Main Manuscript for

Prenatal environmental variation, alternative reproductive tactics and the formation of a mixed-kin cooperative society

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1 **Abstract**

2 Although animal societies often evolve due to limited natal dispersal that results in kin clustering

3 and facilitates cooperation among relatives, many species form cooperative groups with low and

4 variable kin structure. To understand how such mixed-kin societies form despite their potential

5 for social conflict, we investigated the environmental causes and subsequent fitness

6 consequences of dispersal decisions in male cooperatively breeding superb starlings

7 (*Lamprotornis superbus*) living in a climatically unpredictable environment. We show that the

8 two alternative reproductive tactics—natal dispersal vs. philopatry—exhibit reproductive

9 tradeoffs resulting in equal lifetime inclusive fitness. The tactic an individual adopts is governed

10 by the environment its parents experience prior to laying rather than the environment it

11 experiences as an adolescent. When individuals adopt the tactic not predicted by early life

12 environmental conditions, their fitness is reduced. Ultimately, climate-driven oscillating

13 selection may help stabilize mixed-kin animal societies by influencing alternative reproductive

14 trajectories early in life.

15

16 **Main Text**

17 **Introduction**

18 Dispersal decisions that enable individuals to escape unfavorable environmental conditions or

19 reduce inbreeding risk also influence ecological and evolutionary processes like range expansion,

20 gene flow, and the formation of animal societies (Matthysen, 2012; Taylor, 1992). Limited natal

21 dispersal—the permanent movement of an individual from its natal to breeding site—plays a

22 crucial role in social evolution by creating spatial clustering of kin that facilitates cooperative

23 care of young by relatives (Emlen, 1994; Hamilton, 1964a, 1964b). Although most animal

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24   societies are therefore characterized by groups with high kin structure, a surprising number of

25   species form social groups with low kin structure (Riehl, 2013) that consist of same-sex residents

26   and immigrants, which often compete for breeding opportunities (Baglione et al., 2002; Davidian

27   et al., 2016; Kaiser et al., 2018; Reyer, 1980). Since kin selection alone cannot explain the

28   evolution of these mixed-kin societies (Liu et al., 2015; Riehl and Jara, 2009; Rubenstein and

29   Abbot, 2017), direct reproductive or survival benefits may underlie their formation (Baglione et

30   al., 2002; Clutton-Brock, 2002; Kaiser et al., 2018). Understanding how mixed-kin cooperative

31   societies form and remain stable despite their reduced kin structure and potential for high social

32   conflict will require examining the causes and lifetime fitness consequences of individual

33   dispersal decisions to determine why some individuals choose to remain in their natal groups

34   with kin while others do not.

35

36   Dispersal decisions are influenced not only by aspects of the social or ecological environment

37   that individuals experience after birth (termed postnatal factors) (Baglione et al., 2006; Eikenaar

38   et al., 2010; Nelson-Flower et al., 2018), but also by how these factors impact their development

39   early-in-life or affect their parents prior to birth (termed prenatal factors) (Duckworth, 2009;

40   Tschirren et al., 2007). The influence of prenatal factors typically manifests via parental effects,

41   modifications provided by the mother or father to the offspring during development that alter

42   offspring phenotype (Mousseau and Fox, 1998). Parental effects may be particularly important in

43   cooperatively breeding species (Russell and Lummaa, 2009), where parents can limit offspring

44   dispersal by influencing helping behavior or promote dispersal to reduce kin competition

45   (Dantzer et al., 2019; Duckworth, 2009; Silk and Brown, 2008). Although dispersal in most

46   social species tends to be sex-biased (Greenwood and Harvey, 1982), in many cooperative

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47   breeders, individuals of one sex can adopt either of two alternative reproductive tactics: natal

48   dispersal or philopatry (Davidian et al., 2016; Nelson-Flower et al., 2018). Such sex-specific

49   behavioral polymorphisms can exist either because (i) individuals face conditional constraints in

50   adopting the tactic with higher fitness and must instead make "the-best-of-a-bad-job" by

51   choosing the tactic with lower fitness (Dawkins, 1980; Koprowski, 1993), or (ii) the relative

52   fitness payoffs are environmentally-dependent such that both tactics can persist within a

53   population when conditions fluctuate from year-to-year (Moran, 1992; West Eberhard, 1989).

54   Consistent with the "best-of-a-bad-job" hypothesis, the fitness benefits of alternative

55   reproductive tactics in cooperative breeders tend to be unequal in the short-term (Bergmüller et

56   al., 2005; Ekman et al., 2001; Kingma et al., 2016; Walters et al., 1992). Yet, few studies have

57   compared the lifetime inclusive fitness outcomes of alternative reproductive tactics, especially in

58   mixed-kin societies where dispersal polymorphisms are most common (Davidian et al., 2016).

59   Thus, the evolutionary mechanism underlying the formation of mixed-kin societies remains

60   largely unknown and can only be revealed by considering the lifetime inclusive fitness

61   consequences of alternative reproductive tactics.

62

63   Here, we leveraged a 15-year longitudinal dataset from Kenya to examine how reproductive

64   tactics in male cooperatively breeding superb starlings (*Lamprotornis superbus*) are influenced

65   by pre- and postnatal social and ecological factors and impact lifetime inclusive fitness. Superb

66   starlings are plural cooperative breeders in which both sexes help (Rubenstein, 2016, 2007a), and

67   although males tend to be more philopatric than females, these mixed-kin social groups have low

68   but variable kin structure overall as well as within both sexes (Pollack and Rubenstein, 2015;

69   Rubenstein, 2016). While resident females never breed in their natal groups, both resident and

70   immigrant males can acquire breeding status (Rubenstein, 2016). These savanna-dwelling birds

71   inhabit one of the most variable and unpredictable environments on earth (Rubenstein and

72   Lovette, 2007), where high annual variability and unpredictability in seasonal rainfall governs

73   insect prey availability (Rubenstein, 2007b). Rainfall is most variable during the dry season

74   (Rubenstein, 2011), and both pre- and postnatal variation in dry season rainfall has been shown

75   to influence many aspects of starling social behavior and life-history. In particular, prenatal

76   rainfall influences offspring sex ratio (Rubenstein, 2007a), epigenetic modification of genes

77   related to the avian stress response (Rubenstein et al., 2016), and male reproductive decisions

78   (Rubenstein et al., 2016), whereas postnatal rainfall influences access to breeding opportunities

79   for both sexes (Rubenstein, 2007c) and helping behavior (Guindre-Parker and Rubenstein, 2018).

80   In addition, the social environment also impacts superb starling fitness, both survival (Guindre-

81   Parker and Rubenstein, 2020) and reproductive success (Rubenstein, 2011).

82

83   To examine the environmental causes of alternative reproductive tactics in superb starlings, we

84   first investigated how pre- and postnatal ecological and social factors influence male dispersal

85   decisions. We predicted that in a harsh prenatal environment with low rainfall, particularly for

86   small groups with a skewed sex ratio, parental effects may indirectly limit dispersal of male

87   offspring by promoting helping behavior. Thus, males that remain in their natal group would be

88   more likely to provide alloparental care prior to the age of dispersal than males that ultimately

89   disperse. Similarly, in a harsh postnatal environment, male superb starlings would be more likely

90   to remain in their natal group to evade the costs of dispersal or reap the benefits of philopatry,

91   particularly in a social environment conducive to higher survival (large group size) and with

92   greater access to reproductive opportunities (female-skewed sex ratio). Next, to understand the

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93   fitness consequences of these alternative reproductive tactics, we compared access to

94   reproductive opportunities, reproductive success, lifetime inclusive fitness, and survivorship of

95   resident and immigrant males. According to the best-of-a-bad-job hypothesis, we predicted that

96   the two alternative tactics would result in unequal lifetime inclusive fitness, regardless of the pre-

97   or postnatal environments. Alternatively, if both dispersal and philopatry maximize individual

98   fitness, then the two tactics would have equal lifetime inclusive fitness but exhibit reproductive

99   tradeoffs such that individuals would have lower lifetime fitness when they adopt a phenotype

100   not predicted by the prevailing environmental conditions. Ultimately, by linking the

101   environmental causes and fitness consequences of alternative reproductive tactics in a

102   cooperative breeder, we will be able to determine how a behavioral polymorphism of two

103   fundamentally different reproductive phenotypes can persist and potentially give rise to mixed-

104   kin cooperative societies.

105

106   **Results**

107   ***Patterns of male dispersal***

108   Consistent with previous reports in this species (Rubenstein, 2016), we found that males were the

109   primary philopatric sex; only 59 of 162 males (36%) in our marked social groups for whom we

110   had complete lifetime data—from birth to death for natal males and immigration to death for

111   immigrant males—were immigrants (compared to 121 of 224 (54%) of females). However, more

112   than half of male breeders (30 of 59; 51%) were immigrants.

113

114   ***Pre- and postnatal ecological and social predictors of male dispersal***

115   Next, we examined the role pre- and postnatal ecological and social factors play in influencing

116   male dispersal decisions. We found that harsh prenatal ecological conditions limited dispersal

117   such that males were less likely to disperse when they were born in years following low prenatal

118   rainfall ($Z = 1.97$, $P = 0.049$, $CI = 0.002$-0.72; Fig. 1, Table 1). However, both postnatal

119   ecological and social conditions had no significant impact on the likelihood of males dispersing

120   (Table 1), suggesting that male dispersal is influenced more by (i) prenatal than postnatal

121   conditions and (ii) ecological rather than social factors. In addition, we found that males that

122   subsequently dispersed were less likely to act as alloparents in their first year of life than males

123   that subsequently remained in their natal group ($\chi^2_1 = 5.05$, $P = 0.02$).

124

125   ***Fitness consequences of male dispersal decisions***

126   We then explored the fitness consequences of the different male dispersal decisions. More than

127   half the males in the population (87 of 162 males; 54%) accrued zero inclusive fitness in their

128   lifetimes (Fig. S3) (Rubenstein, 2016). While residents accrued higher indirect fitness than

129   immigrants (Fig. 2C, $U = 2350$, $P = 0.05$), resident and immigrant males had equal direct and

130   inclusive lifetime fitness (Fig. 2A-B; inclusive: $U = 2828$, $P = 0.43$; direct: $U = 3115$, $P = 0.66$),

131   as well as equal survival likelihoods ($Z = -0.04$, $P = 0.97$, $CI = -0.33$-0.32) (Fig. S4). Despite

132   equal lifetime inclusive fitness, immigrants were more likely than residents to breed at least once

133   in their lifetimes ($\chi^2_1 = 7.39$, $P = 0.01$), had higher lifetime breeding effort (the number of

134   breeding attempts as a proportion of an individual's adult lifespan) ($U = 3689$, $P = 0.006$), and

135   began breeding at a younger age ($U = 265.5$, $P = 0.01$). In contrast, residents that did breed had

136   higher nest success than immigrant breeders ($Z = 2.48$, $P = 0.01$, $CI = 0.28$-2.33). In addition,

137   only lifetime breeding effort, and not birth status, affected a male's likelihood of accruing some

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138   nonzero inclusive fitness during his lifetime (Fig. 3A, Table 2). However, among males with

139   some lifetime inclusive fitness, residents accrued higher inclusive fitness than immigrants with

140   the same amount of lifetime breeding effort (Fig. 3B, Table 2).

141

142   Finally, we assessed whether there were reproductive tradeoffs for individuals that adopted the

143   tactic not predicted by prenatal ecological conditions. Since we did not have precise rainfall data

144   from the immigrants' natal sites (though rainfall is highly correlated spatially and temporally

145   synchronous within the dispersal radius of our study site; see *SI*), we used a categorical measure

146   of prenatal rainfall based on mean long-term prenatal rainfall at our study site (see *Methods* and

147   *SI*). Consistent with the idea of reproductive tradeoffs and the hypothesis that the fitness

148   consequences of alternative reproductive tactics depend on prenatal environmental conditions,

149   we found that immigrant males were more likely to accrue nonzero lifetime inclusive fitness

150   when born following periods of high prenatal rainfall, but that residents were more likely to

151   accrue nonzero lifetime inclusive fitness when born following periods of low prenatal rainfall

152   (Fig. 4, Table 3).

153

154   **Discussion**

155   Although mixed-kin cooperative groups characterized by low relatedness are surprisingly

156   common (Riehl, 2013), how these societies arise and are maintained given the potential for high

157   social conflict among unrelated group members competing for reproductive opportunities

158   remains unclear. We examined the environmental causes and inclusive fitness consequences of

159   dispersal decisions in male superb starlings living in a climatically variable and unpredictable

160   savanna environment (Guindre-Parker and Rubenstein, 2020; Rubenstein and Lovette, 2007), for

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161   whom philopatry and dispersal can both be pathways to reproductive opportunities (Rubenstein,

162   2016). We found that dispersal in males is influenced by their parents' prenatal environment

163   rather than the postnatal environment that the males experience as adolescents, suggesting that

164   prenatal parental effects play an important role in governing dispersal decisions. Ultimately,

165   natal dispersal and philopatry had equal lifetime inclusive fitness outcomes, meaning that they

166   are two equal, alternative male reproductive tactics. Yet, the two tactics showed reproductive

167   tradeoffs—immigrants had greater access to reproductive opportunities via the acquisition of

168   dominant breeding positions, whereas residents that bred had higher reproductive success. When

169   males adopted a tactic not predicted by prevailing prenatal environmental conditions, their

170   lifetime inclusive fitness was reduced. Together, these results suggest that environmental

171   variability experienced early in life may help maintain a reproductive polymorphism with equal

172   lifetime inclusive fitness, which ultimately enables the formation and persistence of a mixed-kin

173   cooperative society in an unpredictable environment.

174

175   Unlike in other cooperatively breeding species where the postnatal environment shapes dispersal

176   decisions (Baglione et al., 2006; Nelson-Flower et al., 2018; Suh et al., 2020), male dispersal in

177   superb starlings was only governed by prenatal ecological conditions. The effect of prenatal

178   conditions on dispersal suggests that parental effects influence the dispersal phenotype of male

179   superb starlings, a result that has been suggested previously for male reproductive opportunities

180   in this species (Rubenstein et al., 2016). Parental effects, which can result from physiological or

181   molecular modifications to offspring during development (Mousseau and Fox, 1998), may be

182   particularly important in cooperatively breeding species (Russell and Lummaa, 2009) and

183   species inhabiting unpredictable environments (Meylan et al., 2012). While the specific

184   physiological mechanisms of prenatal parental effects on dispersal remain unknown for this

185   species, previous studies have demonstrated an effect of maternal condition on offspring sex

186   allocation, maternal investment in eggs, and DNA methylation in superb starlings (Rubenstein,

187   2007a; Rubenstein et al., 2016) and other vertebrates (Meylan et al., 2002; Silk and Brown,

188   2008; Van Petegem et al., 2015). Studies of two other avian species, western bluebirds (*Sialia*

189   *mexicana*) and great tits (*Parus major*), found an effect of maternal androgen deposition on

190   offspring dispersal in response to ecological conditions (Duckworth, 2009; Tschirren et al.,

191   2007). Viviparous lizards (*Lacerta vivipara*) show a similar effect (Meylan et al., 2002), and

192   maternal hormones have also been shown to increase helping behavior in subordinate female

193   meerkats (*Suricata suricatta*) (Dantzer et al., 2019). Further work in this and other cooperatively

194   breeding species should examine the mechanism by which environmentally-mediated parental

195   effects might influence future reproductive tactics adopted by offspring.

196

197   Parental effects can be selfish, to manipulate offspring phenotype in order to increase parental

198   fitness, or anticipatory, to maximize offspring fitness (Marshall and Uller, 2007; Russell and

199   Lummaa, 2009). We know that offspring sex ratio in superb starlings is male-biased when

200   mothers are in poorer body condition following harsher prenatal conditions, a pattern that

201   suggests that females maximize their inclusive fitness in an unpredictable environment by

202   investing in the sex with lower fitness variance (Rubenstein, 2007a). However, our results here

203   suggest that mothers could also be influencing cooperative behavior in their offspring because

204   males that participated in alloparental care in their first year of life were subsequently more

205   likely to remain in their natal group. Male superb starlings are more likely to become alloparents

206   and help more than females (Rubenstein, 2011), and alloparents buffer the detrimental effects of

207 harsh environmental conditions on reproductive success in this species (Guindre-Parker and

208 Rubenstein, 2018). Thus, prenatal parental effects promoting alloparental behavior following

209 harsher prenatal conditions might serve to selfishly increase the parents' short-term future

210 reproductive success and indirectly limit dispersal of male offspring (Dantzer et al., 2019).

211 Although males born following benign prenatal conditions could, conversely, be more likely to

212 disperse so as to reduce kin competition, this seems less probable because kin competition has

213 actually been shown to decrease under benign environmental conditions in other cooperative

214 species (Korb and Schmidinger, 2004; Nichols et al., 2012). Additionally, our results are

215 consistent with the hypothesis that prenatal parental effects on dispersal in males are anticipatory

216 because when males adopted the tactic predicted by the prevailing prenatal ecological conditions,

217 they were more likely to accrue some inclusive fitness in their lifetimes. Since more than half of

218 superb starling males fail to accrue any fitness in their lifetimes, largely due to high nest

219 predation pressure (Rubenstein, 2016), securing any amount of nonzero lifetime fitness is crucial

220 in this species, an idea consistent with the bet-hedging hypothesis proposed for this (Rubenstein,

221 2011) and other social species (Kennedy et al., 2018). Males born following harsh prenatal

222 conditions thus appear to benefit from avoiding the costs of dispersal and remaining in their natal

223 group (Eikenaar et al., 2010; Stacey and Ligon, 1991), whereas males born following benign

224 conditions might be better able to cope with the costs of dispersal and maximize their fitness by

225 immigrating into another social group (Bergmüller et al., 2005).

226

227 In contrast to other studies in kin-only cooperatively breeding societies (e.g., Ekman et al., 2001;

228 Ligon and Ligon, 1982; MacColl and Hatchwell, 2004; Sparkman et al., 2011; Walters et al.,

229 1992), we found that the two reproductive tactics adopted by males—natal dispersal and

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230   philopatry—have equal lifetime inclusive fitness in a mixed-kin cooperative society. Although

231   resident males had significantly higher lifetime indirect reproductive success than immigrants, an

232   unsurprising result given the kin structuring among males in superb starling social groups

233   (Rubenstein, 2016), this was more than balanced out by the relatively larger contribution of

234   lifetime direct fitness. While it was not logistically possible to compare the fitness of resident

235   and dispersing males born to the same social group, our approach of comparing resident to

236   immigrant males has proven informative in other avian studies (Green and Hatchwell, 2018).

237   Furthermore, we show that the equal lifetime inclusive fitness outcomes of the two dispersal

238   tactics are due to a reproductive tradeoff, an idea that has been proposed theoretically (Moran,

239   1992; Stearns, 1989) but rarely tested empirically. Although immigrant superb starlings had

240   greater access to reproductive opportunities via the acquisition of dominant breeding positions

241   with the group, residents that acquired breeding positions were more likely to successfully fledge

242   young. Residents can therefore afford to have lower access to breeding opportunities over their

243   lifetimes since they have higher nest success. This higher nest success is likely due to greater

244   alloparental care at nests of resident males who have more kin in the group to act as helpers than

245   do immigrants (Emlen and Wrege, 1988; Komdeur, 1994; Wright et al., 2010). Thus, for superb

246   starling males, philopatry leads to lower reproductive quantity but higher quality, whereas

247   dispersal results in higher reproductive quantity but lower quality. Since immigrants and

248   residents are equally likely to survive from one breeding season to the next, these differences in

249   reproductive quality and quantity are unrelated to longevity (Walters et al., 1992). Together these

250   results suggest that the two alterative dispersal tactics are equivalent in terms of lifetime

251   inclusive fitness and refute the hypothesis that remaining in the natal group—the tactic favored

252   following harsh prenatal conditions—is simply making "the-best-of-a-bad-job" (Dawkins, 1980;

253   Koprowski, 1993). The coexistence of resident and immigrant males in cooperative social groups

254   has been shown to be similarly facilitated by equal reproductive rates in spotted hyenas (*Crocuta*

255   *crocuta*) (Davidian et al., 2016) and inclusive fitness at different age stages in dwarf mongooses

256   (*Helogale parvula*) (Creel and Rabenold, 1994), both species that live in mixed-kin societies.

257   However, to the best of our knowledge, ours is the first study in a cooperatively breeding

258   vertebrate to demonstrate equal lifetime inclusive fitness outcomes of alternative dispersal

259   tactics.

260

261   This behavioral polymorphism in reproductive tactics is likely maintained by a flexible response

262   to high and unpredictable environmental variability (West Eberhard, 1989). A temporally

263   variable and unpredictable environment has been shown both theoretically (Moran, 1992) and

264   empirically (Lampert and Linsenmair, 2002) to generate conditional strategies that result in a

265   developmental switch between alternative tactics. If a behavioral polymorphism has a genetic (or

266   perhaps epigenetic) basis (Beldade et al., 2011; Saastamoinen et al., 2018), environmental

267   variability can reverse the selective differential between two tactics from one year to the next,

268   resulting in alternative tactics with equal fitness outcomes (Gibbs and Grant, 1987; Moran,

269   1992). The savanna habitat inhabited by superb starlings has high temporal ecological variability

270   (Rubenstein, 2011; Rubenstein and Lovette, 2007) that may allow both dispersal tactics to

271   persist, resulting in the formation of mixed-kin cooperative groups. Interestingly, spotted hyenas

272   (Holekamp and Smale, 1998) and dwarf mongooses (Creel and Rabenold, 1994) experience the

273   same unpredictable savanna environments, suggesting that environmental uncertainty—and

274   perhaps oscillating selection pressures more generally—maintains alternative dispersal tactics

275   and leads to the formation of and/or stabilizes societies with low kin structure. Oscillating

276   selection may be particularly important in arid and semi-arid environments where climatic

277   variability is high (Gibbs and Grant, 1987), and may help explain the evolution of both mixed-

278   kin societies and plural breeding more generally. Indeed, many other plural cooperatively

279   breeding birds across the globe live in harsh arid and semi-arid environments characterized by

280   unpredictable variation in rainfall and food resources (e.g. Brown et al., 1997; Clarke, 1984;

281   Curry and Grant, 1990; Hegner et al., 1982; Riehl and Jara, 2009; Rowley, 1978; Rowley et al.,

282   1989; Russell et al., 2010; Veltman, 2008). While we do not yet know whether dispersal has a

283   genetic basis in superb starlings—though there are indications of a potential epigenetic basis

284   (Rubenstein et al., 2016)—our results suggest that the two tactics face oscillating selection since

285   the relative lifetime inclusive fitness of the two tactics fluctuates in response to prenatal

286   environmental conditions. Ultimately, identifying the mechanism by which prenatal parental

287   effects lead to developmental differences that determine male reproductive tactics will be

288   important for understanding the role that environmentally-driven selection pressures play in

289   shaping behavioral polymorphisms in this and other social species.

290

291   In summary, we have shown that natal dispersal and philopatry in male cooperatively breeding

292   superb starlings represent two alternative reproductive tactics with equal fitness. The tactics are

293   mediated by parental effects during development and are likely maintained by oscillating

294   selection pressures characteristic of their variable and unpredictable savanna environment. Our

295   study suggests a direct link between environmental uncertainty, behavioral polymorphism, and

296   the evolution of mixed-kin animal societies that cannot be explained by kin selection alone. Our

297   work also underscores the importance of prenatal environmental conditions and parental effects

298   in determining offspring phenotype, especially in cooperative societies where early life

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299   conditions have direct implications on the future fitness of both parents and offspring. Moreover,

300   the direct benefits derived from environmental selective pressures appear to play a significant

301   role in the evolution and maintenance of cooperative societies, alongside or in the absence of kin

302   selection. Ultimately, understanding how fluctuation in early life environmental conditions helps

303   mediate reproductive tradeoffs and lifetime fitness is critical in an era of rapid anthropogenic

304   climate change because climatic uncertainty is only likely to increase across much of the globe

305   for the foreseeable future.

306

307   **Materials and Methods**

308   ***Data collection***

309   Nine superb starling social groups have been monitored continuously since 2001 at the Mpala

310   Research Centre, Kenya (0° 17'N 37° 52'E) (Rubenstein, 2016, 2006). Groups (mean size ± SD

311   = 22 ± 12) defend stable territories year-round and consist of breeding (mean ± SD = 2.70 ± 1.49

312   pairs per group) and non-breeding individuals, some of whom act as alloparents that guard

313   and/or provision young (Guindre-Parker and Rubenstein, 2018; Rubenstein, 2016). Birds breed

314   twice a year during the long (March-June) and short rains (October-November) (Rubenstein,

315   2016). We used data from the beginning of the 2003 long rains breeding season through the end

316   of the 2017 long rains breeding season ($N = 31$ breeding seasons over 15 years), since not all

317   birds in the study population were banded until 2003.

318

319   Birds were banded with a unique combination of colored leg bands and a numbered metal ring.

320   Hatchlings were banded in the nest at seven days of age; all other individuals were captured in

321   baited pull-string traps or mist nets and banded after fledging from the nest (Rubenstein, 2006).

322   If banded post-fledgling, age was assessed via eye color as juvenile (black eyes), sub-adult (less

323   than one year of age; cloudy eyes), or adult (one year of age or older; white eyes) (Guindre-

324   Parker and Rubenstein, 2020). Birth status (i.e., resident or immigrant) was assigned based on

325   age at banding and genetic parentage. Residents were either banded as hatchlings in the nest or

326   as juveniles whose parents were genetically identified as members of the same group using 15

327   microsatellite markers (Rubenstein, 2005). We also used the same microsatellite markers to

328   estimate (i) parentage and direct reproductive success in Cervus v3.0 (Kalinowski et al., 2007)

329   using methods described previously for this species (*sensu* Apakupakul and Rubenstein, 2015;

330   Rubenstein, 2007c, 2007d; Weinman et al., 2015) and (ii) pairwise relatedness (*sensu* Queller

331   and Goodnight, 1989) between all individuals with the R package *related* (Pew et al., 2015).

332   Immigrants were defined as those banded as juveniles or older whose parents were not

333   genetically identified as belonging to the same group. Sex was determined genetically (Griffiths

334   et al., 1998) as previously described for this species (Rubenstein, 2006).

335

336   We performed daily nest searches throughout the breeding season. Active nests were observed

337   with a spotting scope for 60-120 min per observation period (total observation time per nest:

338   mean $\pm$ SD = 314.33 $\pm$ 248.82 min). All superb starlings within 30 m of the nest were identified,

339   and their times of arrival and departure were recorded (Rubenstein, 2007d). Parents are the

340   primary nest builders, and only the mother incubates the eggs (Rubenstein, 2007d). All other

341   members of the social group seen visiting or guarding the nest were categorized as alloparents

342   (Guindre-Parker and Rubenstein, 2018).

343

344   Census data were used to estimate pre- and postnatal group size and sex ratio (calculated by

345   dividing the number of males by the sum of number of males and immigrant females in the

346   group to estimate potential mate competition). Groups were opportunistically censused year-

347   round and each individual marked as either present or absent in its social group twice a year in 6-

348   month increments. Individuals not seen for five or more breeding seasons (i.e. 2.5 years) were

349   assumed to be dead (Guindre-Parker and Rubenstein, 2020; Pollack and Rubenstein, 2015). We

350   inferred that the dispersal window for males is around one year of age using four lines of

351   evidence: (i) the modal age at which males disappear from their natal group; (ii) the categorical

352   age of immigrant males dispersing into the study population (< 1 year of age or ≥ 1 year of age);

353   (iii) the likelihood of males being detected in the census in their first year of life; and (iv) the

354   minimum age of first breeding by resident males (see *SI* for details). If a male was observed in its

355   natal group after one year of age, we classified it as a resident; if not, we classified it as having

356   dispersed. Although we could not completely distinguish between dispersal and mortality, the

357   positive relationship between likelihood of dispersal and prenatal rainfall (see *Results*) suggests

358   that these males did indeed disperse since we would have expected a negative relationship if

359   mortality were higher following harsh prenatal environmental conditions. Following the same

360   lines of evidence, immigrant males were assumed to have entered the group at about one year of

361   age (see *SI*). Since most immigrants into the study population are first detected in the period

362   between the short and long rains breeding seasons, we defined the postnatal period and dispersal

363   window as the pre-breeding season before an individual turned one year old. Ecological and

364   social conditions experienced by an individual during this period were termed postnatal factors.

365   In contrast, ecological and social conditions experienced by parents before the breeding season

366   of an individual's birth were termed prenatal factors.

367

368 Daily rainfall was measured using an automated Hydrological Services TB3 Tipping Bucket

369 Rain Gauge at Mpala Research Centre (Caylor et al., 2017), supplemented by a manual gauge at

370 the same location when the automated gauge failed (Rubenstein, 2011). To calculate pre- and

371 postnatal rainfall, we summed the rainfall between the two weeks after the last nest of the

372 previous breeding season through the two weeks before the first nest of the next breeding season

373 for each short or long rains breeding season (Fig. S1). This approach differs slightly from

374 previously published studies in this system that used a fixed time window to approximate

375 prenatal conditions (e.g., Guindre-Parker and Rubenstein, 2020; Rubenstein, 2007c; Rubenstein

376 et al., 2016) because here we are using data from both the long and short rains breeding seasons.

377

378 ***Data analysis***

379 For all analyses, we only used data from individuals for whom we had complete lifetime life

380 histories (386 of 1177 birds; 33% of banded individuals in the study population), excluding birds

381 that were born prior to 2003 when monitoring in all social groups began, as well as those that

382 were still alive in 2017. First, we examined patterns of male dispersal by quantifying the

383 proportion of immigrant adult males and females in the study population ($N_M = 162$, $N_F = 224$).

384 We determined how breeding opportunities were shared between immigrants and residents by

385 calculating the proportion of immigrant breeders of both sexes in the study population ($N_M = 59$,

386 $N_F = 121$).

387

388 Next, we investigated the effect of pre- and postnatal ecological and social factors on the

389 likelihood of a male dispersing using a general linear model (GLM) with a binomial error

17

390   structure and "logit" link function. We used the binomial response of reproductive tactic (1 =

391   dispersed, 0 = remained) as the dependent variable ($N_{dispersed}$ = 52, $N_{remained}$ = 99). Fixed effects in

392   the full model, which were standardized using z-scores (Schielzeth, 2010), included pre- and

393   postnatal rainfall, postnatal group size, and postnatal sex ratio. Since pre- and postnatal group

394   size and sex ratio were highly correlated (group size: R^2 = 0.95; sex ratio: R^2 = 0.80), we only

395   included postnatal group size and sex ratio in the final model. Including pre- instead of postnatal

396   group size and sex ratio in the model yielded qualitatively similar results. All two-way

397   interactions were included in the model, but later removed if their effect was not significant

398   (Engqvist, 2005). Since including breeding season and social group as random effects led to

399   singular model fits, they were excluded from the full model. We constructed models with all

400   possible combinations of the fixed effects and averaged the best-fitting models (AICc < 2)

401   (Grueber et al., 2011) using the functions "dredge" and "model.avg" in the R package *MuMIn*

402   (Bartoń, 2019) (Table S1). Furthermore, to investigate the relationship between alloparental care

403   provided by males prior to reaching one year of age and their subsequent reproductive tactic, we

404   used a Chi-square test to compare alloparental status (ever alloparent/never alloparent) and

405   reproductive tactic (dispersed/remained) for all natal males (N = 155).

406

407   Finally, we sought to understand the fitness consequences of the alternative reproductive tactics.

408   Although it was not possible to compare the fitness consequences of the alternative reproductive

409   tactics adopted by males born from same social group (since dispersers rarely remain within the

410   study population; only 3 males in 15 years), we compared access to reproductive opportunities,

411   reproductive success, lifetime inclusive fitness, and survivorship of resident and immigrant

412   males (N_{Imm} = 59, N_{Res} = 103). Previous studies of cooperatively breeding birds have used the

413   same approach (e.g,. Green and Hatchwell, 2018). Access to reproductive opportunities was

414   quantified as: (i) the likelihood of a male ever breeding in its lifetime (Chi-squared test); (ii)

415   lifetime breeding effort, or the number of breeding attempts as a proportion of an individual's

416   adult lifespan (Mann-Whitney test with continuity correction); and (iii) for males that bred at

417   least once ($N_{Imm} = 30$, $N_{Res} = 29$), the age at first breeding (Mann-Whitney test with continuity

418   correction). To evaluate the likelihood of a male obtaining any reproductive success in their

419   lifetimes, we modeled the effect of birth status on nest success (1 = succeeded, 0 = failed) using

420   a GLM with a binomial error structure and "logit" link function ($N_{Succeeded} = 49$, $N_{Failed} = 229$).

421   Since some males nested multiple times in their lifetimes, we included individual as a random

422   effect in the model.

423

424   Following Green and Hatchwell (Green and Hatchwell, 2018), we calculated lifetime inclusive

425   fitness (I) as the sum of lifetime direct and indirect fitness according to the equation

426

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

428

429   where direct fitness was calculated as the product of the number of fledglings per nest (M_j),

430   paternal care effort ($E = 0.5$, the other half being attributed to the mother), and the mean

431   offspring-father relatedness ($R = 0.5$) summed over all successful nests (J), minus half of the

432   indirect fitness attributed to alloparents (the other half being subtracted from the mother's direct

433   fitness). Indirect fitness attributed to alloparents at each nest was calculated as the product of the

434   mean alloparental effort at a nest per social group per breeding season (e_{nj}) and the alloparent's

435   relatedness to the fledglings (r_{mnj}), summed over all fledglings (M_j) and alloparents at the nest

19

436   (N_j) for all successful nests (J). Alloparents with $r_{mnj} \leq 0$ received no indirect fitness. Indirect

437   fitness of the focal male was similarly calculated as the product of the mean alloparental effort

438   (e_o) and its relatedness to the fledglings (r_{mo}), summed over all of the nests he visited in his

439   lifetime (O). We used population means instead of individual measures of alloparental effort

440   because total observation time for nests varied. Alloparental effort was calculated as the

441   proportion of time an individual spent attending a nest (both guarding and bringing food) relative

442   to the length of the observation period (*sensu* Guindre-Parker and Rubenstein, 2018).

443

444   We compared the lifetime inclusive, direct, and indirect fitness of resident and immigrant males

445   using a Mann-Whitney test with continuity correction (N_{Imm} = 59, N_{Res} = 103). To determine

446   whether differences in reproductive access and success between resident and immigrant males

447   affected their lifetime inclusive fitness, we used GLMs to model the effect of lifetime breeding

448   effort and birth status on lifetime inclusive fitness of males. The first model had a binomial

449   response (zero/nonzero lifetime inclusive fitness) and a "logit" link function (N_{Imm} = 59, N_{Res} =

450   103). The second model had a continuous dependent variable of all nonzero inclusive fitness

451   observations (N_{Imm} = 25, N_{Res} = 50) with an "identity" link function and a gamma error

452   distribution. The fixed effects for both models were lifetime breeding effort and birth status.

453

454   We also built a GLM to investigate the lifetime fitness consequences of adopting the tactic not

455   predicted by the prevailing environmental conditions, with a binomial response variable

456   (zero/nonzero lifetime inclusive fitness) and prenatal rainfall and birth status as fixed effects

457   (N_{Imm} = 53, N_{Res} = 99). Although we did not have precise rainfall data from the immigrants' natal

458   sites, we used monthly rainfall data from three sites within the dispersal radius (~30 km) of our

459   study population (Mpala Research Centre, MRC)—UHURU Central (12 km from MRC)

460   (Goheen et al., 2013), UHURU North (20 km from MRC) (Goheen et al., 2013), and Nanyuki

461   (38 km from MRC) (East African Livestock Early Warning System)—to demonstrate high

462   spatiotemporal correlation of prenatal rainfall for immigrant and natal males (Table S2).

463   Nonetheless, to take a more conservative approach, we used a categorical measure based on

464   mean long-term prenatal rainfall at Mpala Research Centre (low prenatal rainfall: rainfall < long-

465   term mean; high prenatal rainfall: rainfall > long-term mean).

466

467   Finally, we used a time-varying Cox proportional hazard model to determine whether birth status

468   affected male survival (N_{Imm} = 59, N_{Res} = 103) (*sensu* Guindre-Parker and Rubenstein, 2020).

469   The model was built using the R package *survival* (Therneau, 2020). We checked that our dataset

470   did not violate the proportional hazard assumption using the "cox.zph" function. We performed

471   all data analysis in R (R Core Team, 2019).

472

473   **Data Availability.** Data and R code are available on Dryad at

474   https://doi.org/10.5061/dryad.m37pvmd1p

475

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704

705   **Figures**

706

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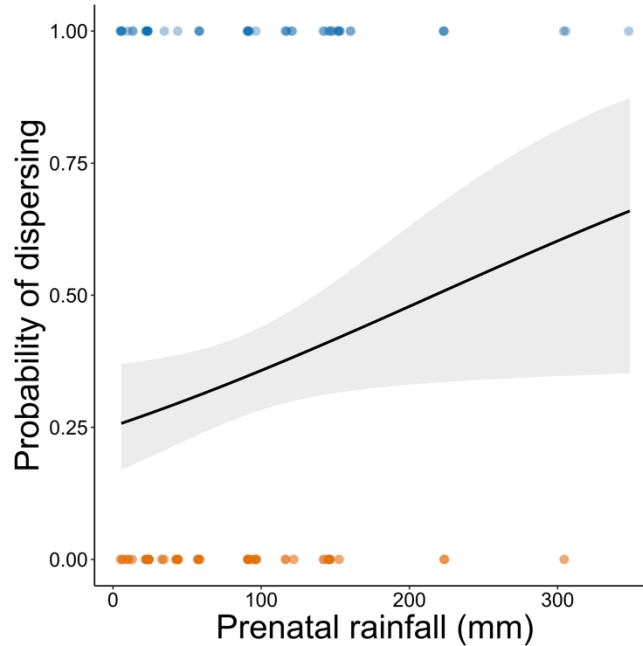
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710   **Figure 1. Effect of prenatal rainfall on the probability of male superb starlings dispersing**
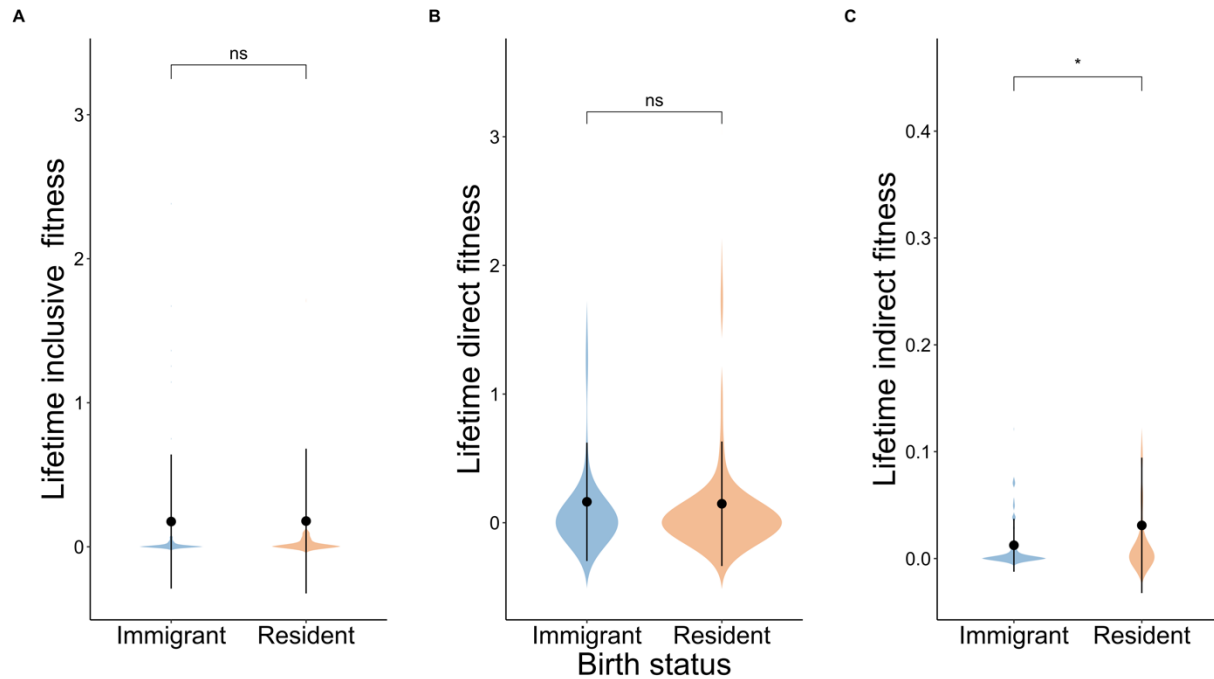
711   **from their natal groups.** Males were more likely to disperse when born following periods of

712   higher prenatal rainfall ($N = 151$, $P = 0.049$). Model estimate (solid line) is bounded by the 95%

713   confidence interval (shaded areas). Circles indicate raw data (blue = dispersed, orange =

714   remained).

715

716

717

718   **Figure 2. Mean lifetime fitness of immigrant and resident male superb starlings.** Immigrant

719   and resident males ($N_{Imm} = 59$, $N_{Res} = 103$) have equal lifetime (A) inclusive (P = 0.43), and (B)

720   direct (P = 0.66) fitness, though residents have higher (C) indirect fitness (P = 0.05). Black dots

721   represent means and error bars denote standard deviation. Shaded areas are kernel probability

722   densities illustrating the distribution of the data.

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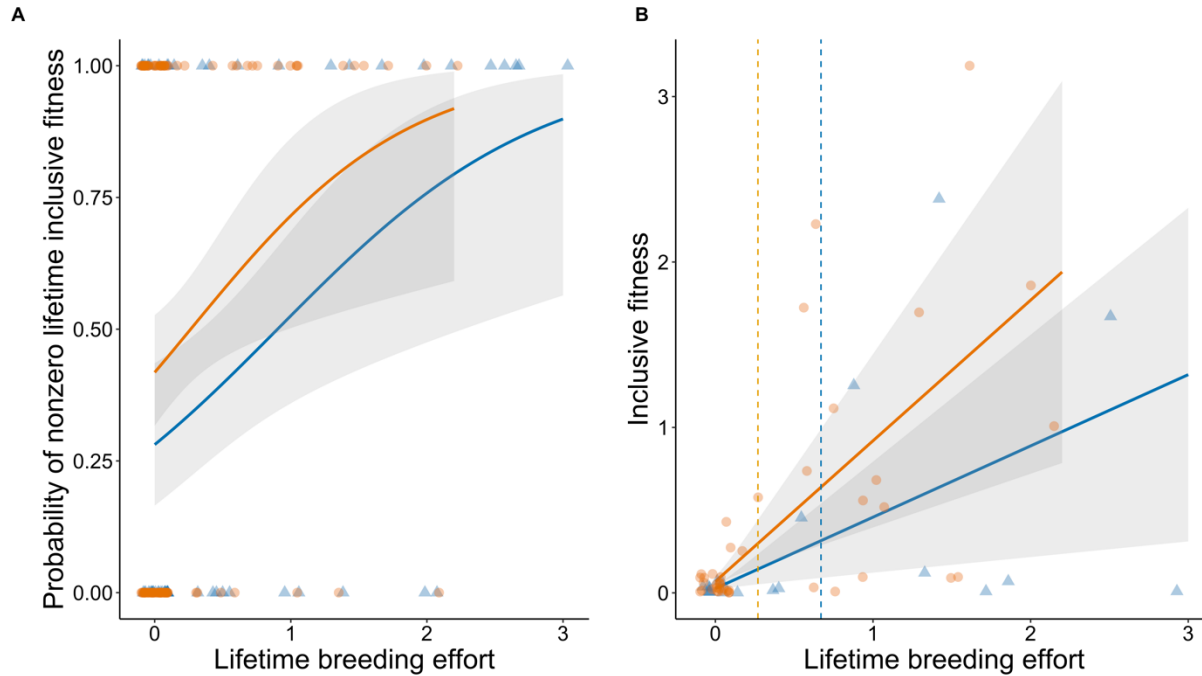
Figure 3. Effect of reproductive tradeoffs on lifetime inclusive fitness of male superb starlings. The effect of lifetime breeding effort and birth status (immigrants = blue, triangles; residents = orange, circles) on (A) the probability of accruing any nonzero lifetime inclusive fitness ($N = 161$), and (B) the value of nonzero lifetime inclusive fitness ($N = 74$). For visualization purposes, we excluded one individual with lifetime breeding effort greater than three standard deviations above the mean; this individual was included in the statistical analysis, though 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), but not birth status, affected a male's likelihood of accruing some nonzero inclusive fitness during his lifetime ($P < 0.001$). However, 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% confidence intervals (shaded areas). Points indicate raw data. Dashed vertical lines indicate mean lifetime breeding effort.

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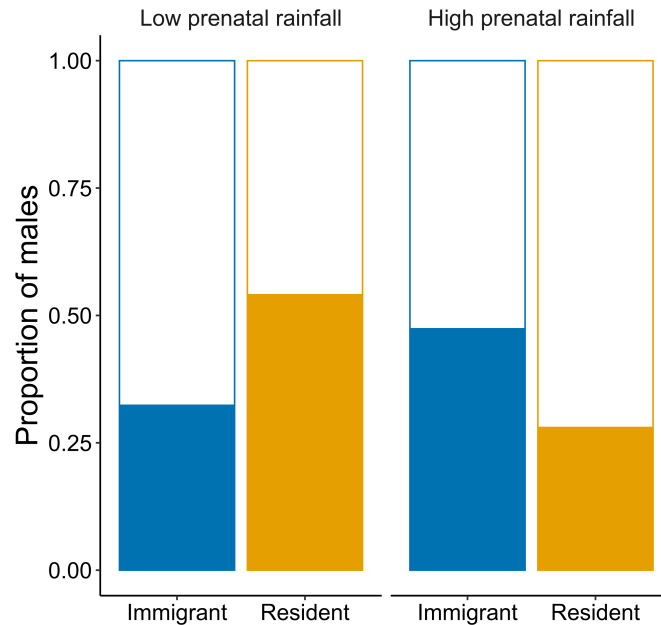
Figure 4. Fitness consequences of male superb starlings adopting the tactic not predicted by the prevailing prenatal environmental conditions. The effect of prenatal rainfall and birth status (immigrants = blue, residents = orange) on the probability of accruing any nonzero lifetime inclusive fitness (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 ($P = 0.03$).

745 **Table 1. Factors affecting dispersal decisions of natal males.** Model-averaged coefficients

746 (full average) of best fit general linear models (AICc < 2) with a binomial response (dispersed

747 vs. remained) variable for natal males (N = 151). Since pre- and postnatal sex ratio and group

748 size are highly correlated, we only included the latter in the final full model.

749

Effect	Estimate	Std. Error	Adjusted Std. Error	Z value	95% CI		p-value
Intercept	-0.63	0.17	0.18	3.59	-0.97	-0.28	<0.001
Prenatal rainfall	0.36	0.18	0.18	1.97	0.002	0.72	0.049
Postnatal sex ratio	-0.02	0.09	0.09	0.24	-0.45	0.24	0.81
Postnatal group size	0.02	0.08	0.08	0.19	-0.26	0.43	0.85
Postnatal rainfall	0.01	0.09	0.09	0.15	-0.32	0.47	0.88

750

751 **Table 2. Effects of lifetime breeding effort and birth status on lifetime inclusive fitness of**

752 **males.** Results of general linear models with a (A) binomial (zero vs. nonzero) ($N = 162$) and

753 (B) continuous, positive ($N = 75$) response variable for lifetime inclusive fitness of males.

(A) Response variable: binomial (zero/nonzero) lifetime inclusive fitness

Effect	Estimate	Std. Error	Z value	95% CI		p-value
Intercept	-0.98	0.33	-2.97	-1.66	-0.35	0.003
Lifetime breeding effort	1.12	0.30	3.72	0.58	1.77	<0.001
Birth status	0.67	0.37	1.82	-0.04	1.42	0.07

(B) Response variable: continuous, positive lifetime inclusive fitness

Effect	Estimate	Std. Error	t value	95% CI		p-value
Intercept	0.03	0.01	2.45	0.01	0.06	0.02
Lifetime breeding effort	0.62	0.14	4.37	0.40	1.00	<0.001
Birth status	0.04	0.02	2.07	-0.005	0.08	0.04

754

755 **Table 3. Effects of male superb starlings adopting the tactic not predicted by the prevailing**

756 **prenatal ecological conditions on the likelihood of gaining nonzero inclusive fitness during**

757 **their lifetimes.** Results of a general linear model with a binomial response (zero vs. nonzero

758 lifetime inclusive fitness) variable for males ($N = 152$). Since including breeding season and

759 social group as random effects led to singular model fits, they were excluded from the full

760 model.

761

Effect	Estimate	Std. Error	Z value	95% CI		p-value
Intercept	-0.74	0.36	-2.01	-1.50	-0.04	0.04
Categorical prenatal rainfall	0.63	0.59	1.08	-0.52	1.80	0.28
Birth status	0.90	0.43	2.07	0.06	1.78	0.04
Categorical prenatal rainfall x Birth status	-1.74	0.77	-2.25	-3.29	-0.24	0.02

762

Supplementary Information for
Prenatal environmental variation, alternative reproductive tactics and the formation of a mixed-kin cooperative society

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This PDF file includes:

Supplementary Information Text
Figures S1 to S4
Table S1 to S2
SI References

Supplementary Information Text

Methods. We inferred age of dispersal of males indirectly using four lines of evidence: (i) the modal age at which males disappear from their natal group ($N = 155$); (ii) the categorical age of immigrant males dispersing into the study population (< 1 year of age or ≥ 1 year of age) ($N = 97$); (iii) the likelihood of males being detected in the census in their first year of life ($N = 103$); and (iv) the minimum age of first breeding by resident males ($N = 29$). We found that (i) 33% of natal males disappeared within the first six months of hatching (Fig. S2A). If six months is the modal age of dispersal, most immigrants into the study population should be in juvenile or sub-adult (< 1 year of age) plumage. However, (ii) 90% of male immigrants into the study population were in adult plumage (i.e., ≥1 year of age) (Fig. S2B). Thus, we reasoned that natal males disperse at 1 year of age but the majority of them are likely missed in the census during the one breeding season they spend in their natal group before they disperse, largely because of our methods for performing censuses. Since our census effort is mostly opportunistic, it is common for individuals to be missed for multiple breeding seasons before being seen again, especially if they did not breed or act as an alloparent (Guindre-Parker and Rubenstein, 2020). We found that (iii) of all the males that remained in their natal group past 1 year of age, 64% were missed in the census at age 0.5 years (six months). Further, the likelihood of missing individuals was higher in the period preceding the short breeding seasons (70%) than in the period preceding the long breeding seasons (48%), which directly matches the variation in census effort. Finally, when we set age of dispersal as 1 year, 52 of 155 natal males (34%) were classified as "dispersed" in our dataset, a proportion that closely matches the proportion of male immigrants in the study population (see *Results*) and gives us more confidence in our inference of dispersal age. Moreover, (iv) the minimum age of first breeding by resident males was at one and a half years

old, further suggesting that males are reproductively immature in their first year of life and may

thus disperse at around one year of age. While we cannot confirm that males dispersed, not died,

the increased likelihood of dispersal following benign prenatal conditions (see *Results*) suggests

that these males did indeed disperse, since mortality would be higher following harsher
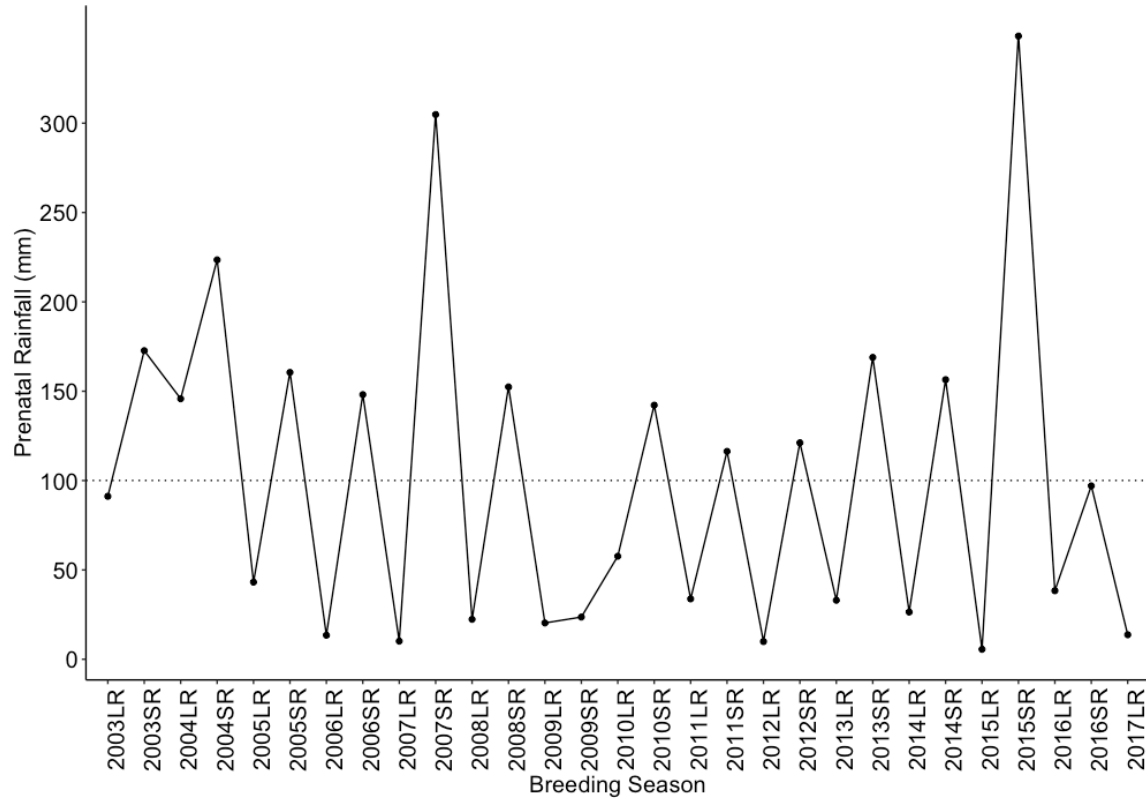
conditions.

Figure S1. Variation in prenatal rainfall during the study period. Superb starlings in the study population breed twice a year in the long (LR) and short (SR) breeding seasons. Dotted line indicates the mean level of prenatal rainfall during the study period.
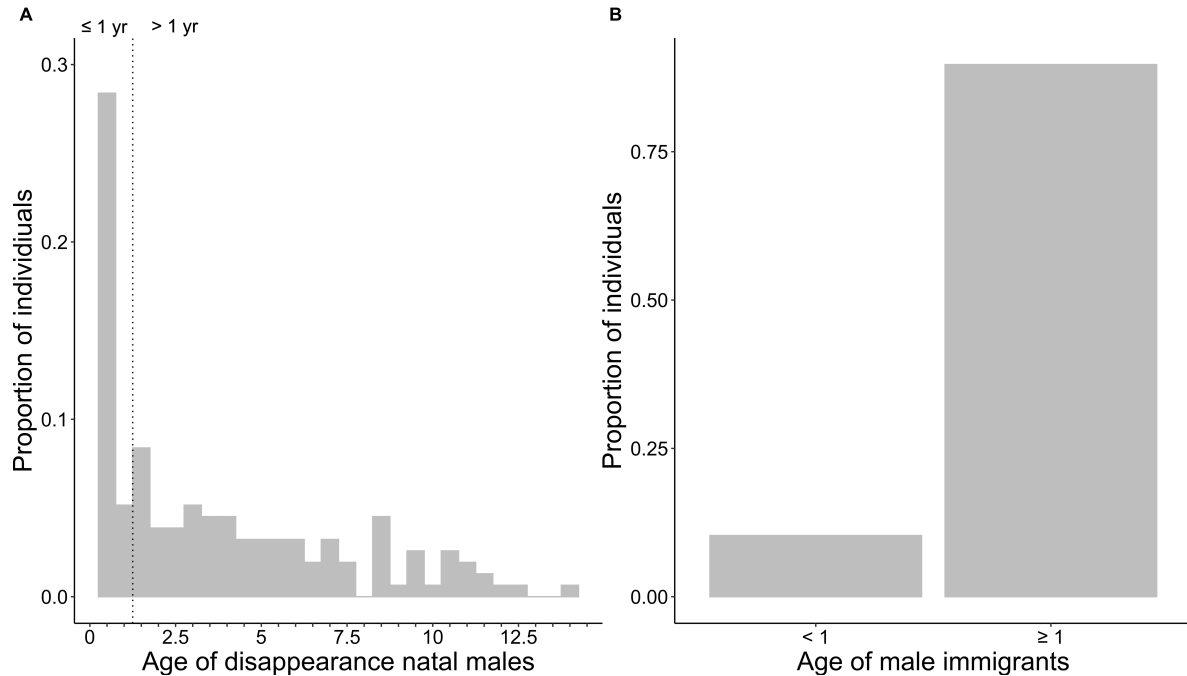
Figure S2. Evidence for age of dispersal of male superb starlings. (A) The modal age of disappearance of natal males is six months ($N = 155$). Age is in 0.5-year (six month) increments. However, (B) the majority of immigrant males are caught in adult plumage (≥ 1 year of age) ($N = 97$). Thus, we concluded that males disperse at 1 year of age and are likely missed in the census during the one breeding season they spend in their natal group before dispersing.
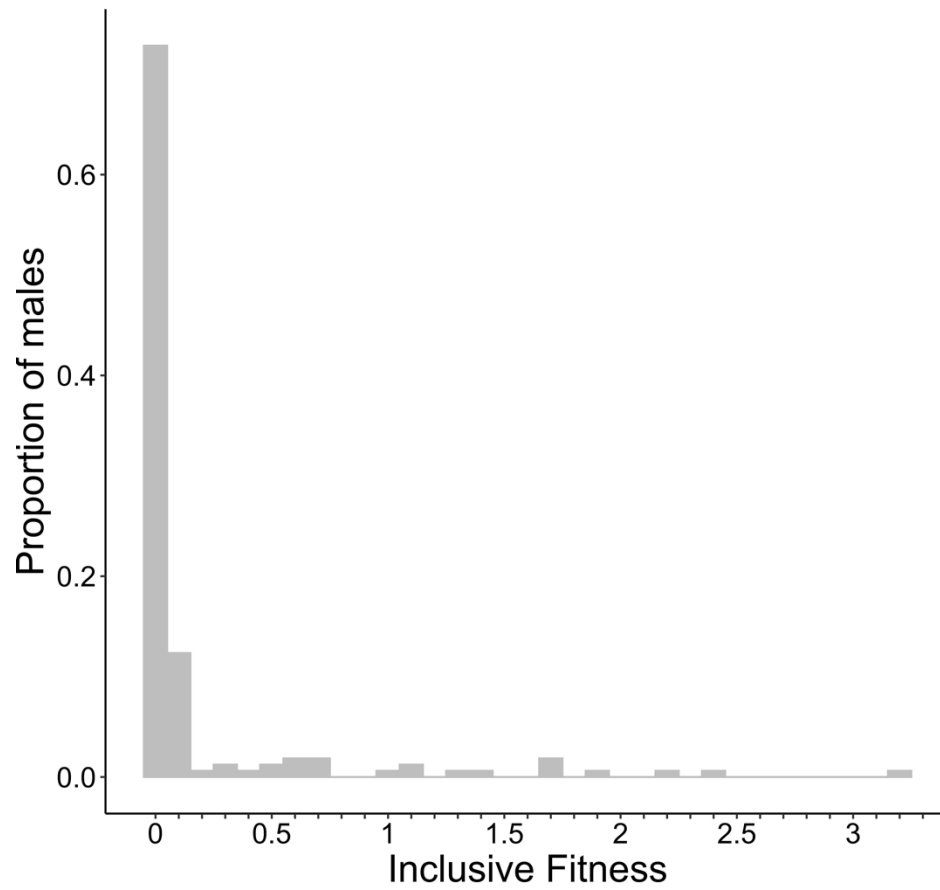
Figure S3. Lifetime inclusive fitness of male superb starlings. Histogram shows the distribution of lifetime inclusive fitness of males ($N = 162$).
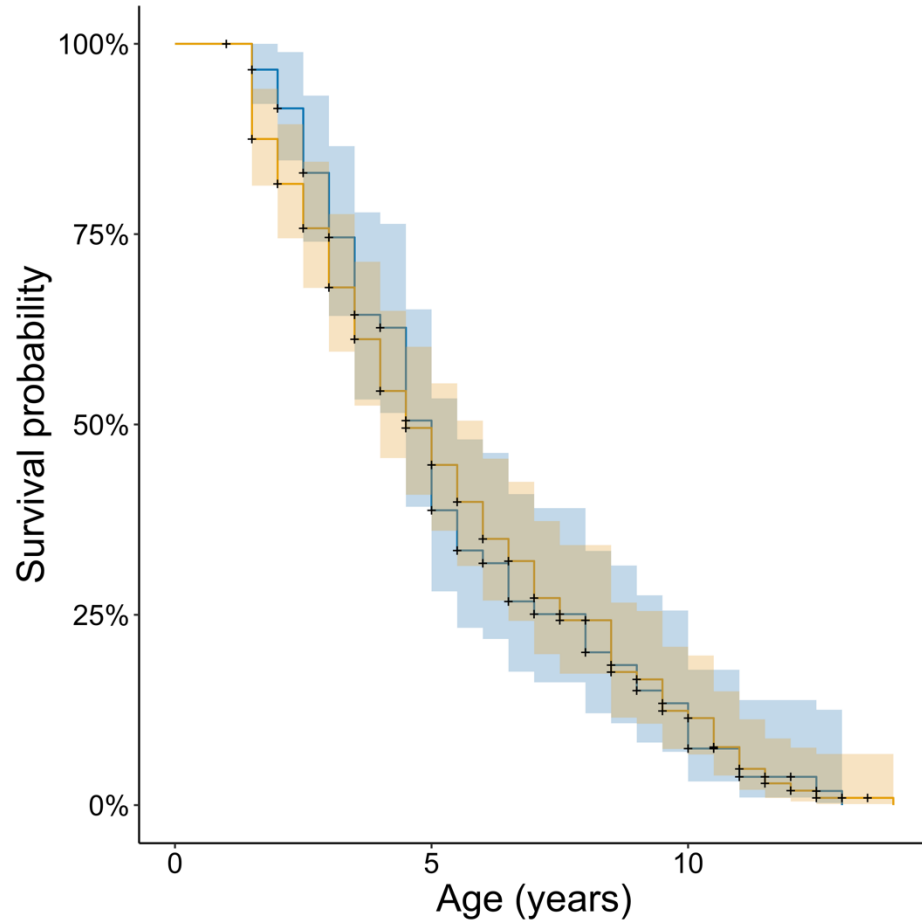
Figure S4. Survivorship of resident and immigrant male superb starlings. Male survival did not differ by birth status (immigrants = blue, residents = orange) (N_{Imm} = 59, N_{Res} = 103, P = 0.97). Model estimates (solid lines) are bound by 95% confidence intervals.

Table S1. Model ranking for factors affecting dispersal decision of natal males using an information theoretic approach. "x" indicates predictors used as fixed effects in the model. Since pre- and postnatal group size and sex ratio were highly correlated, we only included the latter in the full model. Since including breeding season and social group as random effects led to singular model fits, they were excluded from the full model. Models are ranked by AICc score (Akaike Information Criterion corrected for small sample sizes) and arranged in order from best to worst fit.

Model	Intercept	Postnatal group size	Prenatal rainfall	Postnatal Rainfall	Postnatal sex ratio	df	ΔAICc
m3	x		x			2	0.00
m11	x		x		x	3	1.69
m4	x	x	x			3	1.84
m7	x		x	x		3	1.94
m1	x					1	2.36
m5	x			x		2	2.82
m12	x	x	x		x	4	3.37
m15	x		x	x	x	4	3.68
m8	x	x	x	x		4	3.70
m9	x				x	2	3.72
m2	x	x				2	4.20
m6	x	x		x		3	4.34
m13	x			x	x	3	4.37
m16	x	x	x	x	x	5	5.26
m10	x	x			x	3	5.34
m14	x	x		x	x	4	5.61

Table S2. Correlation in rainfall between sites within dispersal radius of the study site.

Numbers represent R^2 values of correlation of monthly rainfall (2008-2017; $N = 103$) between three sites within the approximate dispersal radius of the study site, Mpala Research Centre (MRC); UHURU Central (12 km), UHURU North (20 km), and Nanyuki (38 km).

	MRC	UHURU Central	UHURU North	Nanyuki
MRC	-	-	-	-
UHURU Central	0.85	-	-	-
UHURU North	0.82	0.87	-	-
Nanyuki	0.78	0.73	0.70	-

SI References

Guindre-Parker S, Rubenstein DR. 2020. Survival benefits of group living in a fluctuating

environment. *Am Nat* **195**:1027–1036. doi:10.1086/708496