SCIENCE ADVANCES | RESEARCH ARTICLE

EVOLUTIONARY BIOLOGY

Prenatal environmental conditions underlie alternative reproductive tactics that drive the formation of a mixed-kin cooperative society

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

Although animal societies often evolve due to limited natal dispersal that results in kin clustering and facilitates cooperation among relatives, many species form cooperative groups with low kin structure. These groups often comprise residents and immigrants of the same sex that compete for breeding opportunities. To understand how these mixed-kin societies form, we investigated the causes and fitness consequences of dispersal decisions in male cooperatively breeding superb starlings (*Lamprotornis superbus*) inhabiting a climatically unpredictable environment. We show that the two alternative reproductive tactics—natal dispersal or philopatry—exhibit reproductive trade-offs resulting in equivalent lifetime inclusive fitness. Unexpectedly, an individual's tactic is related to the prenatal environment its parents experience before laying rather than the environment it experiences as a juvenile. Individuals that adopt the tactic not predicted by prenatal environmental conditions have lower fitness. Ultimately, climate-driven oscillating selection appears to stabilize mixed-kin societies despite the potential for social conflict.

INTRODUCTION

Dispersal decisions that enable individuals to escape unfavorable environmental conditions or reduce inbreeding risk also influence ecological and evolutionary processes like range expansion, gene flow, and the formation of animal societies (*1*). Limitations on natal dispersal—the permanent movement of an individual from its natal to breeding site—play a crucial role in social evolution by creating spatial clustering of kin that facilitates cooperative care of young by relatives (*1*, *2*). Natal dispersal may be limited due to environmental constraints, such as habitat saturation (*2*), or due to the benefits of philopatry, including those resulting from kin selection (*3*). Although most animal societies are therefore characterized by groups with high kin structure, an unexpected number of species form social groups with low kin structure (*4*) that consist of same-sex residents and immigrants who often compete for breeding opportunities (*5*, *6*). Since indirect fitness benefits [i.e., those gained by positively influencing the reproduction of relatives (*3*)] alone cannot explain the evolution of these mixed-kin societies, direct fitness benefits are thought to underlie their formation (*7*). Given the low genetic relatedness among same-sex individuals that compete for reproduction, social conflict in mixed-kin cooperative societies can be high and potentially destabilizing (*8*). Understanding how these societies form and remain stable despite their reduced kin structure and potential for high social conflict will require examining not only the causes and lifetime fitness consequences of individual reproductive decisions but also the mechanisms underlying dispersal decisions to determine why some individuals remain in their natal groups with kin while others do not.

Dispersal decisions are influenced not only by aspects of the social or ecological environment that individuals experience during their lifetime affect reaching nutritional independence (*9*–*11*) but also by how these factors affect their development early in life, including how they affect their parents before birth (termed prenatal factors, which can also influence development into the natal stage via carryover effects) (*12*, *13*). The influence of the parental environment can manifest via parental effects, modifications provided by the mother or father to the offspring during various stages of development (*14*), that alter offspring phenotype (*15*) through mechanisms such as hormonal and epigenetic manipulation (*16*, *17*), variable parental investment early in life (*18*), and other behavioral mechanisms such as aggression and eviction (*19*). Parental effects may be particularly important in cooperatively breeding species because parents may benefit from limited offspring dispersal by accruing more helpers or from reduced kin competition from when offspring disperse (*13*, *16*). Although dispersal in most social species tends to be sex-biased (*20*), in many cooperative breeders, individuals of one sex can adopt either of two alternative reproductive tactics: natal dispersal or philopatry (*6*, *9*). These sex-specific behavioral polyphenisms can exist either because (i) individuals face conditional constraints in adopting the tactic with higher fitness and must instead make "the best of a bad job" by choosing the tactic with lower fitness (*21*, *22*), or (ii) the relative fitness payoffs are environmentally dependent such that both tactics can persist within a population when conditions fluctuate (*23*, *24*). Consistent with the best-of-a-bad-job hypothesis, the fitness benefits of alternative reproductive tactics in cooperative breeders tend to be unequal in the short term (*25*–*28*). Yet, few studies have compared the lifetime inclusive fitness outcomes of alternative reproductive tactics, especially in mixed-kin societies where they are most common (*6*). Thus, the evolutionary mechanism underlying the formation of mixed-kin societies remains largely unknown and can only be revealed by considering the lifetime inclusive fitness consequences of alternative reproductive tactics.

Here, we leveraged a 16-year longitudinal dataset from Kenya to examine how reproductive tactics in male cooperatively breeding superb starlings (*Lamprotornis superbus*) are influenced by ecological and social factors in both the prenatal stage (including possible carryover effects into the natal stage) and the juvenile stage, and ultimately how these alternative tactics affect lifetime inclusive

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[1]Department of Ecology, Evolution, and Environmental Biology, Columbia University, 1200 Amsterdam Avenue, New York, NY 10027, USA. [2]Center for Integrative Animal Behavior, Columbia University, New York, NY 10027, USA.
*Corresponding author. Email: sss2254@columbia.edu

fitness. Superb starlings are plural cooperative breeders in which both sexes help (*29*, *30*), and although males tend to be more philopatric than females, these mixed-kin social groups have low but variable kin structure overall and within both sexes (*29*, *31*). Whereas resident females never breed in their natal groups, both resident and immigrant males can acquire breeding status (*29*). These savanna-dwelling birds inhabit one of the most variable and unpredictable environments on earth (*32*), where annual fluctuation in seasonal rainfall governs insect prey availability (*33*) and climate-driven oscillating selection affects many aspects of their social behavior and life history (*29*). In particular, rainfall experienced by the parents (prenatal rainfall) influences their offspring in terms of the clutch sex ratio (*30*), epigenetic modification of genes related to the avian stress response (*34*), and ultimately male reproductive decisions (*34*). Dry season rainfall experienced by individuals of both sexes also influences access to breeding opportunities (*35*) and helping behavior (*36*). In addition, the social environment (group size) also affects superb starling fitness, with increased survival (*37*) and reproductive success (*38*) in larger groups.

To examine the environmental causes of alternative reproductive tactics in superb starlings, we first investigated how ecological and social factors early in life during the prenatal stage (which could influence offspring development during the natal stage via carryover effects), as well as later in life during the juvenile stage, influence male dispersal decisions. We predicted that under harsh prenatal environmental conditions (low rainfall), dispersal of male offspring will be limited and helping behavior will be promoted. This effect may be intensified in smaller groups with a female-skewed sex ratio because group size is correlated with helper number and males help more than females (*38*). Similarly, male superb starlings that experience harsh environmental conditions as juveniles, the life history stage when dispersal decisions are likely made (*29*), would be more likely to remain in their natal group to avoid the costs of dispersal or reap the benefits of philopatry. Furthermore, a social environment conducive to higher survival (i.e., when in larger groups) and with greater access to reproductive opportunities (i.e., groups with female-skewed sex ratios) may also promote philopatry. In addition, we predicted that males that remain in their natal group may be more likely to provide alloparental care in their first year of life than males that ultimately disperse, since parents may manipulate males to stay and help to increase their own future reproductive success (*16*). In addition to potentially gaining indirect fitness benefits, males that adopt the tactic of not dispersing may also stand to gain future inclusive fitness benefits by increasing offspring recruitment in their natal group (*39*, *40*).

Next, to understand the fitness consequences of these alternative reproductive tactics, we compared access to reproductive opportunities, reproductive success, lifetime inclusive fitness, and survivorship of resident and immigrant males. According to the best-of-a-bad-job hypothesis, we predicted that the two alternative tactics would result in unequal lifetime inclusive fitness. Alternatively, if both dispersal and philopatry maximize individual fitness, then the two tactics would have equivalent lifetime inclusive fitness but exhibit reproductive trade-offs such that individuals would have lower lifetime fitness when they adopt the reproductive tactic not predicted by the prevailing environmental conditions. Ultimately, by linking the environmental causes and fitness consequences of alternative reproductive tactics in a cooperative breeder that experiences variable and unpredictable climatic oscillations, we will be able to determine how two fundamentally different reproductive phenotypes can persist and potentially give rise to mixed-kin cooperative societies.

RESULTS

Patterns of male dispersal

Consistent with previous reports in this species (*29*), we found that males were the primary philopatric sex; only 59 of 198 (30%) males in our marked social groups for whom we had data on dispersal status [i.e., excluding individuals already present in the groups at the beginning of 2001 (dispersal status unknown) and individuals not seen past 1 year of age (presumed dispersed)] were immigrants [compared to 121 of 248 (49%) females]. However, among all male breeders for whom we had complete life history data (i.e., males who bred at least once during their lifetime) ($N = 59$), more than half the individuals [30 of 59 (51%) males] were immigrants.

Ecological and social predictors of male dispersal

Next, we examined the role of ecological and social factors experienced by males during their juvenile stage (i.e., the period when dispersal occurs) and by their parents (i.e., prenatal stage) in influencing male dispersal decisions. We found that harsh prenatal ecological conditions were associated with limited dispersal such that males were less likely to disperse when they were born in years following low prenatal rainfall [$Z = 2.03$, $P = 0.04$, 95% confidence interval (CI) = 0.02 to 0.74; Fig. 1 and Table 1]. Since including natal stage rainfall in the model did not affect the results and prenatal ecological conditions did not affect hatchling mass before fledging (see the Supplementary Materials), this pattern was likely driven by dispersal, and not mortality, due to poor offspring condition during development. In contrast, the social environment and the ecological

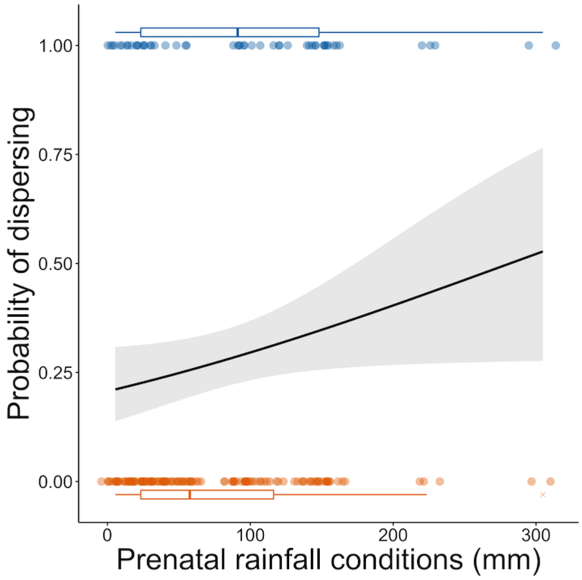

Fig. 1. Effect of prenatal rainfall on the probability of male superb starlings dispersing from their natal groups. Males were more likely to disperse when born following periods of higher prenatal rainfall ($N = 185$, $P = 0.04$). Model estimate (solid line) is bounded by the 95% CI (shaded areas). Circles indicate raw data and boxplots indicate median, upper, and lower quartiles, and range of prenatal rainfall for birds that dispersed (blue) and those that did not (orange).

Table 1. Factors affecting dispersal decisions of natal male superb starlings. Results of a generalized linear mixed model with a binomial response (dispersed versus remained) for natal males ($N = 185$). Since sex ratio and group size are highly correlated across consecutive breeding seasons, we only included the prenatal sex ratio and group size in the final model. Breeding season was included as a random effect. Random effects of social group, father ID, mother ID, and season (short versus long rains) had variance components equal to zero and were thus excluded from the final model to facilitate the computation of 95% CIs.

Effect	Estimate	SE	*Z* value	95% CI		*P* value
Intercept	−0.97	0.18	−5.45	−1.36	−0.60	<0.001
Prenatal rainfall	0.36	0.18	2.03	0.02	0.74	0.04
Prenatal sex ratio	−0.13	0.20	−0.68	−0.54	0.24	0.50
Prenatal group size	0.05	0.19	0.27	−0.34	0.44	0.78
Juvenile rainfall	−0.12	0.17	−0.69	−0.48	0.24	0.49

conditions experienced during the juvenile stage had no significant impact on the likelihood of males dispersing (Table 1 and table S1). Together, these results suggest that male dispersal is influenced more by (i) conditions experienced by their parents (and therefore the chicks early in life) than the conditions that they experience as juveniles and (ii) ecological rather than social factors. Last, we also found that males that subsequently dispersed were less likely to act as alloparents in their first year of life than males that subsequently remained in their natal group ($Z = -2.75$, $P = 0.006$, 95% CI = −2.23 to −0.41).

Fitness consequences of male dispersal decisions

We then explored the fitness consequences of the different male dispersal decisions. More than half of the males in the population [85 of 152 (56%) males] failed to accrue any inclusive fitness in their lifetimes (fig. S4) (*29*). Residents expectedly accrued higher indirect fitness than immigrants ($U = 2103$, $P = 0.02$; Fig. 2C) who were also unlikely to accrue meaningful indirect fitness in their natal group before dispersal (see the Supplementary Materials). In contrast, resident and immigrant males had similar direct and inclusive lifetime fitness (inclusive: $U = 2337$, $P = 0.22$; direct: $U = 2701$, $P = 0.59$; Fig. 2, A and B). Although this analysis does not quantify indirect fitness accrued by immigrants in their natal group before dispersing, natal males that dispersed accrued significantly lower fitness in their first year than residents, suggesting that immigrants into our study population also did not likely accrue considerable fitness before dispersing (see the Supplementary Materials). Nonetheless, to account for the possibility that immigrant males accrued at least some indirect fitness in their natal group before dispersal, we repeated our analysis after excluding fitness accrued by residents in their first year of life. We found qualitatively similar results, with residents and immigrants still having equivalent direct and inclusive fitness, as well as equivalent indirect fitness (see the Supplementary Materials). Furthermore, to account for any biases introduced in our analysis of lifetime fitness due to the exclusion of males that were still alive at the end of the study period, we repeated our analysis after excluding all males from birth cohorts that had at least one male still alive in the 2017 long rains breeding season and found that our results remained unchanged (see the Supplementary Materials).

Although the survival likelihood of immigrants after successful dispersal is not significantly different from that of residents ($Z = 0.06$, $P = 0.95$, 95% CI = −0.36 to 0.38) (fig. S6), our analysis did not account for any potential mortality of immigrants during dispersal. Although we expected the mortality of immigrants to be low because there are no floaters in this system (*29*), to account for potential immigrant mortality during dispersal, we ran a sensitivity analysis that added immigrants with zero fitness in 10% increments to the analyses of direct, indirect, and inclusive lifetime fitness. Our sensitivity analysis found that the mortality threshold for immigrants at which direct fitness would be higher in residents than immigrants was 70% (table S3). In addition, the mortality threshold for immigrants at which inclusive fitness would be higher in residents than immigrants was 20% when first-year resident males were included in the analysis, and 50% when first-year resident males were excluded from the analysis (table S3). These thresholds were much higher than the mean mortality for both immigrant and resident males, which was 4% (SD immigrants = 4%; SD residents = 3%) for each 6-month interval over their adult lifetime (table S4). Together, these results indicate that resident and immigrant males have similar lifetime inclusive fitness, even when accounting for the potential of mortality during dispersal.

Despite similar lifetime inclusive fitness, immigrants were more likely than residents to breed at least once in their lifetimes ($Z = 2.74$, $P = 0.006$, 95% CI = 0.27 to 1.64), had higher lifetime breeding effort (the number of breeding attempts as a proportion of an individual's adult lifespan) ($U = 2388$, $P = 0.006$), and began breeding at a younger age ($U = 604.5$, $P = 0.01$). In contrast, residents that did breed had higher nest success than immigrant breeders ($Z = 2.46$, $P = 0.01$, 95% CI = 0.27 to 2.34). In addition, both lifetime breeding effort and dispersal status (i.e., immigrant or resident) affected a male's likelihood of accruing some nonzero inclusive fitness during his lifetime (Fig. 3A and Table 2). Among males with some lifetime inclusive fitness, residents accrued higher inclusive fitness than immigrants with the same amount of lifetime breeding effort (Fig. 3B and Table 2).

Last, we assessed whether there were reproductive trade-offs for individuals that adopted the tactic not predicted by prenatal ecological conditions. Since we did not have precise rainfall data from the immigrants' natal sites (although rainfall is highly spatially correlated and temporally synchronous within the dispersal radius of our study site; table S4), we used a categorical measure of prenatal rainfall based on the mean long-term prebreeding rainfall at our study site (see Materials and Methods and the Supplementary Materials). Consistent with the idea of reproductive trade-offs and the hypothesis that the fitness consequences of alternative reproductive tactics depend on prenatal environmental conditions, we found that immigrant males were more likely to accrue nonzero lifetime inclusive fitness when born following periods of high prenatal

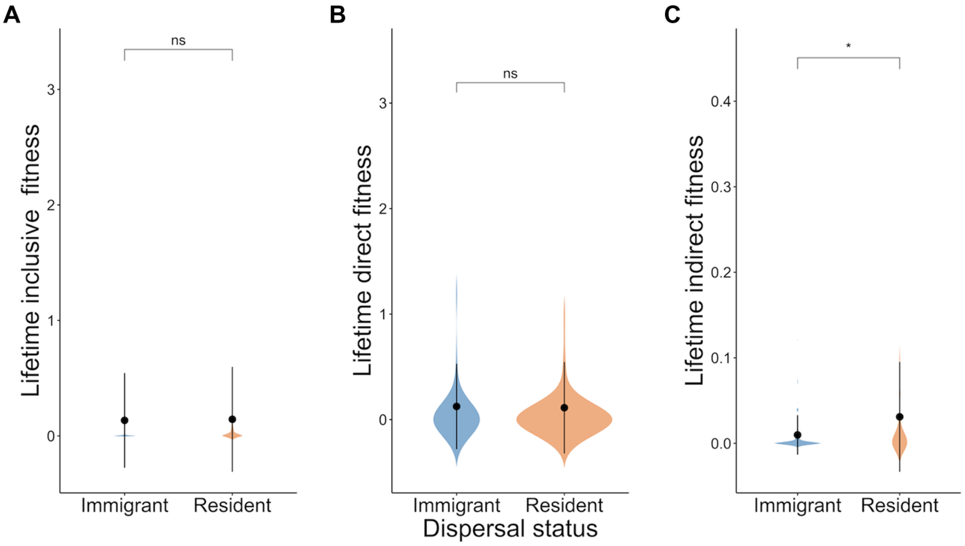

Fig. 2. Mean lifetime fitness of immigrant and resident male superb starlings. Immigrant and resident males ($N_{\text{immigrant}} = 59$, $N_{\text{resident}} = 99$) have equivalent lifetime (**A**) inclusive ($P = 0.22$) and (**B**) direct fitness ($P = 0.59$), although residents have higher (**C**) indirect fitness ($P = 0.02$). Black dots represent means and error bars denote SD. Shaded areas are kernel probability densities illustrating the distribution of the data. Asterisks indicate significance (ns, not significant; $P > 0.05$; $*P < 0.05$).

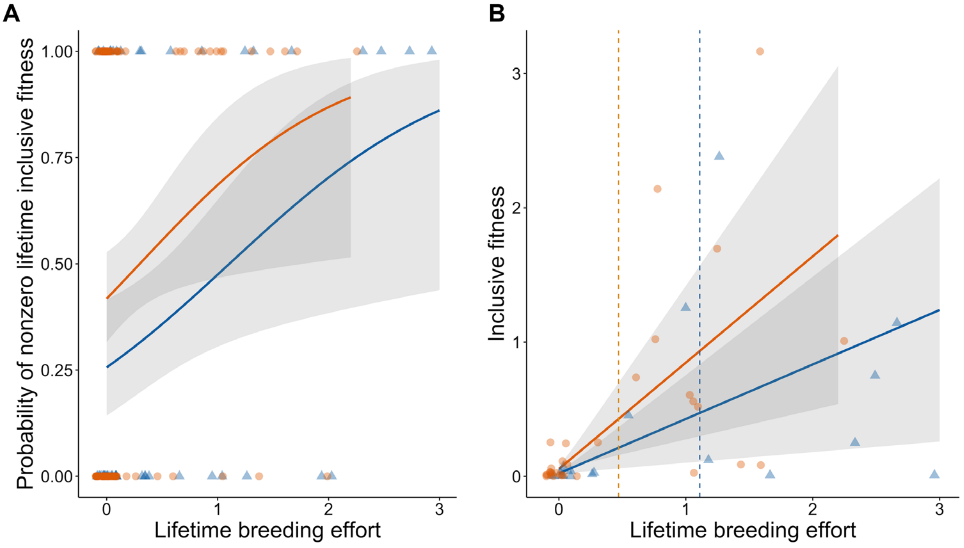

Fig. 3. Effect of reproductive trade-offs on lifetime inclusive fitness of male superb starlings. The effect of lifetime breeding effort and dispersal status (immigrants = blue, triangles; residents = orange, circles) on (**A**) the probability of accruing any nonzero lifetime inclusive fitness ($N = 152$) and (**B**) the value of nonzero lifetime inclusive fitness ($N = 67$). For visualization purposes, we excluded one individual with lifetime breeding effort greater than three SDs above the mean; this individual was included in the statistical analysis, although excluding it did not alter the results. Lifetime breeding effort (i.e., the number of breeding attempts as a proportion of an individual's adult lifespan) ($P = 0.001$) and dispersal status ($P = 0.04$) affected a male's likelihood of accruing some nonzero inclusive fitness during his lifetime. Among males with some lifetime inclusive fitness, residents accrued higher inclusive fitness than immigrants for the same amount of lifetime breeding effort ($P = 0.04$). Model estimates (solid lines) are bound by 95% CIs (shaded areas). Points indicate raw data. Dashed vertical lines indicate mean lifetime breeding effort.

rainfall, but that resident males were more likely to accrue nonzero lifetime inclusive fitness when born following periods of low prenatal rainfall (Fig. 4 and Table 3). Repeating this analysis using a continuous rather than a categorical value of rainfall collected at the Mpala Research Centre (MRC) yielded qualitatively similar results (fig. S5).

DISCUSSION

Although mixed-kin cooperative groups characterized by low relatedness are unexpectedly common (45% of all cooperatively breeding birds) (*4*), it remains unclear how these societies arise and are maintained given the potential for high social conflict among unrelated group members competing for reproductive opportunities. We

Table 2. Effects of lifetime breeding effort and dispersal status on lifetime inclusive fitness of male superb starlings. Results of generalized linear mixed models with (top) a binomial (zero versus nonzero) ($N = 152$) or (bottom) continuous, positive ($N = 67$) response variable for lifetime inclusive fitness of males. Social group was included as a random effect in the binomial model, but since it explained none of the variance and hindered the calculation of 95% CIs for the fixed effects, we removed it from the continuous model.

Response variable: Binomial (zero/nonzero) lifetime inclusive fitness

Effect	Estimate	SE	*Z* value	95% CI		*P* value
Intercept	−1.10	0.35	−3.14	−1.86	−0.44	0.002
Lifetime breeding effort	1.03	0.31	3.28	0.46	1.72	0.001
Dispersal status	0.78	0.39	2.02	0.01	1.56	0.04

Response variable: Continuous, positive lifetime inclusive fitness

Effect	Estimate	SE	*t* value	95% CI		*P* value
Intercept	0.02	0.01	2.04	0.01	0.06	0.04
Lifetime breeding effort	0.55	0.15	3.73	0.33	0.95	<0.001
Dispersal status	0.04	0.02	2.27	−0.00	0.08	0.03

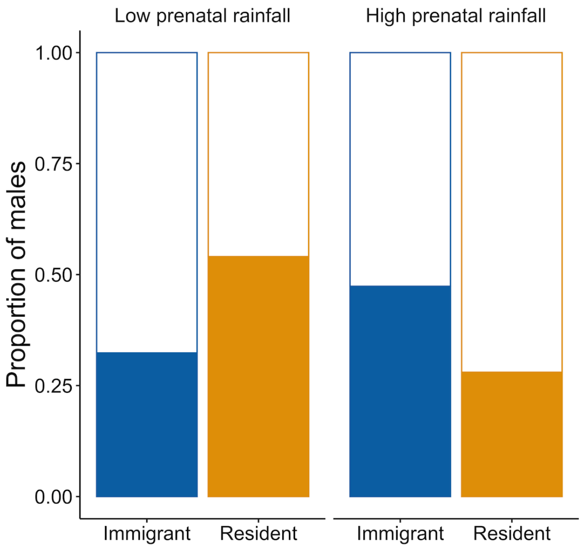

Fig. 4. Fitness consequences of male superb starlings adopting the tactic not predicted by the prevailing prenatal environmental conditions. The effect of prenatal rainfall and dispersal status (immigrants = blue; residents = orange) on the probability of accruing any nonzero lifetime inclusive fitness (fill = nonzero fitness; no fill = zero fitness) ($N = 152$). Immigrants were more likely to accrue nonzero lifetime inclusive fitness when born following periods of high prenatal rainfall, whereas residents were more likely to accrue nonzero lifetime inclusive fitness when born following periods of low prenatal rainfall ($P = 0.02$).

examined the environmental causes and inclusive fitness consequences of dispersal decisions in male superb starlings living in a climatically variable and unpredictable savanna environment (*32*, *37*), for whom philopatry and dispersal can both be pathways to reproductive opportunities (*29*). We found that dispersal in males is influenced by their parents' prenatal ecological environment rather than the environment that the males experience as juveniles, suggesting that parental effects during offspring development or carryover effects early in life play an important role in governing dispersal decisions. Ultimately, natal dispersal and philopatry had similar lifetime inclusive fitness outcomes, meaning that they are two equivalent, alternative male reproductive tactics. Yet, the two tactics showed reproductive trade-offs—immigrants had greater access to reproductive opportunities via the acquisition of breeding positions, whereas residents that bred had higher reproductive success. When males adopted a tactic not predicted by prevailing prenatal environmental conditions, their lifetime inclusive fitness was reduced. Together, these results suggest that environmental variability driven by oscillating climatic conditions experienced by parents before laying may help maintain a reproductive polyphenism with equivalent lifetime inclusive fitness, which ultimately enables the formation and persistence of a mixed-kin cooperative society in an unpredictable environment. Our study is one of very few to use lifetime inclusive fitness rather than just point-in-time reproductive rates, contributing a more robust understanding of the formation and maintenance of cooperative societies.

Unlike in other cooperatively breeding species where conditions experienced during the juvenile stage shape dispersal decisions (*9*, *10*, *41*), male dispersal in superb starlings was only governed by prenatal ecological conditions. Although we were unable to directly distinguish between dispersal and mortality, several lines of evidence—including the modal age at which natal males disappear from our study population, the modal age at which immigrants arrive into our study population, the age at which males reach sexual maturity, the close match in the proportions of dispersers and immigrants, the increased likelihood of dispersal following benign ecological conditions, no effect of prenatal ecological conditions on hatchling mass before fledging, and the high likelihood of post-fledgling survival from year-to-year (*37*)—strongly suggest that the pattern we observed is driven by dispersal, and not mortality (see Materials and Methods and the Supplementary Materials for further details). The effect of prenatal conditions on dispersal suggests that parental effects during development influence the dispersal phenotype of male superb starlings, a result that has been suggested previously for male reproductive opportunities in this species (*34*). Parental effects, which can result from physiological or molecular modifications to offspring during development (*15*), may be particularly important in cooperatively breeding species (*14*) and species inhabiting

Table 3. Effects of male superb starlings adopting the tactic not predicted by the prevailing prenatal ecological conditions on the likelihood of gaining nonzero inclusive fitness during their lifetimes. Results of a generalized linear mixed model with a binomial response (zero versus nonzero lifetime inclusive fitness) variable for males ($N = 152$). Social group was included in the model as a random effect.

Effect	Estimate	SE	*Z* value	95% CI		*P* value
Intercept	−0.10	0.46	−0.23	−1.03	0.80	0.82
Categorical prenatal rainfall	−0.63	0.59	−1.08	−0.80	0.52	0.28
Dispersal status	−0.84	0.64	−1.31	−2.13	0.40	0.19
Categorical prenatal rainfall × Dispersal status	1.74	0.77	2.25	0.24	3.29	0.02

unpredictable environments (*42*). While the specific physiological mechanisms of early-life parental effects on dispersal remain unknown for this species, previous studies have demonstrated an effect of maternal condition on offspring sex allocation, maternal investment in eggs, and DNA methylation in superb starlings (*30*, *34*) and other vertebrates (*42*, *43*). Studies of two other avian species, western bluebirds (*Sialia mexicana*) and great tits (*Parus major*), found an effect of maternal androgen deposition on offspring dispersal in response to ecological conditions (*12*, *13*). Viviparous lizards (*Lacerta vivipara*) show a similar effect (*44*), and maternal hormones have also been shown to increase helping behavior in subordinate female meerkats (*Suricata suricatta*) (*16*).

Parental effects can also manifest during the natal and early postnatal stages (*45*) because environmental conditions experienced by parents before birth may affect their behavior toward their offspring after birth, such that dispersal is driven purely by behavioral interactions before offspring becoming self-sufficient (*19*). Carryover effects may also influence offspring phenotypes, including competitive ability (*46*) or personality traits (*47*), which subsequently affect dispersal decisions. Although we were only able to examine the effect of prenatal conditions on nestling mass, there may be more subtle parental effects on offspring condition early in life that govern their subsequent reproductive tactics and lifetime fitness (*48*). Since conditions preceding the breeding season are known to affect behavioral phenotypes of adult superb starlings during the breeding season [e.g., breeding status (*35*) and helping behavior (*36*)], it is likely that prenatal conditions govern development throughout early life. Although directly examining the role of factors such as helper number, territory quality, and average relatedness to group members (i.e., potential for indirect benefits) was outside the scope of the present study, all three factors are correlated with group size in this species (*29*, *36*, *37*), which did not have a significant effect on dispersal decisions. Ultimately, further work in this and other cooperatively breeding species should examine the mechanisms by which environmentally mediated parental effects at different developmental stages might influence future reproductive tactics adopted by the offspring.

Parental effects can be selfish, to manipulate offspring phenotype to increase parental fitness, or anticipatory, to maximize offspring fitness (*14*). We know that offspring sex ratio in superb starlings is male-biased when mothers are in poorer body condition following harsher prenatal conditions, a pattern that suggests that females maximize their inclusive fitness in an unpredictable environment by investing in the sex with lower fitness variance (males in the case of superb starlings) (*30*). However, our results suggest that mothers could also be influencing cooperative behavior in their offspring because males that participated in alloparental care in their first year of life were subsequently more likely to remain in their natal group. Male superb starlings are more likely to become alloparents and help more than females (*38*), and alloparents buffer the detrimental effects of harsh environmental conditions on reproductive success in this species (*36*). Thus, parental effects promoting alloparental behavior following harsher prenatal conditions might serve to selfishly increase the parents' short-term future reproductive success and indirectly limit dispersal of male offspring (*16*). Although males born following benign prenatal conditions could, conversely, be more likely to disperse so as to reduce kin competition, this seems less probable because kin competition has actually been shown to decrease under benign environmental conditions in other cooperatively breeding species (*49*). In addition, our results are consistent with the hypothesis that parental effects on dispersal in males are anticipatory because when males adopted the tactic predicted by the prevailing prenatal ecological conditions, they were more likely to accrue some inclusive fitness in their lifetimes. Since more than half of superb starling males fail to accrue any fitness in their lifetimes, largely due to high nest predation pressure (*29*), securing any amount of nonzero lifetime fitness is crucial in this species, an idea consistent with the bet-hedging hypothesis proposed for this (*38*) and other social species (*50*–*52*). Furthermore, increased alloparental care by males that subsequently remained in their natal group may result not only in higher indirect benefits in their first year of life but also in increased likelihood of future inclusive fitness benefits as has been shown in other cooperatively breeding species (*39*, *40*). Males born following harsh prenatal conditions thus appear to benefit from avoiding the costs of dispersal and remaining in their natal group (*11*, *53*), whereas males born following benign conditions might be better able to cope with the costs of dispersal and maximize their fitness by immigrating into another social group (*27*).

In contrast to other studies in kin-only cooperatively breeding societies (*25*, *26*, *54*–*56*), we found that the two reproductive tactics adopted by males—natal dispersal and philopatry—have equivalent lifetime inclusive fitness in a mixed-kin cooperative society. Although resident males had significantly higher lifetime indirect reproductive success than immigrants, an expected result given the kin structuring among males in superb starling social groups (*29*), this was more than balanced out by the relatively larger contribution of lifetime direct fitness, even when accounting for potential mortality during dispersal. While it was not logistically possible to compare the fitness of resident and dispersing males born to the same social group, our approach of comparing resident to immigrant males has proven informative in other avian studies (*40*). Although we do not have an estimate of dispersal mortality in this species, we have never observed floaters in our study area, suggesting that individuals move from their natal group to their nonnatal group over a relatively short time period and likely do not incur significant mortality in transit (*29*). Yet, when even accounting for this possibility, immigrant and resident males still had equivalent lifetime inclusive fitness. Following successful dispersal, our results show that the survival likelihood of immigrants is similar to that of resident males. Furthermore, males that remain in their natal group provide more alloparental care and accrue significantly higher indirect fitness in their first year of life than natal males that subsequently disperse. Since most males disperse at around 1 year of age, this suggests that immigrants are unlikely to accrue considerable indirect fitness in their natal group before dispersing. Similar variation in alloparental effort and indirect fitness in relation to dispersal tactics has been shown in other cooperatively breeding species (*39*, *40*).

Last, we also show that the equivalent lifetime inclusive fitness outcomes of the two dispersal tactics are due to a reproductive trade-off, an idea that has been proposed theoretically (*24*) but rarely tested empirically. Although immigrant male superb starlings had greater access to reproductive opportunities via the acquisition of dominant breeding positions within the group, residents that acquired breeding positions were more likely to successfully fledge young. Resident males can therefore afford to have lower access to breeding opportunities over their lifetimes since they have higher nest success. This higher nest success is likely due to greater alloparental care at nests of resident males who have more kin in the group to act as helpers than do immigrants (*57*–*59*). Thus, for superb starling males, philopatry leads to lower reproductive quantity but higher quality, whereas dispersal results in higher reproductive quantity but lower quality. Since immigrants and residents are equally likely to survive from one breeding season to the next, these differences in reproductive quality and quantity are unrelated to longevity (*25*). Together, these results suggest that the two male alternative dispersal tactics are equivalent in terms of lifetime inclusive fitness and refute the hypothesis that remaining in the natal group—the tactic favored following harsh prenatal conditions—is simply making the best of a bad job (*21*, *22*). The coexistence of resident and immigrant males in cooperative social groups has been shown to be similarly facilitated by equivalent reproductive rates in spotted hyenas (*Crocuta crocuta*) (*6*) and inclusive fitness at different age stages in dwarf mongooses (*Helogale parvula*) (*60*), both species that live in mixed-kin societies. However, to the best of our knowledge, ours is the first study in a cooperatively breeding vertebrate to demonstrate equivalent lifetime inclusive fitness outcomes of alternative dispersal tactics.

This behavioral polyphenism in male reproductive tactics is likely maintained by a flexible response to high and unpredictable environmental variability (*23*). A temporally variable and unpredictable environment has been shown both theoretically (*24*) and empirically (*61*) to generate conditional strategies that result in a developmental switch between alternative tactics. If alternative reproductive tactics have a strong genetic (or perhaps epigenetic) basis (*62*, *63*), environmental variability can reverse the selective differential between the two tactics from one year to the next, resulting in alternative tactics with equivalent fitness outcomes (*24*, *64*). The savanna habitat inhabited by superb starlings has high temporal ecological variability (*32*, *38*) that may allow both dispersal tactics to persist as conditions oscillate unpredictability from year to year, resulting in the formation of mixed-kin cooperative groups. Spotted hyenas (*65*) and dwarf mongooses (*60*) experience the same unpredictable African savanna environments as superb starlings, suggesting that environmental uncertainty—and perhaps oscillating selection pressures more generally—maintains alternative dispersal tactics and leads to the formation of and/or stabilizes societies with low kin structure. Oscillating selection may be particularly important in arid and semiarid environments where climatic variability is high (*64*) and may help explain the evolution of both mixed-kin societies and plural breeding more broadly. Many other plural cooperatively breeding birds across the globe live in harsh arid and semiarid environments characterized by unpredictable variation in rainfall and food resources (*66*–*72*). More generally, any variation in the social or ecological environment that results in reversals of selective differentials of alternative dispersal tactics may lead to the rise of mixed-kin societies in cooperatively breeding species. While we do not yet know whether dispersal has a genetic basis in superb starlings—although there are indications of a potential epigenetic basis (*34*)—our results suggest that the two tactics face oscillating selection since the relative lifetime inclusive fitness of the two tactics fluctuates in response to prenatal environmental conditions. Ultimately, identifying the mechanism by which prenatal parental effects lead to developmental differences that determine male reproductive tactics will be important for understanding the role that environmentally driven selection pressures play in shaping behavioral polyphenisms in this and other social species.

In summary, we have shown that natal dispersal and philopatry in male cooperatively breeding superb starlings represent two alternative reproductive tactics with equivalent lifetime inclusive fitness. The tactics are likely mediated by parental effects before and during development and are maintained by oscillating selection pressures characteristic of their variable and unpredictable savanna environment. Our study suggests a direct link between environmental uncertainty, behavioral polyphenism, and the evolution of mixed-kin animal societies that cannot be explained by indirect fitness benefits alone. Our work also underscores the importance of prenatal environmental conditions and parental effects in determining offspring phenotype, especially in cooperative societies where early life conditions have direct implications on the future fitness of both parents and offspring. Moreover, the direct benefits derived from environmental selective pressures appear to play a significant role in the evolution and maintenance of cooperative societies, alongside or in the absence of kin selection. Ultimately, understanding how fluctuation in early-life environmental conditions helps mediate reproductive trade-offs and lifetime fitness is critical in an era of rapid anthropogenic climate change because climatic uncertainty is only likely to increase across much of the globe for the foreseeable future.

MATERIALS AND METHODS

Data collection

Nine superb starling social groups have been monitored continuously since 2001 at the MRC, Kenya (0° 17′N 37° 52′E) (*29*). The study population is distributed across a 9-km distance from north to south. Groups (mean size ± SD = 22 ± 12 individuals) defend stable territories year-round and consist of breeding (means ± SD = 2.70 ± 1.49 pairs per group) and nonbreeding individuals, some of whom act as alloparents that guard and/or provision the young (*29*, *36*). Birds breed twice a year during the long (March–June) and short rains (October–November) (*29*). We used data from the beginning of the 2001 short rains breeding season to the end of the 2017 long rains breeding season ($N = 33$ breeding seasons over 16 years), since not all birds in the study population were banded in the first long rains breeding season.

Birds were banded 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 (*35*). If birds were banded after fledging, age was assessed via eye color as "fledgling" (black eyes), "subadult" (less than 1 year of age; cloudy eyes), or "adult" (1 year of age or older; white eyes) (*37*). Individuals were classified as "natal" or "immigrant" based on age at banding, as well as genetic parentage data from 15 microsatellite markers analyzed in Cervus v3.0 (*73*) with methods described previously for this species (*33*, *74*, *75*). Natal individuals were defined as those either banded as hatchlings in the nest or as juveniles whose parents were genetically identified as members of the same group. Immigrants were defined as those banded as juveniles or older whose parents were not genetically identified as belonging to the same group. In addition to parentage, we used the same microsatellite markers to estimate pairwise relatedness (*76*) between all individuals with the R package related (*77*). Sex was determined genetically (*78*) as previously described for this species (*75*).

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 (total observation time per nest: means ± SD = 314.33 ± 248.82 min, $N = 391$). All superb starlings within 30 m of the nest were identified, and their times of arrival and departure were recorded (*75*). Parents are the primary nest builders, and only the mother incubates the eggs (*75*). All other members of the social group seen visiting or guarding the nest were categorized as alloparents (*36*).

Census data were used to estimate group size and operational sex ratio (calculated by dividing the number of males by the sum of the number of males and immigrant females in the group to estimate potential mate competition; 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 marked as either present or absent in its social group twice a year in 6-month increments. Individuals not seen for five or more breeding seasons (i.e., 2.5 years) were assumed to be dead (*31*, *37*). We inferred that the dispersal window for males is between fledging and around 1 year of age (age of sexual maturity) using four lines of evidence: (i) the modal age at which males disappear from their natal group (6 months); (ii) the categorical age of immigrant males dispersing into the study population (≥1 year); (iii) the likelihood of males being detected in the census in their first year of life [30% in the period preceding and during the short rains breeding season (July–November) and 52% in the period preceding and during the long rains breeding season (December–June), which directly matches the intraannual variation in census effort]; and (iv) the minimum age of first breeding by resident males (1.5 years) (see the Supplementary Materials for details). If a male was observed in its natal group after 1 year of age, then we classified it as a resident; if not, we classified it as having dispersed. Although we could not distinguish between dispersal and mortality, the positive relationship between the likelihood of dispersal and benign ecological conditions (see Results) suggests that these males did disperse, since we would have expected a negative relationship if mortality was higher following harsh ecological conditions as has been shown in this study system (*37*). In addition, we found no association between hatchling mass before fledging (measured at 10 days of age) and variation in ecological conditions, further suggesting that this pattern is driven by dispersal and not mortality, unlike in other studies where the effect of harsh ecological conditions on post-fledging survival has been shown to be mediated by hatchling mass pre-fledging (*79*, *80*) (see the Supplementary Materials). Following the same lines of evidence, immigrant males were assumed to have entered the group at about 1 year of age (see the Supplementary Materials). There is no evidence of breeding dispersal (i.e., dispersal between two successive breeding attempts) in our study population (*29*).

We considered the period between the end of the breeding season when a male is born to the beginning of the breeding season 1 year later (i.e., its juvenile stage) as its "dispersal window" (see the Supplementary Materials for more details). Ecological and social conditions experienced by juveniles in this period were termed "juvenile stage conditions." In contrast, ecological and social conditions experienced by parents in the prebreeding period preceding the breeding season of an individual's birth were termed "prenatal conditions." The breeding season of an individual's birth was termed its "natal stage." A "breeding season" was defined as the period between 2 weeks before the first nest and 2 weeks after the last nest of the season. The period between the two consecutive breeding seasons was termed the "prebreeding period." Daily rainfall was measured using an automated Hydrological Services TB3 Tipping Bucket Rain Gauge at MRC (*81*), supplemented by a manual gauge at the same location when the automated gauge failed (*38*). To calculate prenatal, natal, and juvenile rainfall, we summed the rainfall within the relevant stages of an individual's lifetime, as defined above (fig. S1). Rainfall from different life stages was not correlated (Pearson's $r < 0.15$).

Data analysis

Our dataset comprises individuals that (i) are known to have been born in the groups (natal), (ii) are known to have immigrated into the group (immigrant), and (iii) were already part of the group in 2001 when the study population was banded. All individuals are either known to have disappeared (classified as either "dead" or "dispersed" depending on age at disappearance) or were still present in the study population in 2017. Natal individuals that did not disperse were termed "residents." Thus, individuals with "known complete life histories" are natal and immigrant individuals who were classified as dead.

Using data from individuals with known complete life histories and natal individuals that are still alive and present in the study population past 1 year of age ($N_{\text{male}} = 198$, $N_{\text{female}} = 248$), we first examined patterns of male dispersal by quantifying the proportion of immigrant adult males and females in the study population. We then determined how breeding opportunities were shared between immigrants and residents by calculating the proportion of immigrant breeders of both sexes in the study population using data from breeders with known complete life histories ($N_{\text{male}} = 59$, $N_{\text{female}} = 121$).

Next, using data from all natal males—including those classified as dispersed or dead and those still present in the study population past the age of 1 year in 2017—we investigated the effect of ecological and social conditions during the prenatal and juvenile stages on the likelihood of a male dispersing. We built a generalized linear mixed model (GLMM) with a binomial error structure and "logit" link function. We used the binomial response of reproductive tactic (1 = dispersed, 0 = remained) as the dependent variable ($N_{\text{dispersed}} = 52$, $N_{\text{remained}} = 133$). Fixed effects, which were standardized using *z* scores (*82*), included prenatal and juvenile stage rainfall, prenatal group size, and prenatal sex ratio. Since group size and sex ratio were highly correlated across consecutive breeding seasons and thus highly correlated across the prenatal and juvenile stages (group size: Pearson's $r = 0.95$; sex ratio: Pearson's $r = 0.80$), we were unable to distinguish between the effects of prenatal and juvenile stage social factors and only included prenatal group size and sex ratio in the final model. However, prenatal rainfall and juvenile stage rainfall were not correlated (Pearson's $r = 0.12$; fig. S3) and could therefore both be included in the final model. All two-way interactions were included in the model, but later removed if their effect was not significant (*83*). Breeding season of birth, season (long versus short rains), social group, mother ID, and father ID were included as random effects. All random effects other than breeding season of birth had variance components equal to zero and were thus removed from the final model to facilitate the computation of 95% CIs. This had no effect on the estimates of fixed effects (*84*). Furthermore, to investigate the relationship between alloparental care provided by males before reaching 1 year of age and their subsequent reproductive tactic, we used a GLMM with a binomial error structure and logit link function with alloparental status (ever alloparent/never alloparent) as the response variable, reproductive tactic (dispersed/remained) as a fixed effect, and social group as a random effect for all natal males ($N = 185$).

Last, we sought to understand the fitness consequences of the alternative reproductive tactics using data from males with known complete life histories (i.e., only including males classified as dead). Although it was not possible to compare the fitness consequences of the alternative reproductive tactics adopted by males born in the same social group (since dispersers rarely remain within the study population; only three dispersing males were resighted in the study population in 16 years), we compared access to reproductive opportunities, reproductive success, lifetime inclusive fitness, and survivorship of resident and immigrant males. Previous studies of cooperatively breeding birds have used the same approach (*40*). Access to reproductive opportunities was quantified as (i) the likelihood of a male ever breeding in its lifetime (GLMM with a binomial error structure and logit link function, with social group as a random effect) ($N_{\text{immigrant}} = 59$, $N_{\text{resident}} = 103$); (ii) lifetime breeding effort or the number of breeding attempts as a proportion of an individual's adult lifespan (Mann-Whitney test with continuity correction) ($N_{\text{immigrant}} = 59$, $N_{\text{resident}} = 103$); and (iii) for males that bred at least once ($N_{\text{immigrant}} = 30$, $N_{\text{resident}} = 29$), the age at first breeding (Mann-Whitney test with continuity correction). To evaluate the likelihood of a male obtaining any reproductive success in their lifetimes, we modeled the effect of dispersal status on nest success (1 = succeeded, 0 = failed) using a GLMM with a binomial error structure and logit link function ($\mathrm{N}_{\text{succeeded}} = 49$, $\mathrm{N}_{\text{failed}} = 229$). Since some males nested multiple times in their lifetimes, we included individual ID as a random effect in the model along with social group and breeding season.

Following Green and Hatchwell (*40*), we calculated lifetime inclusive fitness (I) as the sum of lifetime direct and indirect fitness according to the equation

$$I = \left[\sum_{j=1}^{J} M_j E R - \frac{\sum_{j=1}^{J}\sum_{n=1}^{N_j}\sum_{m=1}^{M_j} e_{nj}\, r_{mnj}}{2}\right]_{\text{direct fitness}} + \left[\sum_{o=1}^{O}\sum_{m=1}^{M_o} e_o\, r_{mo}\right]_{\text{indirect fitness}} \tag{1}$$

where direct fitness was calculated as the product of the number of fledglings per nest (M_j), paternal care effort ($E = 0.5$, the other half being attributed to the mother), and the mean offspring-father relatedness ($R = 0.5$) summed over all successful nests (J), minus half of the indirect fitness attributed to alloparents (the other half being subtracted from the mother's direct fitness). Indirect fitness attributed to alloparents at each nest was calculated as the product of the mean alloparental effort at a nest per social group per breeding season (e_{nj}) and the alloparent's relatedness to the fledglings (r_{mnj}), summed over all fledglings (M_j) and alloparents at the nest (N_j) for all successful nests (J). Alloparents with $r_{mnj} \leq 0$ received no indirect fitness. Indirect fitness of the focal male was similarly calculated as the product of the mean alloparental effort (e_o) and its relatedness to the fledglings (r_{mo}), summed over all the nests he visited in his lifetime (O). We used population means instead of individual measures of alloparental effort because total observation time for nests varied. Alloparental effort was calculated as the proportion of time an individual spent attending a nest (both guarding and bringing food) relative to the length of the observation period (*36*).

We compared the lifetime inclusive, direct, and indirect fitness of resident and immigrant males using a Mann-Whitney test with continuity correction ($N_{\text{immigrant}} = 53$, $N_{\text{resident}} = 99$). Since males accrue indirect fitness as juveniles, we excluded males born in 2001 short rains, the earliest breeding season in our dataset, during which limited focal observations were conducted at nests. To account for indirect fitness accrued by immigrant males in their natal group before dispersing, we additionally compared the fitness (i) of residents and immigrants after excluding fitness accrued by residents during the first year of their life (see the Supplementary Materials) and (ii) of natal males accrued in the first year of life that remained in their natal group to that accrued by natal males that subsequently dispersed (see the Supplementary Materials). To account for mortality during dispersal, we conducted a sensitivity analysis by adding incremental proportions of immigrants with zero lifetime fitness to the dataset (see the Supplementary Materials).

To determine whether differences in reproductive access and success between resident and immigrant males affected their lifetime inclusive fitness, we used GLMMs to model the effect of lifetime breeding effort and dispersal status on lifetime inclusive fitness of males. The first model had a binomial response (zero/nonzero lifetime inclusive fitness) and a logit link function ($N_{\text{immigrant}} = 53$, $N_{\text{resident}} = 99$). The second model had a continuous dependent variable of all nonzero inclusive fitness observations ($N_{\text{immigrant}} = 20$, $N_{\text{resident}} = 47$) with an "identity" link function and a gamma error distribution. The fixed effects for both models were lifetime breeding effort and dispersal status. Social group was included as a random effect but later removed from the second model, where its variance component equaled zero, to facilitate the computation of 95% CIs (*84*).

We also built a GLMM to investigate the lifetime fitness consequences of adopting the tactic not predicted by the prevailing environmental conditions, with a binomial response variable (zero/nonzero lifetime inclusive fitness) and prenatal rainfall and dispersal status as fixed effects ($N_{\text{immigrant}} = 53$, $N_{\text{resident}} = 99$). Although we did not have precise rainfall data from the immigrants' natal sites, we used monthly rainfall data from three sites within the dispersal radius (~30 km) (*29*) of our study population (MRC)—UHURU Central (12 km from MRC) (*85*), UHURU North (20 km from MRC) (*85*), and Nanyuki (38 km from MRC) (East African Livestock Early Warning System)—to demonstrate high spatiotemporal correlation of prenatal rainfall for immigrant and resident males (table S5). Nonetheless, to take a more conservative approach, we used a categorical measure based on mean long-term prebreeding rainfall at MRC ("low prenatal rainfall": rainfall ≤ long-term mean; "high prenatal rainfall": rainfall > long-term mean). Rainfall within 10 mm of the long-term mean was categorized as "low" to account for the accuracy of the rainfall gauge (*81*).

Last, we used a time-varying Cox proportional hazards model to determine whether dispersal status affected male survival ($N_{\text{immigrant}} = 59$, $N_{\text{resident}} = 103$) (*37*). The model was built using the R package survival (*86*). We checked that our dataset did not violate the proportional hazard assumption using the "cox.zph" function. Social group was included as a random factor. We performed all data analysis in R (*87*); variance inflation factor < 2 for all fixed effects in GLMMs, excluding interaction terms (*88*).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at https://science.org/doi/10.1126/sciadv.abk2220

View/request a protocol for this paper from *Bio-protocol*.

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Shailee S. ShahDustin R. Rubenstein

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