1 **Implications of adult sex ratios on natal dispersal in a cooperative breeder.**

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ABSTRACT

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31   In cooperatively breeding species, sexually mature individuals may delay natal dispersal and

32   become subordinates, helping a dominant pair raise offspring. To understand how

33   cooperative breeding evolved, it is important to determine the mechanisms leading to delayed

34   dispersal. Adult sex ratio (ASR) variation may affect dispersal through limiting breeding

35   vacancies available to the more abundant sex, and cooperative breeders often have a more

36   biased ASR than non-cooperative breeders. However, no studies of cooperative breeders have

37   related ASR at both the local and population level with dispersal. Using the long-term

38   Seychelles warbler (*Acrocephalus sechellensis*) dataset, we test the influence of population-

39   wide and local ASR, and density, on natal dispersal of yearlings. Our ASR-density hypothesis

40   predicts that the probability of natal dispersal is lower when the ASR is biased towards the sex

41   of the focal individual, but only when the population density is high. Dispersal was associated

42   with population density and ASR in males, but not in females; males were likely to delay

43   dispersal when ASR was male-biased and density was high. Our findings illustrate a complex

44   association between demographic factors and cooperative breeding, and suggest that

45   individuals alter their dispersal behaviour in response to the demographic composition of the

46   population.

47

48   **HIGHLIGHTS**

49   • Natal dispersal is associated with ASR in a facultative cooperative breeder

50   • Male but not female yearlings disperse in response to population ASR and density

51   • Population-wide rather than local demographic composition predicted male dispersal

52   • Our study links demographic factors with behaviour that drives cooperative breeding

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57
58   **INTRODUCTION**

59   Many social animals live and reproduce in stable groups. Cooperative breeding, although once

60   considered as a rare phenomenon (Brown, 1987; Emlen, 1982), is commonly observed across

61   taxa (Choe & Crespi, 1997; Cockburn, 2006; Lukas & Clutton-Brock, 2012; Solomon & French,

62   1997; Taborsky, 1994). It is often characterised by a dominant breeding pair being assisted by

63   non-breeding sexually mature subordinates that provide offspring care (Cockburn, 1998).

64   Delayed dispersal, whereby offspring remain in the natal territory after they reach sexual

65   maturity is a common route to cooperative breeding (Ekman et al., 2004; Griesser et al., 2017;

66   Kingma et al., 2021; Koenig et al., 1992). A central question in the study of cooperative

67   breeding is which circumstances drive such philopatric to individuals delay dispersal instead

68   of leaving to breed independently (Ekman et al., 2004; García-Ruiz et al., 2022; Hatchwell,

69   2009; Koenig et al., 1992; Wiley & Rabenold, 1984).

70   The adult sex ratio (ASR, the proportion of adults that are male) is a major potential

71   determinant of the costs and benefits of dispersal, since the scarcity of one sex directly

72   influences the availability of potential mates for the other (Brown, 1987; Hatchwell &

73   Komdeur, 2000). ASR can strongly influence life-history trajectories and vice versa (Székely et

74   al., 2014). A meta-analysis found that ASRs are more biased in cooperatively breeding species

75   compared to non-cooperatively breeding species, and that within cooperatively breeding

76   species ASR is positively associated with helper sex ratio (Komdeur, Székely, et al., 2017). Sex-

77   biased dispersal and helping behaviour could result in consistent biases in ASR. Alternatively,

78   population ASR may influence dispersal propensity and can lead to an increase in group

79   formation and be a pathway to cooperative breeding behaviour, although the direction of

80   causality is unclear. For instance, if the ASR is male biased, males will have more difficulty

81   finding independent breeding vacancies, and therefore may benefit by staying in the natal

82   territory. This effect can act both on the local social neighbourhood and population level

83   within species. At the population level, ASR may affect direct costs and benefits of dispersal,

84   whereas at the local level, ASR could provide a proxy of direct social information on the

85   number of adult males and females that individuals have access to when deciding whether to

86   disperse from their natal territory or not. Additionally, ASR is an important demographic driver

87   of inter- and intraspecific behavioural variability across the sexes (Jennoins & Kokko, 2010;

88   Liker et al., 2013; McNamara et al., 2000; Rosa et al., 2017; Zheng et al., 2021). Dispersing

89   individuals are often, but not always, changing their status from subordinate to dominant

90   breeder (Groenewoud et al., 2018; Jungwirth et al., 2023; Kutsukake & Clutton-Brock, 2007;

91   Nelson-Flower et al., 2011), meaning availability of mates often dictates the opportunities of

92   successful dispersal. Males are less likely to search for additional female mates and increase

93   parental care when the ASR is male-biased compared to when it is female-biased (Eberhart-

94   Phillips et al., 2018; Fromhage & Jennions, 2016). This suggests that ASR may also be an

95   important driver of social behaviours that could lead to cooperative breeding. The effect of

96   ASR on cooperative breeding has mainly been observed in between-species comparisons,

97   whereas within species different mechanisms may be at play (Komdeur, Székely, et al., 2017),

98   but see (Curry & Grant, 1989; Pruett-Jones & Lewis, 1990). One study which explored

99   cooperative breeding and manipulated local ASR in brown-headed nuthatches (*Sitta pusilla*)

100   found that males postpone breeding due to a shortage of available mates (Cox et al., 2019;

101   Kingma & Székely, 2019).

102   Most studies do not account for an accurate assessment of ASR and density for entire

103   populations, usually due to a combination of migration and difficulty in tracking individuals.

104   Consequently, it is difficult to assess the impact of demographic effects such as ASRs in wild

105   populations. Moreover, studies often assume biases in ASR to be a consequence of sex

106   differences in dispersal (i.e. a sex-bias in dispersal costs driving a bias in ASR), rather than as a

107   driving mechanism of dispersal (i.e. ASR bias limits breeding opportunities leading to different

108   dispersal decisions in the sexes) (Gros et al., 2008; Leturque & Rousset, 2004; Pen & Weissing,

109   2000; Wild & Taylor, 2004). Therefore, to assess if and to what extent ASR drives sex-biased

110   dispersal, it is of key importance to measure ASR just prior to dispersal and to monitor its

111   effect on dispersal propensity, instead of measuring ASR during or after dispersal.

112   Population density can also influence the strength of evolutionary drivers of cooperative

113   breeding, for example through the degree of habitat saturation and number of sexual partners

114   in a population (Brown, 1987; Pen & Weissing, 2000). ASR often covaries with population

115   density (Donald, 2007; Kokko & Rankin, 2006), and population density can potentially alter the

116   ASR-dependent change in natal dispersal propensity. For example, the direction and

117   magnitude of the effect of ASR on dispersal costs and benefits may vary over different

118   population densities, as this indicates the potential availability of breeding partners as well as

119   the level of competition for breeding vacancies (Kokko & Rankin, 2006). This makes it

120   important to include both parameters when studying the demographic drivers of cooperative

121   breeding. However, we are not aware of previous studies on cooperatively breeding species

122   that have investigated the combined effects of density and ASR on dispersal.

123

124   Here, we investigate the importance of local and population-wide ASR, and how these interact

125   with density, for dispersal in a species with facultatively cooperative breeding. We determine

126   which parameters influence the dispersal probability of juveniles (see Table 1 for details) in

127   the Seychelles warbler (*Acrocephalus sechellensis*). This system provides an excellent model

128   for this question since the species is a facultative cooperative breeder, meaning breeders are

129   not fully dependent on having helping subordinates in their territory at all times. Most

130   dispersals happen within the first two years of life (Eikenaar et al., 2008). The Cousin Island

131   study population is contained, and dispersal off the island is extremely rare (~0.1%, Komdeur

132   et al. 2004), almost all individuals (>96%) are individually colour-ringed (Hammers et al., 2019;

133   Komdeur, 1992), and resighting rates are high (Brouwer et al., 2009), thus dispersal and

134   mortality are not confounded in this species. The whole population has been continuously

135   monitored since 1985, with data being most complete from 1995 onwards, and we have

136   accurate measures of population ASR and density for 25 years. Moreover, the dataset includes

137   individual life histories, individual environmental and social conditions, and bi-annual

138   assessment of dispersal of all individuals. Although a negative association between dispersal

139   probability and population density has been reported in the Seychelles warbler (Eikenaar et

140   al., 2007), how ASR affects natal dispersal and whether density affects the slope and direction

141   of this relationship have not yet been investigated. Here, we focus on ASR rather than OSR

142   (operational sex ratio, proportion of sexually active individuals that are male), since we are

143   specifically interested in the potential frequency-dependent aspects of sexual selection and

144   intrasexual competition on individual behaviour since. ASR is a product of demographic

145   processes (therefore including non-reproducing subordinates) whereas OSR is influenced by

146   reproductive decisions of individuals (Székely et al., 2014). Moreover, ASR strongly predicts

147   mating systems (Székely et al., 2014), parental investment (Fromhage & Jennions, 2016) and

148   sex roles (Gonzalez-Voyer et al., 2022; Kokko & Jennions, 2008; Liker et al., 2013). Therefore,

149   OSR bias emerges as a consequence of sex-biased behaviour e.g. dispersal to independent

150   breeding) rather than being a driver (Komdeur, Székely, et al., 2017; Long et al., 2022; Székely

151   et al., 2014). In socially monogamous mating systems, OSR is expected to emerge from ASR

152   through monogamous pair-bonds, whereas for polygamous species OSR is largely dependent

153   on the rate of mate monopolisation and parental care that can be sex-biased (Carmona-Isunza

154   et al., 2017; Székely et al., 2014). Seychelles warblers often pair for life, meaning there is hardly

155   any mate acquisition during breeding (Edwards et al., 2018; Komdeur, 1991). Thus, the

156   cooperatively breeding and socially monogamous Seychelles warbler provides an excellent

157   opportunity to assess the interplay between ASR variation and dispersal propensity. We assess

158   the effect of ASR the breeding season before potential dispersal, because this can provide

159   insights into whether variation in ASR predicts subsequent individual dispersal decisions. As

160   inheriting a natal territory is extremely rare in the Seychelles warbler (8% of individuals),

161   acquiring a dominant breeding position happens primarily through dispersal (Kingma, et al.,

162   2016). Thereby, dispersal propensity is likely strongly driven by intrasexual competition for

163   breeding vacancies. Since we expect yearling males and females to explore their local

164   neighbourhood more intensively than the entire population, and might use this as a proxy for

165   demographic information on the population (Eikenaar et al., 2008), we assessed the effects of

166   ASR on dispersal at both a local (neighbouring territory level) and population level. Our ASR-

167   density hypothesis predicts an interacting effect of ASR and density on natal dispersal:

168   specifically, with a biased ASR and high density, the abundant sex is predicted to delay

169   dispersal, since under these conditions we expect competition for residency and breeding

170   positions in territories to be very high, thereby increasing costs of dispersal. We expect this

171   effect will decrease or disappear when ASR is less biased and/or the density is low, since the

172 competition for residency will be lower. The effect of ASR and density on dispersal is predicted

173 to be less pronounced in subordinate females than in subordinate males, since subordinate

174 females often produce offspring within their territory through co-breeding with the dominant

175 female when they delay dispersal, whereas subordinate males rarely gain parentage as a

176 subordinate (Groenewoud et al., 2018; D. S. Richardson et al., 2001, 2002). This study provides

177 novel insights on the combined effects of ASR and population density on natal dispersal in

178 cooperative breeders.

179

180 **METHODS**

181 *Study population and data collection*

182 The Seychelles warbler is a small insectivorous passerine endemic to the Seychelles

183 archipelago. The population on Cousin island (29 ha, 04°20'S, 55°40'E) consists of ca. 320 birds

184 in ca. 110 territories, which are maintained year round (Brouwer et al., 2009; Hammers et al.,

185 2019; Komdeur, 1992). In each year as many Seychelles warblers as possible are

186 caught/recaught using mistnets to ring birds and take morphometric measures (including

187 tarsus length ± 0.5 mm as a measure of skeletal size), and collect DNA (using ca. 25 µl blood

188 taken from the brachial vein) to determine sex using up to three sexing markers (following

189 Richardson et al. 2001). We used data from 1995 to 2019, since >96% of the population had

190 been ringed with a unique metal and colour ring during this period (Hammers et al., 2019;

191 Komdeur, 1992). Breeding occurs during the main breeding season (May – September) in the

192 period when food availability is highest (breeding occurs in 94% of territories in this period),

193 although individuals in 18% of territories breed during a minor breeding season (January –

194 March; Komdeur & Daan, 2005). The number of yearlings assessed for dispersal ranged

195 between 1 and 28 individuals per breeding season. Seychelles warblers are facultative

196 cooperative breeders, with approximately 50% of breeding pairs being accompanied by up to

197 four subordinates (average ± SE = 0.7 ± 0.02) of either sex, which are often retained offspring

198 from previous breeding attempts (Kingma et al., 2016). Remaining subordinates of either sex

199 can become helpers, but most helpers are female (88%; Komdeur, 1996; 68%; Richardson et

200 al., 2002). Dispersal likelihood is not sex biased (although females disperse further than

201 males), nor is likelihood of becoming a dominant breeder after dispersal (Groenewoud et al.,

202 2018). However, females are much more likely to become non-natal subordinates whereas

203 males are more likely to become floaters (dispersing individuals that are not part of a group).

204 Breeding attempts usually consist of a single egg (91%; Richardson et al., 2002). After

205 hatching, fledglings are fed for up to 3 months until independence (Komdeur, 1994). Post-

206 fledgling survival in the first year is 0.61 ± 0.09 SE, and increases to 0.81 ± 0.04 in adulthood

207 (i.e. 1 year of age; Brouwer et al., 2006). There is no sex difference in annual survival likelihood

208 of adults (Brouwer et al., 2006). Adults that acquire a dominant breeding position usually

209 defend their territory and remain with the same partner until death (Richardson et al., 2007).

210 Therefore, territory boundaries are relatively stable between years (Komdeur, 1991).

211 In each breeding season, every territory was monitored to regularly throughout the breeding

212 season determine group membership and social status by assessing an individual's presence

213 for 15 minutes, and antagonistic and affiliative interactions with conspecifics (Kingma,

214 Komdeur, et al., 2016; D. S. Richardson et al., 2002). Dominant breeders were identified mainly

215 via pair and courtship behaviour and mate guarding. Sexually mature individuals within

216 a breeding group that were not dominant breeders were classified as subordinates. In

217 territories with nests, one-hour watches were performed to reliably verify residency and social

218 status of individuals by assessing incubation and feeding behaviour of individuals (Van de

219 Crommenacker et al., 2011). Since inter-island dispersal is extremely rare (<0.1%; Komdeur et

220 al., 2004) and annual resighting probabilities are extremely high in the study population

221 (Brouwer et al., 2010), individuals that are not resighted in two consecutive breeding seasons

222 could be assumed to be dead. As Seychelles warblers mainly feed on insects on leaves and

223 lack natural predators, an index of territory quality was calculated using insect prey

224 abundance. Every breeding season, the numbers of insects on the underside of leaves (where

225 Seychelles warblers forage) were counted, and foliage cover and species abundance

226 measured. Next, mean monthly insect density was calculated per territory, corrected for the

227 plant species present (for a detailed description of the territory quality calculations, see

228 Brouwer et al., 2009; Komdeur, 1992). We excluded two field seasons in 2004 and 2011

229 because 58 and 59 birds respectively were translocated to another island just before the

230 breeding season as part of a conservation programme (Richardson et al., 2006; Wright et al.,

231 2014).

232 *ASR and density*

233 ASR and density were measured at the population level and at the local level. 'Population ASR'

234 was calculated as the proportion of adult individuals sighted in the population during a field

235 season that were male, with 0.5 indicating an equal number of adult males and females.

236 Population size was used as a measure of 'population density', since the number of territories

237 was almost constant over time. 'Local ASR' and 'local density' were assessed using all resident

238 individuals from territories located within two territory borders away from the home territory

239 of the focal individual in all directions during a field season. We defined local groups as such

240 since males disperse ≤2 territories away from their home territory more often than females

241 who typically disperse further from their natal territory (56% and 33% respectively; Eikenaar

242 et al., 2008). Additionally, most extra-group fathers (59% of paternities) are resident dominant

243 males within 2 territories distance from the focal offspring's territory (Richardson et al., 2001),

244 meaning that short- and long-distance dispersal likely have different costs and benefits

245   associated with them (Kingma et al., 2017). Since there is nearly no migration off the island

246   (Komdeur et al., 2004), ASR and density are dependent on recruitment and death of adult

247   individuals. We expect the variability in ASR and density to be small on fine temporal scales,

248   meaning seasonal demographic measurements of the breeding season prior to dispersal will

249   capture a close estimate of the measures during the moment individuals decide whether to

250   disperse. We classified natal dispersal as establishment (i.e. consistently seen in territory

251   during weekly checks throughout the breeding season) in a territory other than the natal

252   territory. Individuals rarely visit other territories, as they are attacked by the territory owners

253   when doing so (Kingma, Komdeur, et al., 2016). Natal dispersal was determined for yearlings

254   only (dispersal until 1 year of age) to exclude potential influences from previous potential

255   dispersal events (i.e. if individuals 'choose' not to disperse before, they might be more/less

256   likely to do so later) and age-dependent effects on dispersal. Only including yearlings also

257   eliminates pseudoreplication due to the same individual being included repeatedly. Since

258   most Seychelles warblers disperse from their natal territory as yearlings (Groenewoud et al.,

259   2018), most natal dispersal events are still captured by our analyses. As we could not

260   determine whether juveniles that did not survive to one year of age had attempted to disperse

261   from their natal territory, we cannot directly infer the mortality of dispersing and thus the

262   direct cost of dispersing *per se*.

263
264   *Statistical analysis*

265   We separately assessed the natal dispersal probability of male (*N* = 145) and female (*N* = 132)

266   yearlings, since we expect that ASR will affect male and female dispersal propensities in

267   opposite directions. The dataset included the following fixed effects: population and local ASR

268   during the breeding season before potential yearling dispersal is tracked (between fledgling

269 and reaching one year of age), population density and local density, tarsus length, (natal)

270 territory quality, number of female subordinates (split into <2 years and ≥2 years old, see

271 below), and number of male subordinates on the natal territory (Table 1). Individuals can

272 disperse when they are 3 months old, but the exact timing of dispersal could not be

273 determined since the populations are only monitored in the breeding seasons. Thus, we

274 assumed the ASR and density at time of dispersal to be that when individuals reached one

275 year of age. Female subordinates were categorised as <2 and ≥2 years old, since subordinates

276 older than 2 were never observed to prospect away from their resident territory (Kingma et

277 al., 2016). Since male subordinates >2 years old were very rare ($N = 8$, 3% of all natal

278 territories) all male subordinates were pooled in the analysis. Tarsus length might affect

279 dispersal probability (see Camacho et al., 2013) as it describes overall body size and serves as

280 a proxy for physiological condition (e.g. telomere length) (Bebbington et al. 2017; Spurgin et

281 al. 2018, Brown et al., 2022) and might be correlated with social dominance (Vedder et al.,

282 2010). Natal territory quality might affect dispersal probability, since yearlings can benefit

283 more from staying in a high-quality territory than in a low-quality territory (Komdeur, 1992).

284 Finally, territory group composition potentially affects dispersal; e.g. more subordinates in the

285 territory increases competition, especially if they are of the same sex as the focal individual,

286 thereby increasing dispersal likelihood (Groenewoud et al., 2018). To account for pseudo-

287 replication, we included the breeding season and breeding group (i.e. all individuals in a

288 territory in a given field period) as random effects, since two yearlings can come from the

289 same breeding group ($N =21$ individuals born in the same group in the same breeding season).

290 We used a model averaging approach in R (4.2.2; R Core Team, 2020), using global generalised

291 mixed effect models (GLMMs) containing all fixed effects. Global GLMMS were built with

292 binomial error structure and a logit link function using the *lme4* (1.1-23) package (Bates et al.,

293   2015), with the 'Bobyqa' non-linear optimization (Powell, 2009) to aid model convergence.

294   Territory quality measures were log transformed to correct for the right skew in these data.

295   All continuous variables were z-transformed (mean centred and scaled by one SD) over the

296   entire observation period to facilitate interpretation and comparison of model coefficients. To

297   assess whether there was an overall sex difference in ASR-dependent dispersal probability,

298   we built a separate global GLMM including two three-way interactions between 1) sex,

299   population ASR and population density and between 2) sex, local ASR, and local density

300   respectively. However, we may not have sufficient power to model three-way interactions

301   with the sample size of this study, especially for dispersal, a complex behaviour that may be

302   driven by multiple factors that explain variance. Therefore, we did test the effect of population

303   ASR and population density and local ASR and local density separately for each sex. The global

304   model included interaction effects between population density and population ASR, as well as

305   between local density and local ASR. Using the variance inflation factor (VIF) we found no

306   substantial collinearity between fixed effects (all VIF ≤ 3). There was no correlation between

307   population ASR and population density (Pearson's correlation: r = 0.137, t_{31} = 0.771, P = 0.45)

308   and local ASR and local density (Pearson's correlation: r = -0.006, t_{252} = -0.087, P = 0.93), which

309   allowed them to be included in the same model. From each global model, we built competing

310   models based on all possible combinations of fixed effects and ranked these models by AICc

311   score (*MuMIn* package, 1.43.17; Bartoń, 2020). All models with ΔAICc ≤ 7 were included in the

312   top model set (Burnham et al., 2011). We re-analysed our top model set with a more

313   conservative cut-off of ΔAICc = 2 and found our results to be consistent. We calculated

314   conditional averaged estimates for each variable containing the natural averages, i.e. model-

315   weighted predictions for the variable of interest at the mean of all other parameters. We used

316   natural averages rather than full averaged models since we were specifically interested in the

317 effects of ASR and density on dispersal, and these could otherwise be masked by other

318 covariates on the models (Grueber et al., 2011).

319

320 *Ethical note*

321 The research adhered to the ASAB/ABS Guidelines for ethical treatment of nonhuman animals

322 in research. Fieldwork was conducted with the permission of the Seychelles Bureau of

323 Standards and the Seychelles Ministry of Environment, Energy and Climate Change, and

324 adhered with all local ethical guidelines and regulations. Nature Seychelles provided

325 permission to work on Cousin Island.

Parameter	Predicted effect on dispersal probability	Prediction met?
Population ASR	Stronger population sex-bias leads to decreased dispersal by the more abundant sex, due to lack of breeding opportunities	Males: yes (Table 2, Figure 1) Females: no
Local ASR	Stronger local sex-bias leads to decreased dispersal by the more abundant sex, due to apparent lack of breeding opportunities	No
Population density	A more pronounced effect of population ASR when population is close to saturation, due to more pronounced lack of breeding opportunities	Males: yes (Table 2, Figure 1) Females: no
Local density	A more pronounced effect of local ASR when local group is (close to) being saturated, due to more pronounced lack of breeding opportunities	No
Territory quality	A higher natal territory quality will reduce dispersal probability	No
Natal territory composition	If same-sex (and for females similar aged) subordinates are present, dispersal probability increases due to local competition	No
Body size (tarsus length)	Increase in dispersal probability, since larger individuals can afford the costs of dispersal better	No

326

327 *Table 1. Parameters of interest, the predictions on their relationship with dispersal probability*

328 *of yearling Seychelles warblers, and whether these predictions were met in the present study.*

329

330
331 **RESULTS**

332 Over the 33 (main and minor) breeding seasons monitored in our study, the population

333 density ranged between 26 -369 individuals (mean ± SD = 338 ± 37, Figure S1). Of all territories

334 with fledglings that survived to one year of age for which we had access to all fixed effect data

335 ($N_{fledglings}$ = 277, Table 1), 57% contained subordinates (range 25-68% per year, $N_{territories}$ = 146),

336 with 1–4 subordinates per territory. Population ASR was on average female biased (range =

337 0.44 − 0.54; mean ± SD = 0.48 ± 0.03, Figure S1) and deviated significantly from 0.5 (one-

338 sample t-test: t = -4.096, $N_{seasons}$ = 33, P < 0.001). Local ASR varied more widely, but was still

339 on average female biased (range = 0.35 − 0.68; mean ± SD = 0.48 ± 0.05) and deviated

340 significantly from 0.5 (one-sample t-test: t = -5.450, $N_{territories}$ = 256, P < 0.001). Of all yearling

341 warblers, 40% (N = 79) of males and 41% (N = 73) of females dispersed.

342 Natal dispersal of juvenile males was best described by an interaction between population

343 ASR and population density (Table 2, Figure 1). This interaction indicates that in years with

344 moderate to high population density male dispersal probability increased when the

345 population ASR was more female biased, whereas, in years with a lower population density

346 (i.e. below the long term saturation level of the population) there was no effect of ASR on

347 dispersal propensity (95% CI of the mean ASR effect for the 33% lowest population densities

348 overlaps zero). All other variables tested, including population ASR and population density

349 separately, had 95% CIs overlapping zero, meaning they were not associated with male natal

350 dispersal.

351 The probability of female juvenile natal dispersal was not associated with any of the variables

352 in the model (Table S1, Figure 1). Finally, the top model set of natal dispersal probability for

353 both sexes found no interaction between sex, ASR and density (neither at the local or

354 population level) (Table S2). None of the models in the model set that included the interaction

355 between sex, ASR and density showed a significant interaction, indicating that neither overall

356 ASR nor density significantly differ in how they influence the dispersal propensity of either sex.

357

358

Fixed	β	SE	z	95% CI
(Intercept)	-0.48	0.24	1.97	-0.96, -0.001
Population ASR	-0.45	0.25	1.77	-0.94, 0.05
Local group density	-0.36	0.24	1.47	-0.84, 0.12
Population density	0.08	0.22	0.34	-0.36, 0.51
Population ASR * Population density	**-0.74**	**0.34**	**2.16**	**-1.41, -0.07**
Territory quality	0.29	0.22	1.29	-0.15, 0.72
Local ASR	0.28	0.24	1.14	-0.20, 0.76
Male subordinates	-0.21	0.23	0.87	-0.68, 0.26
Young female subordinates	-0.08	0.20	0.40	-0.48, 0.32
Old female subordinates	-0.06	0.20	0.27	-0.46, 0.35
Tarsus length	-0.01	0.24	0.06	-0.49, 0.46
Local ASR * Local group density	0.29	0.33	0.86	-0.37, 0.95
Random	σ^2	N		
Field period : Breeding group	0.687	139		
Field period	0	30		

Response: juvenile male dispersal likelihood (N = 145)
Candidate models: 800. Top set models: 332

359

360 *Table 2. Model-averaged parameters: the effect of socio-ecological predictors on the*

361 *probability of dispersal in male Seychelles warblers until the age of 1. Conditional model-*

362 *averaged estimates (β), standard errors (SE), z-values, and 95% confidence intervals (CIs) are*

363 *shown for all predictors featuring the top model set (ΔAICc ≤ 7). Random effect variances (σ^2)*

364 *and number of levels (N) in the best model are also shown. Significant predictors whose CIs do*

365 *not overlap with zero are given in bold.*

366
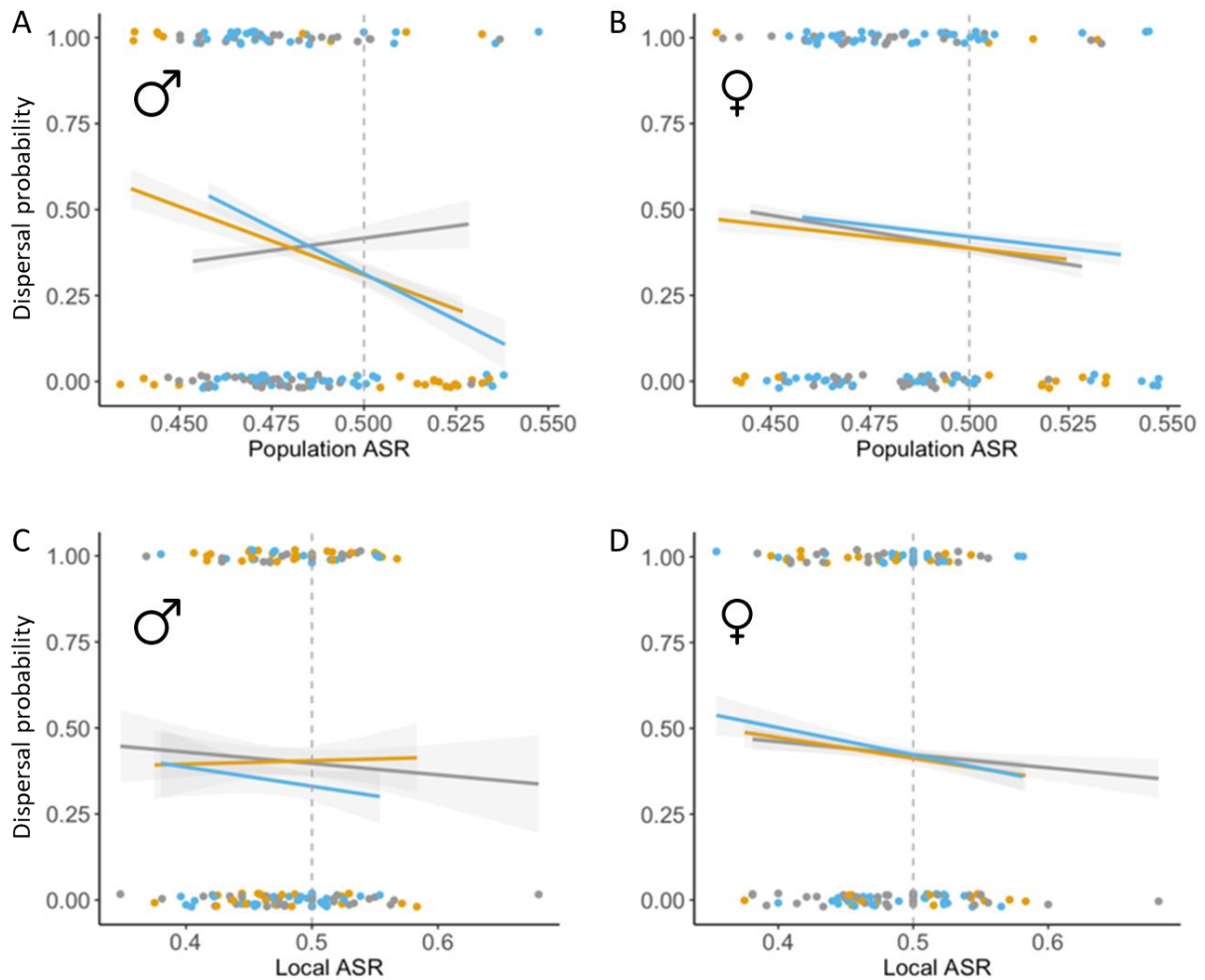
Figure 1. Dispersal probability of yearlings in relation to adult sex ratio (ASR) and density in the Seychelles warbler. The interaction between population ASR and population density is depicted for (A) male and (B) female yearlings. The interaction between local ASR and local density is depicted in (C) male and (D) female yearlings.

For the sake of visualisation, population (N = 33) and local density (N = 256) are categorised in even sample sizes as low (in grey, lowest 33%), middle (in orange, middle 33%) and high (in blue, highest 33%) but are used as continuous variables in the analyses. Lines depict the model averaged predictions (see main text), with the 95% CI (shaded area). Each point refers to one individual (N = 145 in males, N = 132 in females). The dashed line depicts an equal ASR. The

377 *interaction effect of population ASR and population density is significant for males, whereas*

378 *all the other effects are not significant (Table 2).*

379 **DISCUSSION**

380 Demographic composition may play a key role in explaining some of the considerable inter-

381 specific and intraspecific variation in dispersal behaviour observed in cooperative breeders.

382 Our study reveals that population ASR and population density predict the natal dispersal

383 probability of male, but not female, yearlings in the Seychelles warbler. We found no evidence

384 for a 3-way interaction between ASR, density, and sex in an analysis with both sexes combined

385 - indicating that there is no significant sex difference in dispersal in relation to ASR and density.

386 However, an analysis performed for both sexes separately showed that there was evidence

387 for a density-dependent effect of ASR on dispersal in males, but not in females. The effect of

388 ASR on male natal dispersal probability varied with population density, i.e. the propensity of

389 male yearlings to disperse in response to biases in ASR changed with respect to density.

390 Specifically, males are more likely to disperse from their natal territory when the population

391 ASR is female biased and the population density is moderate to high, but this effect disappears

392 when the population density becomes lower.

393 When there are more males in a population, the competition for a breeding vacancy for males

394 will likely increase, independent of the mating system. Indeed, when ASR is male biased and

395 population density is high, there is a high absolute number of males in the population, which

396 may cause high dispersal costs in terms of increased competition among males for residency

397 in a territory and for breeding positions. Therefore, a better strategy for male Seychelles

398 warbler yearlings may be to delay dispersal and remain in a territory either to inherit it

399 (although this is very rare; Kingma et al., 2016), bud off a part of the natal territory as their

400 own breeding territory (Komdeur & Edelaar, 2001), or to wait for breeding vacancies as they

401 become available in nearby territories (Kingma et al., 2016). An alternative to staying is to

402 disperse as a floater: roaming through the population without association with any territory

403 (Groenewoud et al., 2018). However, this is a highly costly strategy as they cannot enjoy

404 group-living benefits generally experienced by cooperative breeders (Koenig et al., 1992;

405 Ridley et al., 2008). The survival of floaters is very low in Seychelles warblers, with only 9% of

406 floaters surviving to the next breeding season compared to 67% of subordinates that are

407 resident in a territory (Kingma et al., 2016). Still, in scenarios with extremely high competition

408 for breeding vacancies, floating might be a valuable strategy as they are more likely to detect

409 potential breeding vacancies as they move freely through the population (Kokko & Sutherland,

410 1998). . In breeding seasons with low population density, there is likely to be reduced overall

411 competition, which makes dispersal less costly, independent of ASRs. Competition among

412 males is likely to be lower even when ASR is still male biased, since the population is not

413 saturated and males may be better able to find residency and perhaps even become a

414 dominant breeder. Even in years with low population densities and a male-biased ASR, usually

415 all breeding vacancies for the rarer sex (here: females) are filled. As this species is socially

416 monogamous, this implies there is no shortage of potential partners per se, but rather a

417 shortage of available territories. This result is congruent with recent findings indicating the

418 relationship between dispersal and cooperation need not be straightforward, and dispersal in

419 cooperative breeders is likely to be strongly influenced by intrasexual competition (Jungwirth

420 et al., 2023). Dispersal propensity of cooperatively breeding species displays strong intrasexual

421 variation (Trochet et al., 2016), which may be strongly dictated by demographic composition.

422 Importantly, male dispersal was associated with population-wide but not local ASR and

423 density. This suggests that males may have access to information on breeding vacancies of the

424 entire population. Although prospecting males are usually observed close to their natal

425   territory (Kingma et al., 2016; Kingma et al., 2017), some survey a considerable part of the

426   population outside of the breeding season (Komdeur, 1991; Komdeur & Edelaar, 2001), when

427   warblers are likely more relaxed in terms of territory defence and antagonistic interactions.

428   Moreover, since individuals can face high fitness costs by being attacked by conspecifics during

429   prospecting trips (Kingma et al., 2016), they are often very inconspicuous to avoid antagonistic

430   interactions (Komdeur, 1991), making it harder to detect them in the field. Finally, selectively

431   prospecting certain territories may increase the likelihood of successful dispersal even when

432   to territories further away as was found in cooperatively breeding fish (Jungwirth et al., 2015).

433   Altogether, when competition for breeding vacancies is expected to be high, prospecting

434   larger areas (here: population rather than local neighbourhood) may provide strong benefits

435   in likelihood of acquiring a breeding position, especially in highly saturated populations.

436   We found no association between any tested variable and natal dispersal probability in

437   females, which was expected since females are less dependent on becoming a dominant

438   breeder to produce offspring since they can also become co-breeder. However, we found no

439   significant difference in the effect of ASR and density on dispersal propensity between males

440   and females. This is consistent with previous work indicating there is no sex bias in dispersal

441   natal dispersal in the Seychelles warbler (Groenewoud et al., 2018). Still, we suggest that the

442   lack of an effect may be due to our limited sample size. The variance in population ASR is

443   relatively small and mostly female biased. Therefore, it might not be possible to find a

444   significant effect of ASR and density on female dispersal probability, as the effect in females

445   is in any case expected to be small due to co-breeding opportunities, and we mostly would

446   expect an effect in years with a male-biased ASR. Thus, finding a significant three-way

447   interaction between sex, ASR and density would probably require more power; also, we

448   expect other factors to have an influence on dispersal (variance that could be considered noise

449   in our model). We expect our results on male dispersal to be important, but they should be

450   considered with care and we hope future research can consider this question as well for

451   comparison.

452   Females can reproduce as a subordinate (natal and non-natal) by becoming a co-breeder,

453   whereas males almost never gain paternity as a subordinate (D. S. Richardson et al., 2002) .

454   Co-breeding occurs frequently: ca. 30–40% of the subordinate females produce offspring in a

455   given year (Richardson et al., 2001, 2002, 2003), totalling to 11% of offspring being produced

456   by subordinate females (Raj Pant et al., 2019). Subordinate reproduction is common among

457   cooperatively breeding species but there is large inter-sex and inter-species variation in

458   reproduction rates (Komdeur, Richardson, et al., 2017), which may in turn affect how strongly

459   ASR dictates intrasexual competition and dispersal propensity among different species.

460   Dominant females also gain benefits from subordinate females in their breeding territory:

461   allowing females to co-breed reduces egg-predation by Seychelles fodies *Foudia sechellarum*

462   (Kingma et al. Unpublished data) and helping by female subordinates is associated with

463   increased lifespan and delayed senescence of the dominants (Hammers et al., 2019). Finally,

464   females can gain substantial inclusive fitness benefits through helping in their natal territory

465   when the dominant breeders are their parents. Helper presence increases the reproductive

466   success of their parents (Komdeur, 1994), and dominant females gain inclusive fitness benefits

467   by allowing subordinates to breed; they increase their own reproductive success and gain

468   indirect benefits from related subordinates producing offspring (Richardson et al., 2002).

469   When parents are replaced by unrelated step-parents, subordinates are more likely to

470   disperse from their natal territory, presumably since future indirect fitness benefits decrease

471   (Eikenaar et al., 2007).

Individuals that disperse and become subordinates in non-natal groups are predominantly female (87%; Groenewoud et al., 2018). Female intruders are attacked less by conspecifics when venturing to new territories than males (Kingma et al., 2017), and therefore may be more likely to be accepted as a non-natal subordinate. Additionally, females may also gain parentage by co-breeding as a non-natal subordinate (Groenewoud et al., 2018; D. S. Richardson et al., 2002). Thus, females can still breed and disperse when dominant breeder vacancies are not readily available. Conversely, males rarely settle as non-natal subordinates (Groenewoud et al., 2018), and only very rarely gain paternity as a subordinate (D. S. Richardson et al., 2001, 2002; Sparks et al., 2021). Therefore, males are more limited in their options and highly dependent on the available breeding vacancies.

Since delayed dispersal is a route to cooperative breeding and group living (Ekman et al., 2004; Griesser et al., 2017; Kingma et al., 2021; Koenig et al., 1992), the association between dispersal probability, population density and adult sex-bias has important implications. In a recent theoretical framework, García-Ruiz et al. (2022) showed that delayed dispersal as a pathway to cooperative breeding can be solely explained by group living benefits, and the possibility of gaining a breeding position in the natal territory by queueing as a subordinate. However, in the Seychelles warbler, territory inheritance as a subordinate is rare (Kingma et al., 2016b), and intrasexual competition is likely a predominant mechanism behind delayed dispersal in this highly saturated population. Our study therefore provides a rare empirical link between demographic drivers and routes to cooperative breeding. To our knowledge, this is the first study on dispersal in which ASR and density are considered on both a local and population level, since accurate measures of population density and ASR are extremely rare in the wild. Our study highlights the importance of taking sex-specific effects into account when studying the evolution of group-living. We suggest to include all adult individuals in the

496 population for assessing sex ratio effects (i.e. ASR) in socially monogamous species. By only

497 including the sexually active individuals (operational sex ratio; OSR), it is impossible to

498 disentangle sex ratio as an external factor that predicts dispersal decisions since it may both

499 be a cause and a consequence of dispersal. We assessed ASR and density seasonally, rather

500 than individually at the moment of maturation, meaning there is some variability in the

501 temporal distance between assessment of demographics and potential dispersal among

502 individuals. Measuring ASR and density at the moment in which a yearling decides whether to

503 disperse or not would provide a more accurate assessment of their effect. However, ASR does

504 not vary greatly among breeding seasons, meaning the noise introduced by the temporal

505 variability is expected to be minimal. Additionally, since we cannot assess exactly when an

506 individual decides to disperse in response to the demographic composition, it is impossible to

507 determine the precise moment ASR and density should be assessed. In order to elucidate the

508 causal relationships between demographic factors and dispersal in cooperative breeders and

509 identify the timeframe of information used for dispersing, it is necessary to experimentally

510 manipulate population ASR and density. For example, dispersal propensity can be

511 experimentally tested in response to temporally removing individuals from a breeding

512 territory, as was done by Heg et al. (2008). Future studies should experimentally manipulate

513 population ASR and density in order to investigate the causal relationships between these

514 factors and dispersal in cooperative breeders. We hope our analyses stimulate future studies

515 to unravel how variation in ASR affects the fitness costs and benefits of dispersal.

516

517

518 **DATA AVAILABILITY STATEMENT**

519 Data will become available on the University X dryad, via the following link:

520

521 Since we might still need to change things (for example after suggestions from reviewers),

522 the above link is not yet publicly available.

523

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