direct benefits should not be overlooked in studies of animal social evolution, even in species that live in groups with substantial kin structure (91). Ultimately, the relative importance of direct versus indirect benefits in the evolution of sociality will depend on both the ecological and social environments that animals experience and how these environmental factors influence their cooperative behaviors and the demography of their social groups (24).

Methods

Long-Term Data Collection. Nine superb starling social groups, distributed across approximately 20 sq. km, have been monitored continuously since 2001 at the Mpala Research Centre, Kenya (0°17′N37° 52′E) (52). Groups defend stable territories year-round and consist of breeding pairs (mean ± SD: 2.58 ± 1.49, range: one to eight breeding pairs per group) and nonbreeding individuals (mean ± SD = 18.6 ± 9.86), some of whom act as alloparents that guard and/or provision the young (52, 64). Birds breed twice a year during the long (March to June) and short rains (October to November) (*SI Appendix*, Fig. S9) (52). We used data from the beginning of the 2003 long-rain breeding season (when all birds in the population were banded) through the end of the 2017 long-rain breeding season (N = 29 breeding seasons over 15 y).

Birds were marked with a unique combination of colored leg bands and a numbered metal ring. Hatchlings were banded in the nest; all other individuals were captured in baited pull-string traps or mist nets and banded after fledging from the nest (56). Blood from adults and hatchlings was collected in Queens lysis buffer and genomic DNA was extracted following the DNeasy Blood and Tissue kit protocol (QIAGEN). Parentage was determined in Cervus v3.0 (92) using 15 microsatellite markers previously identified for superb starlings (93, 94). Immigrants were identified as juveniles or older whose parents were not genetically identified as belonging to the same group. Using the same microsatellite markers, we estimated group relatedness for each social group for every breeding season using the function "grouprel" in the R package related (95), which averages all pairwise relatedness values (96) for group members. Sex was determined genetically (97) as previously described for this species (56).

We performed daily nest searches throughout the breeding season. Active nests were observed with a spotting scope for 60 to 120 min per observation period and all superb starlings within 30 m of the nest were identified (94). Parents are the primary nest builders, and only the mother incubates the eggs (94). Nests were checked daily to determine their ultimate fate (fledged or failed). Census data were used to estimate group size and operational sex ratio (natal females were excluded since they never breed and are thus not viable mates for males in the group). Groups were opportunistically censused year-round, and each individual was marked as either present or absent in its social group twice a year in 6-mo increments. The length of breeding season was calculated as the number of days from 2 wk before the first nest to 2 wk after the last nest of the breeding season (sensu ref. 53). Daily rainfall was measured using an automated Hydrological Services TB3 Tipping Bucket Rain Gauge at Mpala Research Centre (98) supplemented by a manual gauge at the same location when the automated gauge failed (54). Breeding season rainfall was calculated as a sum of total rainfall within the breeding season (sensu ref. 53).

Data Analysis.

Models of group population dynamics. We fit five generalized linear models (GLMs) with a negative binomial error distribution and group size as a fixed effect to estimate the effect of group size on the number of immigrants, the number of offspring recruited (i.e., successfully fledged), and the number of individuals that disappeared (dispersed or died) (*SI Appendix*, Table S1). Although the demographic rates are not highly correlated (*SI Appendix*, Table S8), because group size, the number of breeders, and the genetic relatedness of social groups are all related (*SI Appendix*, Fig. S1), for simplicity, we used only group size as a fixed effect in our models. Further, since our model is not age or stage structured, birds that died or dispersed were put in the same category to simplify the model. We built separate GLMs by sex for two of the three demographic processes resulting in a total of five models, with the number of male immigrants, female immigrants, males that disappeared, females that disappeared, and offspring recruited as the

dependent variables (see *SI Appendix*, Table S1 for model details). To account for optimal group size, we added a quadratic term for the fixed effect of group size for demographic processes that result in the recruitment of new individuals to the group if it significantly improved model fit [offspring recruitment: $X^2(1) = 9.84, P = 0.002$; male immigration: $X^2(1) = 1.30, P = 0.25$; female immigration: $X^2(1) = 2.73, P = 0.10$]. Improvement in model fit was assessed by performing a Chi-squared test between a model with only a linear term for group size and a model with the quadratic term added using the "ANOVA" function in base R (sensu ref. 99). In our final models, only offspring recruitment had a quadratic term for the fixed effect of group size such that it scales linearly with group size at smaller group sizes until an optimum group size is reached, after which offspring recruitment declines as groups get larger (*SI Appendix*, Table S1). Predicted demographic variables from all the five models had good visual fit with real values from the long-term study population (*SI Appendix*, Fig. S10).

We then built a discrete time step population growth model such that group size at time $t+1$ (N_{t+1}) was calculated as a function of group size at time t (N_t), rate of immigration (i), offspring recruitment (r), and disappearance (d) (Eq. **1**).

$$N_{t+1} = N_t + (i_m + i_f)_{\text{immigration}} + (r)_{\text{offspring}} - (d_m + d_f)_{\text{disappearance}}. \quad [\textbf{1}]$$

Demographic rates were parameterized using estimates from fitted GLMs. For each time step (t), we generated a distribution of predicted values for each demographic rate based on group size at that time step (N_t) and randomly picked a value to plug into the equation. We let the model run for 100 iterations over 29 time-steps. We used 29 time-steps to match the time period of our long-term dataset (29 breeding seasons). For each iteration, starting group size (N_0) was randomly set between 10 and 30 individuals, which matches the natural variation in group size (range in means across nine groups = 13 to 41 individuals, mean ± SD = 23 ± 11 individuals). To simulate the effect of no immigration into the social groups, we then set the immigration terms to zero, and reran the model for 29 time-steps for 100 iterations (Eq. **2**).

$$N_{t+1} = N_t + (r)_{\text{offspring}} - (d_m + d_f)_{\text{disappearance}}. \quad [\textbf{2}]$$

We also evaluated the effect of no offspring recruitment into the social groups by setting the offspring recruitment term to zero and running 100 iterations for 29 time-steps (Eq. **3**).

$$N_{t+1} = N_t + (i_m + i_f)_{\text{immigration}} - (d_m + d_f)_{\text{disappearance}}. \quad [\textbf{3}]$$

Moreover, to make our model more generalizable to other animal species that live in similar types of societies, we varied the rates of immigration and offspring recruitment by multiplying values predicted from fitted GLMs by an integer $P = 0, 0.5, 1, 1.5,$ or 2, resulting in 25 simulations with varying rates of the two demographic processes (Eq. **4**). This exploration of a wider parameter space makes our model generalizable to a wide range of cooperatively breeding species. For example, annual immigration into social groups can range from almost zero [e.g., long-tailed tits (*Aegithalos caudatus*)] (100) to high [e.g., greater anis (*Crotophaga major*) and Lake Tanganyika cichlids (*Neolamprologus pulcher*)] (44, 71). Similarly, annual offspring recruitment is also quite variable in cooperatively breeding species, with most well-studied cooperative breeders experiencing higher rates of annual offspring recruitment than superb starlings (see examples in ref. 101).

$$N_{t+1} = N_t + [P * (i_m + i_f)]_{\text{immigration}} + [P * (r)]_{\text{offspring}} - (d_m + d_f)_{\text{disappearance}}. \quad [\textbf{4}]$$

Finally, because setting the disappearance rate to zero would result in infinite population growth, we instead halved the rate of disappearance for both sexes to assess how dispersal and mortality together contribute to a change in group size over time (Eq. **5**).

$$N_{t+1} = N_t + (i_m + i_f)_{\text{immigration}} + (r)_{\text{offspring}} - [0.5 * (d_m + d_f)]_{\text{disappearance}}. \quad [\textbf{5}]$$

For all simulations, we evaluated the percentage of iterations for which group size fell to zero. For the full model, we also assessed the presence of inverse density

dependence in population growth by plotting group size at time N_t against the per capita growth rate [$(N_{t+1} - N_t)/N_t$] using both simulated data and empirical data from the long-term study (*SI Appendix*, Fig. S6). Additionally, we fit a linear model using the empirical data with per capita growth rate [$(N_{t+1} - N_t)/N_t$] as the dependent variable and group size (N_t) as the fixed effect (N = 257). We included a quadratic term for group size to assess whether per capita growth rate shows a unimodal relationship with group size, as would be the case for inverse density dependence in population growth.

Next, to examine the effect of group size on group extinction risk, we set starting group size (N_0) to either 10, 20, or 30 individuals and ran 100 iterations of the model (Eq. **1**) for 29 time-steps. For these simulations, immigration was higher in larger groups, as predicted by models fit to the long-term data (*SI Appendix*, Table S1). However, to simulate a scenario where the relationship between immigrant and group size is reversed [i.e., more immigration into smaller groups as is seen in some cooperatively breeding birds such as Southern pied babblers (102), we reran the same simulations after changing group size values by subtracting real values from the maximum group size (61 individuals) [i.e., $N_{\text{artificial}} = \max(N) - N_i$] (*SI Appendix*, Table S9). The starting group size values were based on the natural variation in group size in our study population (mean ± SD = 23 ± 11 individuals). Models were run 10 times per each N_0 to obtain mean and SD estimates. We fit a beta regression to the model results with the percentage of iterations resulting in group extinction as the dependent variable and N_0 as the fixed effect using the package *betareg* (103). We also estimated the threshold group size, below which superb starling groups cannot successfully fledge offspring, by plotting reproductive success against group size from our long-term dataset and identifying the group size below which no offspring have ever been recruited (Fig. 2), similar to studies of other cooperative breeders (29, 30).

Empirical tests of individual- and group-level benefits driving immigration and plural breeding. Using empirical data from our long-term study, we tested three key predictions regarding variation in reproductive sharing with immigrants based on group size, immigration patterns and reproductive fitness outcomes of dispersing individuals in relation to group size, and group augmentation benefits of plural breeding itself. First, we examined whether smaller groups are in more need of immigrants due to lower offspring recruitment. We fit a generalized linear mixed model (GLMM) with a negative binomial error distribution including number of offspring fledged as the dependent variable and group size as the fixed effect (N = 255). Including a quadratic term for group size to account for nonlinearity in the relationship between offspring recruitment and group size improved model fit [$X^2(1) = 3.86, P = 0.05$], though the sample size was limited for large group sizes (*SI Appendix*).

Next, we examined whether in smaller groups reproductive opportunities are shared to a higher degree, especially among immigrants. We calculated an index of reproductive skew (L) for each group per breeding season as a function of the total number of potential reproductives (N_T) and the effective number of reproductives (Q_E) (sensu ref. 104) (Eq. **6**).

$$L = (N_T - Q_E) / (N_T - 1). \quad [\textbf{6}]$$

Here, Q_E is a function of the proportion of total nesting attempts observed in the group attributed to an individual breeder (p_i) (104) (Eq. **7**). We did not take extra-pair fertilizations into account because previous work has shown that extra-pair paternity is much lower in superb starlings (14% or less) compared to other cooperatively breeding species, especially plural cooperative breeders (52, 94). Moreover, considering extra-pair fertilizations would likely only strengthen our results because previous work has found that extra-pair fertilization rates are higher (i.e., reproductive skew is lower) in groups on low-quality territories (105), which can only support smaller groups (55).

$$Q_E = 1 / \sum p_i^2. \quad [\textbf{7}]$$

Values of L can range from 0 (equitable reproductive sharing) to 1 (complete monopolization of reproduction by a single individual) (104). This reproductive skew index is appropriate for investigating how inequality in reproductive opportunities varies with group-level attributes such as group size, since the lower and upper bounds to the value enable comparison among groups with different numbers of potential reproductives and total nesting attempts (106). We calculated reproductive skew for all males (i.e., both residents and immigrants), only

immigrant males, and only immigrant females (since resident females do not become breeders). Examining the relationship between group size and reproductive skew for both all males and only immigrant males helped us understand whether the variation in skew among male breeders in a group is driven by sharing of reproductive opportunities with immigrant males in particular. We fit a GLMM with a gamma error distribution and an identity link function to assess the effect of group size (fixed effect) on reproductive skew (dependent variable) ($N_{all\ males} = 199$, $N_{immigrant\ males} = 94$, $N_{immigrant\ females} = 199$). We included a quadratic term for group size to account for a nonlinear relationship between group size and reproductive skew. Including the quadratic term significantly improved model fit for all the three models [all males: $X^2(1) = 4.18$, $P = 0.04$; immigrant males: $X^2(1) = 14.66$, $P < 0.001$; immigrant females: $X^2(1) = 7.45$, $P = 0.01$], though the sample size was limited for large group sizes (*SI Appendix*). We also fit a GLMM with a binomial error distribution to investigate the effect of group size on the likelihood of an immigrant attaining a breeding position in its first year in its nonnatal social group to approach the question of reproductive sharing from the point of view of the immigrating individual (*SI Appendix*). Social group ID, breeding season, and proximity to human settlement (yes/no) were included as random effects in all models. Proximity to human settlement was included as the territories of two of the nine social groups overlap the research station which may affect their demography (107).

Next, we investigated the effect of social factors on immigration of both sexes into superb starling social groups (N = 257). We fit separate GLMMs by sex with a binomial error distribution including immigration (yes = 1, no = 0) as the dependent variable and group size, sex ratio, and fledging success in the previous breeding season as fixed effects. Group ID, breeding season, and proximity to human settlement (yes/no) were included as random effects. Further, we examined the reproductive fitness benefits accrued by immigrants of both sexes as well as resident males in groups of varying sizes (resident females were excluded since they do not become breeders in their natal groups). We know from previous studies that the best predictor of lifetime direct reproductive success is the number of lifetime nesting attempts (58), and that immigrant males in particular maximize their lifetime fitness by maximizing nesting attempts (53). Thus, we fit a GLMM with a Poisson error distribution and the number of nesting attempts per individual breeder per breeding season as the dependent variable and group size and the length of breeding season as the fixed effects ($N_{immigrant\ males} = 188$, $N_{immigrant\ females} = 617$, $N_{resident\ males} = 124$). We included the length of breeding season in number of days as a fixed effect to account for its effect on the variation in opportunity to nest multiple times. Additionally, we fit a GLMM with a binomial error distribution modeling the effect of the number of nesting attempts (fixed effect) on the likelihood of achieving any reproductive success (i.e., fledging one or more offspring) for individual breeders in a breeding season (dependent variable) ($N_{immigrant\ males} = 188$, $N_{immigrant\ females} = 618$, $N_{resident\ males} = 124$). We also examined the likelihood of nest success (fledged = 1, failed = 0) of individual nests in relation to group size for individual breeders using a GLMM with a

binomial error distribution ($N_{immigrant\ males} = 323$, $N_{immigrant\ females} = 986$, $N_{resident\ males} = 190$). Group ID, breeder ID, breeding season, and proximity to human settlement (yes/no) were included as random effects in all models.

Finally, we investigated whether group augmentation benefits help maintain plural breeding in superb starlings. Since reproductive opportunities are shared among residents and immigrants only in males, we first examined whether having one or more immigrant male breeders is required for increasing the number of breeding pairs in a group. We fit a GLMM with a binomial error distribution with a "logit" link, the number of breeding pairs as the fixed effect, and the likelihood of one or more male breeders being immigrants (no immigrant males breeding = 0, at least one immigrant male breeding = 1) as the dependent variable. Then, we examined whether more breeding pairs increase the reproductive success of the group under varying environmental conditions by fitting a GLMM with a binomial error distribution with a "logit" link to the likelihood of a group fledging any offspring (dependent variable) (no offspring fledged = 0, some offspring fledged = 1) and the interaction between number of breeding pairs in the group and the total rainfall during the breeding season (fixed effects). Social group ID, breeding season, and proximity to human settlement (yes/no) were included as random effects in both models (N = 200). All analyses were conducted in R (108). For GLMMs and beta regression, all fixed effects were standardized using Z-scores (109). CIs for GLMMs were calculated by bootstrapping (500 iterations) except for models with Gamma error distributions where Wald CIs were used. All GLMs and GLMMs were fit using the package *lme4* (110).

Author affiliations: [a]Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, NY 10027; and [b]Center for Integrative Animal Behavior, Columbia University, New York, NY 10027

1. C. Riehl, Evolutionary routes to non-kin cooperative breeding in birds. *Proc. R. Soc. B.* **280**, 20132245 (2013).
2. T. Clutton-Brock, Social evolution in mammals. *Science* **373**, eabc9699 (2021).
3. J. L. Brown, Avian communal breeding systems. *Annu. Rev. Ecol. Syst.* **9**, 123–155 (1978).
4. B. J. Hatchwell, The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Phil. Trans. R. Soc. B* **364**, 3217–3227 (2009).
5. P. Dierkes, D. Heg, M. Taborsky, E. Skubic, R. Achmann, Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid. *Ecol. Lett.* **8**, 968–975 (2005).
6. D. R. Rubenstein, C. A. Botero, E. A. Lacey, Discrete but variable structure of animal societies leads to the false perception of a social continuum. *R. Soc. Open Sci.* **3**, 160147 (2016).
7. M. Dyble, T. H. Clutton-Brock, Contrasts in kinship structure in mammalian societies. *Behav. Ecol.* **31**, 971–977 (2020).
8. S. T. C. Chak, J. E. Duffy, D. R. Rubenstein, Reproductive skew drives patterns of sexual dimorphism in sponge-dwelling snapping shrimps. *Proc. R. Soc. B.* **282**, 20150342 (2015).
9. D. Lukas, T. Clutton-Brock, Social complexity and kinship in animal societies. *Ecol. Lett.* **21**, 1129–1134 (2018).
10. K. C. Brooks, R. Maia, J. E. Duffy, K. M. Hultgren, D. R. Rubenstein, Ecological generalism facilitates the evolution of sociality in snapping shrimps. *Ecol. Lett.* **20**, 1516–1525 (2017).
11. K. G. Ross, L. Keller, Genetic control of social organization in an ant. *Proc. Natl. Acad. Sci. U.S.A.* **95**, 14232–14237 (1998).
12. J. Purcell, A. Brelsford, Y. Wurm, N. Perrin, M. Chapuisat, Convergent genetic architecture underlies social organization in ants. *Curr. Biol.* **24**, 2728–2732 (2014).
13. D. R. Rubenstein, Family feuds: social competition and sexual conflict in complex societies. *Phil. Trans. R. Soc. B* **367**, 2304–2313 (2012).
14. D. Heg, Reproductive suppression in female cooperatively breeding cichlids. *Biol. Lett.* **4**, 606–609 (2008).
15. E. A. Tibbetts, H. K. Reeve, Two experimental tests of the relationship between group stability and aggressive conflict in Polistes wasps. *Sci. Nat.* **95**, 383–389 (2008).
16. J. S. Mitchell, E. Jutzeler, D. Heg, M. Taborsky, Gender differences in the costs that subordinate group members impose on dominant males in a cooperative breeder. *Ethology* **115**, 1162–1174 (2009).
17. P. Seppa, Reproduction in foundress associations of the social wasp, *Polistes carolina*: Conventions, competition, and skew. *Behav. Ecol.* **13**, 531–542 (2002).
18. M. Chapuisat, S. Bocherens, H. Rosset, Variable queen number in ant colonies: No impact on queen turnover, inbreeding, and population genetic differentiation in the ant *Formica selysi*. *Evolution* **58**, 1064–1072 (2004).
19. M. Taborsky, "Cichlid fishes: A model for the integrative study of social behavior" in *Cooperative Breeding in Vertebrates*, 1st, W. D. Koenig, J. L. Dickinson, Eds. (Cambridge University Press, 2016), pp. 272–293.
20. A. Cockburn, B. J. Hatchwell, W. D. Koenig, "Sociality in birds" in *Comparative Social Evolution*, 1st, D. R. Rubenstein, P. Abbot, Eds. (Cambridge University Press, 2017), pp. 320–353.
21. D. Lukas, T. Clutton-Brock, Monotocy and the evolution of plural breeding in mammals. *Behav. Ecol.* **31**, 943–949 (2020).
22. K. Hultgren, J. Emmett Duffy, D. R. Rubenstein, "Sociality in shrimps" in *Comparative Social Evolution*, 1st, D. R. Rubenstein, P. Abbot, Eds. (Cambridge University Press, 2017), pp. 224–250.
23. H. Kokko, R. A. Johnstone, The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. Lond. B* **268**, 187–196 (2001).
24. I. García-Ruiz, A. Quiñones, M. Taborsky, The evolution of cooperative breeding by direct and indirect fitness effects. *Sci. Adv.* **8**, eabl7853 (2022).

25. D. R. Rubenstein, I. J. Lovette, Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.* **17**, 1414–1419 (2007).

26. W. Jetz, D. R. Rubenstein, Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.* **21**, 72–78 (2011).

27. M. Griesser, S. M. Drobniak, S. Nakagawa, C. A. Botero, Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLoS Biol.* **15**, e2000483 (2017).

28. F. Courchamp, T. Clutton-Brock, B. Grenfell, Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* **14**, 405–410 (1999).

29. O. A. E. Rasa, The costs and effectiveness of vigilance behaviour in the dwarf mongoose: implications for fitness and optimal group size. *Ethol. Ecol. Evol.* **1**, 265–282 (1989).

30. R. G. Heinsohn, Cooperative enhancement of reproductive success in white-winged choughs. *Evol. Ecol.* **6**, 97–114 (1992).

31. F. Courchamp, B. Grenfell, T. Clutton-Brock, Population dynamics of obligate cooperators. *Proc. R. Soc. Lond. B* **266**, 557–563 (1999).

32. T. H. Clutton-Brock *et al.*, Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *J. Anim. Ecol.* **68**, 672–683 (1999).

33. D. Heg, L. Brouwer, Z. Bachar, M. Taborsky, Large group size yields group stability in the cooperatively breeding cichlid Neolamprologus pulcher. *Behaviour* **142**, 1615–1641 (2005).

34. A. W. Bateman, A. Ozgul, J. F. Nielsen, T. Coulson, T. H. Clutton-Brock, Social structure mediates environmental effects on group size in an obligate cooperative breeder, *Suricata suricatta*. *Ecology* **94**, 587–597 (2013).

35. S. A. Kingma, P. Santema, M. Taborsky, J. Komdeur, Group augmentation and the evolution of cooperation. *Trends Ecol. Evol.* **29**, 476–484 (2014).

36. S.-F. Shen, S. T. Emlen, W. D. Koenig, D. R. Rubenstein, The ecology of cooperative breeding behaviour. *Ecol. Lett.* **20**, 708–720 (2017).

37. M. Higashi, N. Yamamura, What determines animal group size? Insider-outsider conflict and its resolution. *Am. Nat.* **142**, 553–563 (1993).

38. T. H. Clutton-Brock, S. J. Hodge, T. P. Flower, Group size and the suppression of subordinate reproduction in Kalahari meerkats. *Anim. Behav.* **76**, 689–700 (2008).

39. M. A. Cant, S. J. Hodge, M. B. V. Bell, J. S. Gilchrist, H. J. Nichols, Reproductive control via eviction (but not the threat of eviction) in banded mongooses. *Proc. R. Soc. B Biol. Sci.* **277**, 2219–2226 (2010).

40. M. A. Cant, E. Otali, F. Mwanguhya, Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose. *Ethology* **108**, 541–555 (2002).

41. S. J. Hodge, Helpers benefit offspring in both the short and long-term in the cooperatively breeding banded mongoose. *Proc. R. Soc. B* **272**, 2479–2484 (2005).

42. S. J. Hodge, A. Manica, T. P. Flower, T. H. Clutton-Brock, Determinants of reproductive success in dominant female meerkats. *J. Anim. Ecol.* **77**, 92–102 (2008).

43. S. Guindre-Parker, D. R. Rubenstein, Survival benefits of group living in a fluctuating environment. *Am. Nat.* **195**, 1027–1036 (2020).

44. M. Zöttl, J. G. Frommen, M. Taborsky, Group size adjustment to ecological demand in a cooperative breeder. *Proc. R. Soc. B* **280**, 20122772 (2013).

45. L. Grinsted, J. Field, Market forces influence helping behaviour in cooperatively breeding paper wasps. *Nat. Commun.* **8**, 13750 (2017).

46. H. K. Reeve, L. Keller, Tests of reproductive-skew models in social insects. *Annu. Rev. Entomol.* **46**, 347–385 (2001).

47. R. Noë, P. Hammerstein, Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* **11** (1994).

48. H. K. Reeve, S. T. Emlen, L. Keller, Reproductive sharing in animal societies: Reproductive incentives or incomplete control by dominant breeders? *Behav. Ecol.* **9**, 267–278 (1998).

49. T. H. Clutton-Brock, Reproductive skew, concessions and limited control. *Trends Ecol. Evol.* **13**, 288–292 (1998).

50. S.-F. Shen, H. Kern Reeve, Reproductive skew theory unified: The general bordered tug-of-war model. *J. Theor. Biol.* **263**, 1–12 (2010).

51. S. L. Vehrencamp, A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.* **31**, 667–682 (1983).

52. D. R. Rubenstein, "Superb starlings: Cooperation and conflict in an unpredictable environment" in *Cooperative Breeding in Vertebrates*, 1st Ed., W. D. Koenig, J. L. Dickinson, Eds. (Cambridge University Press, 2016), pp. 181–196.

53. S. S. Shah, D. R. Rubenstein, Prenatal environmental conditions underlie alternative reproductive tactics that drive the formation of a mixed-kin cooperative society. *Sci. Adv.* **8**, eabk2220 (2022).

54. D. R. Rubenstein, Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 10816–10822 (2011).

55. S. S. Shah, *Socioecological Drivers of Complex Social Structure in an Avian Cooperative Breeder* (Columbia University, 2022).

56. D. R. Rubenstein, Stress hormones and sociality: Integrating social and environmental stressors. *Proc. R. Soc. B.* **274**, 967–975 (2007).

57. D. R. Rubenstein *et al.*, Sex-specific fitness effects of unpredictable early life conditions are associated with DNA methylation in the avian glucocorticoid receptor. *Mol. Ecol.* **25**, 1714–1728 (2016).

58. K. Apakupakul, D. R. Rubenstein, Bateman's principle is reversed in a cooperatively breeding bird. *Biol. Lett.* **11**, 20150034 (2015).

59. P. Capilla-Lasheras, X. Harrison, E. M. Wood, A. J. Wilson, A. J. Young, Altruistic bet-hedging and the evolution of cooperation in a Kalahari bird. *Sci. Adv.* **7**, eabe8980 (2021).

60. S. T. Emlen, An evolutionary theory of the family. *Proc. Natl. Acad. Sci. U.S.A.* **92**, 8092–8099 (1995).

61. W. D. Hamilton, The genetical evolution of social behaviour. I. *J. Theor. Biol.* **7**, 1–16 (1964).

62. W. D. Hamilton, The genetical evolution of social behaviour. II. *J. Theor. Biol.* **7**, 17–52 (1964).

63. C. Duncan, M. B. Manser, T. Clutton-Brock, Decline and fall: The causes of group failure in cooperatively breeding meerkats. *Ecol. Evol.* **11**, 14459–14474 (2021).

64. S. Guindre-Parker, D. R. Rubenstein, Multiple benefits of alloparental care in a fluctuating environment. *R. Soc. Open Sci.* **5**, 172406 (2018).

65. I. Hanski, D. Simberloff, "The metapopulation approach, its history, conceptual domain, and application to conservation" in *Metapopulation Biology* (Elsevier, 1997), pp. 5–26.

66. B. Unglaub *et al.*, Context-dependent dispersal determines relatedness and genetic structure in a patchy amphibian population. *Mol. Ecol.* **30**, 5009–5028 (2021).

67. A. R. Reddon, D. Balk, S. Balshine, Sex differences in group-joining decisions in social fish. *Anim. Behav.* **82**, 229–234 (2011).

68. S.-H. Li, J. L. Brown, Influence of climate on reproductive success in Mexican jays. *Auk* **116**, 924–936 (1999).

69. I. García-Ruiz, M. Taborsky, Group augmentation on trial: Helpers in small groups enhance antipredator defence of eggs. *Biol. Lett.* **18**, 20220170 (2022).

70. A. F. Russell, D. J. Portelli, D. J. F. Russell, H. Barclay, Breeding ecology of the chestnut-crowned babbler: A cooperative breeder in the desert. *Emu* **110**, 324–331 (2010).

71. C. Riehl, L. Jara, Natural history and reproductive biology of the communally breeding greater ani (crotophaga major) at Gatún Lake, Panama. *Wilson J. Ornithol.* **121**, 679–687 (2009).

72. I. Rowley, E. Russell, R. B. Payne, L. L. Payne, Plural breeding in the splendid fairy-wren, Malurus splendens (aves: Maluridae), a cooperative breeder. *Ethology* **83**, 229–247 (2010).

73. J. L. Brown, Cooperative breeding and altruistic behaviour in the Mexican jay, *Aphelocoma ultramarina*. *Anim. Behav.* **18**, 366–378 (1970).

74. H. K. Reeve, P. Nonacs, Within-group aggression and the value of group members: Theory and a field test with social wasps. *Behav. Ecol.* **8**, 75–82 (1997).

75. J. H. Gillespie, Natural selection for variances in offspring numbers: A new evolutionary principle. *Am. Nat.* **111**, 1010–1014 (1977).

76. J. Starrfelt, H. Kokko, Bet-hedging–a triple trade-off between means, variances and correlations. *Biol. Rev.* **87**, 742–755 (2012).

77. A. P. Beckerman, S. P. Sharp, B. J. Hatchwell, Predation and kin-structured populations: An empirical perspective on the evolution of cooperation. *Behav. Ecol.* **22**, 1294–1303 (2011).

78. D. Papageorgiou, D. R. Farine, Group size and composition influence collective movement in a highly social terrestrial bird. *eLife* **9**, e59902 (2020).

79. N. E. Collias, E. C. Collias, Behavior of the grey-capped social weaver (*Pseudonigrita arnaudi*) in Kenya. *Auk* **97**, 213–226 (1980).

80. L. Brown, P. L. Britton, *The Breeding Seasons of East African Birds* (East Africa Natural History Society, 1980).

81. F. Groenewoud *et al.*, Predation risk drives social complexity in cooperative breeders. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 4104–4109 (2016).

82. E. Sorato, P. R. Gullett, S. C. Griffith, A. F. Russell, Effects of predation risk on foraging behaviour and group size: Adaptations in a social cooperative species. *Anim. Behav.* **84**, 823–834 (2012).

83. C. P. van Schaik, M. Hörstermann, Predation risk and the number of adult males in a primate group: A comparative test. *Behav. Ecol. Sociobiol.* **35**, 261–272 (1994).

84. C. M. Bettridge, R. I. M. Dunbar, Predation as a determinant of minimum group size in baboons. *Folia Primatol.* **83**, 332–352 (2012).

85. B. R. Haney, J. H. Fewell, Ecological drivers and reproductive consequences of non-kin cooperation by ant queens. *Oecologia* **187**, 643–655 (2018).

86. M. J. Sheehan *et al.*, Different axes of environmental variation explain the presence vs. extent of cooperative nest founding associations in *Polistes* paper wasps. *Ecol. Lett.* **18**, 1057–1067 (2015).

87. M. M. Ostwald *et al.*, Cooperation among unrelated ant queens provides persistent growth and survival benefits during colony ontogeny. *Sci. Rep.* **11**, 8332 (2021).

88. M. Taborsky, Breeder-helper conflict in a cichlid fish with broodcare helpers: An experimental analysis. *Behaviour* **95**, 45–75 (1985).

89. R. G. Heinsohn, Kidnapping and reciprocity in cooperatively breeding white-winged choughs. *Anim. Behav.* **41**, 1097–1100 (1991).

90. A. R. Ridley, M. J. Nelson-Flower, E. M. Wiley, D. J. Humphries, H. Kokko, Kidnapping intergroup young: an alternative strategy to maintain group size in the group-living pied babbler (*Turdoides bicolor*). *Phil. Trans. R. Soc. B* **377**, 20210153 (2022).

91. S. A. Kingma, Direct benefits explain interspecific variation in helping behaviour among cooperatively breeding birds. *Nat. Commun.* **8**, 1094 (2017).

92. S. T. Kalinowski, M. L. Taper, T. C. Marshall, Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* **16**, 1099–1106 (2007).

93. D. R. Rubenstein, Isolation and characterization of polymorphic microsatellite loci in the plural cooperatively breeding superb starling, *Lamprotornis superbus*. *Mol. Ecol. Notes* **5**, 739–744 (2005).

94. D. R. Rubenstein, Female extrapair mate choice in a cooperative breeder: Trading sex for help and increasing offspring heterozygosity. *Proc. R. Soc. B.* **274**, 1895–1903 (2007).

95. J. Pew, P. H. Muir, J. Wang, T. R. Frasier, related: An R package for analysing pairwise relatedness from codominant molecular markers. *Mol. Ecol. Res.* **15**, 557–561 (2015).

96. D. C. Queller, K. F. Goodnight, Estimating relatedness using genetic markers. *Evolution* **43**, 258–275 (1989).

97. R. Griffiths, M. C. Double, K. Orr, R. J. G. Dawson, A DNA test to sex most birds. *Mol. Ecol.* **7**, 1071–1075 (1998).

98. K. K. Caylor, J. Gitonga, D. J. Martins, Mpala Research Centre Meteorological and Hydrological Dataset.

99. B. M. Bolker *et al.*, Generalized linear mixed models: A practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135 (2009).

100. J. P. Green, B. J. Hatchwell, Inclusive fitness consequences of dispersal decisions in a cooperatively breeding bird, the long-tailed tit (*Aegithalos caudatus*). *Proc. Natl. Acad. Sci. U.S.A.* **115**, 12011–12016 (2018).

101. W. D. Koenig, J. L. Dickinson, Eds., *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior* (Cambridge University Press, 2016) (January 30, 2023), 10.1017/CBO9781107338357.

102. A. R. Ridley, "Southern pied babblers: The dynamics of conflict and cooperation in a group-living society" in *Cooperative Breeding in Vertebrates*, 1st Ed., W. D. Koenig, J. L. Dickinson, Eds. (Cambridge University Press, 2016), pp. 115–132.

103. F. Cribari-Neto, A. Zeileis, Beta Regression in *R. J. Stat. Soft.* **34** (2010).

104. P. Pamilo, R. H. Crozier, Reproductive skew simplified. *Oikos* **75**, 533 (1996).

105. D. R. Rubenstein, Territory quality drives intraspecific patterns of extrapair paternity. *Behav. Ecol.* **18**, 1058–1064 (2007).

106. H. Kokko, A. Mackenzie, J. D. Reynolds, J. Lindström, W. J. Sutherland, Measures of inequality are not equal. *Am. Nat.* **154**, 358–382 (1999).

107. J. M. Marzluff, E. Neatherlin, Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biol. Conserv.* **130**, 301–314 (2006).

108. R Core Team, R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna, Austria, 2019). https://www.R-project.org/.

109. H. Schielzeth, Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**, 103–113 (2010).

110. D. Bates, M. Mächler, B. Bolker, S. Walker, Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).

111. S. S. Shah, D. R. Rubenstein, Data from "*Group* augmentation underlies the evolution of complex sociality in the face of environmental instability". Dryad. https://doi.org/10.5061/dryad.bvq83bkcj. Deposited 2 April 2023.