

1 **Socio-ecological conditions and female infidelity**  
2 **in the Seychelles warbler**

3 Abbreviated title: Conditions promoting infidelity in Seychelles warblers

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## Abstract

18

19 Within socially monogamous breeding systems, levels of extra-pair paternity  
20 can vary not only between species, populations and individuals, but also across  
21 time. Uncovering how different extrinsic conditions (ecological, demographic  
22 and social) influence this behavior will help shed light on the factors driving its  
23 evolution. Here, we simultaneously address multiple socio-ecological conditions  
24 potentially influencing female infidelity in a natural population of the  
25 cooperatively breeding Seychelles warbler, *Acrocephalus sechellensis*. Our  
26 contained study population has been monitored for over 25 years, enabling us  
27 to capture variation in socio-ecological conditions between individuals and  
28 across time and to accurately assign parentage. We test hypotheses predicting  
29 the influence of territory quality, breeding density and synchrony, group size and  
30 composition (number and sex of subordinates), and inbreeding avoidance on  
31 female infidelity. We find that a larger group size promotes the likelihood of  
32 extra-pair paternity in offspring from both dominant and subordinate females,  
33 but this paternity is almost always gained by dominant males from outside the  
34 group (not by subordinate males within the group). Higher relatedness between  
35 a mother and the dominant male in her group also results in more extra-pair  
36 paternity — but only for subordinate females — and this does not prevent  
37 inbreeding occurring in this population. Our findings highlight the role of social  
38 conditions favoring infidelity and contribute towards understanding the evolution  
39 of this enigmatic behavior.

40

## Introduction

41

42 The occurrence of extra-pair paternity (EPP: genetic promiscuity) within socially  
43 monogamous breeding systems is widespread (birds: see e.g. Richardson and  
44 Burke 1999; Foerster et al. 2003; mammals: see e.g. Schulke et al. 2004;  
45 Kitchen et al. 2006; Munshi-South 2007; fish: see e.g. Lee-Jenkins et al. 2015;  
46 Lee et al. 2016; Bose et al. 2018; reptiles: see e.g. Bull et al. 1998; While et al.  
47 2009; insects: see e.g. Dillard 2017), but its evolution remains enigmatic,  
48 despite decades of research (Griffith et al. 2002; Forstmeier et al. 2014; Taylor  
49 et al. 2014). Levels of EPP are highly variable, not only between different  
50 individuals, populations and species, but also across time (Petrie and  
51 Kempnaers 1998; Griffith 2000; Dietrich et al. 2004; Schroeder et al. 2016).  
52 This variation may be partly responsible for the ongoing lack of clarity  
53 surrounding the evolution of this phenomenon. Different extrinsic conditions —  
54 ecological, demographic and social — may play a key role in this variability, with  
55 certain factors promoting, and others suppressing EPP (Griffith et al. 2002;  
56 Westneat and Stewart 2003; Isvaran and Clutton-Brock 2007; Cohan and  
57 Allainé 2009; Brouwer et al. 2017). However, across taxa, which conditions  
58 affect EPP, and how, is still not fully understood (see reviews: Griffith et al.  
59 2002; Isvaran and Clutton-Brock 2007; Uller and Olsson 2008; Hsu et al. 2015).  
60 A potential problem is that the influence of socio-ecological factors on EPP has  
61 been investigated extensively in avian species, and to a lesser extent in  
62 mammals, while other taxa have received very little attention. This narrow  
63 taxonomic focus may have provided results which are limited by a lack of  
64 phylogenetic diversity. Importantly, up until recently, most studies investigating

65 the factors influencing EPP have focused on just one or very few hypotheses.  
66 This may have hampered knowledge on the relative importance of different  
67 conditions shaping levels of EPP (Brouwer et al. 2017).

68 Various ecological, demographic and social conditions have been  
69 proposed to influence EPP within socially monogamous systems, though the  
70 evidence for these hypotheses remains ambiguous (reviewed in Griffith et al.  
71 2002; Westneat and Stewart 2003; Ackay and Roughgarden 2007). For  
72 example, habitat quality (i.e. resource availability) has been predicted to  
73 influence EPP in two opposing ways. According to the constrained female  
74 hypothesis (Gowaty 1996), in species with biparental brood provisioning,  
75 females in high-quality territories can afford to be unfaithful because high  
76 resource availability should compensate for any reduction in paternal care by  
77 males who lose (confidence in) paternity. Alternatively, if females gain extra  
78 resources by mating with more than one male (e.g. access to the extra-pair  
79 male's territory for feeding), EPP may increase in low-quality areas (Gray 1997).  
80 Evidence for these alternative hypotheses is mixed, with some studies finding a  
81 positive (e.g. Hoi-Leitner et al. 1999; Charmantier and Blondel 2003) and others  
82 a negative (e.g. Vaclav et al. 2003; Rubenstein 2007) territory quality–EPP  
83 relationship.

84 Breeding density (i.e. the number of reproductively mature individuals in  
85 an area) has been predicted to increase potential mate encounter rate and,  
86 consequently, EPP frequency (Alexander 1974; Birkhead 1978; Gladstone  
87 1979; Moller and Birkhead 1993). Research assessing the effect of breeding  
88 density on EPP has provided conflicting results, with studies showing a positive

89 correlation (e.g. Moller 1991; Richardson and Burke 2001; Stewart et al. 2010;  
90 Annavi et al. 2014; Hellmann et al. 2015), a negative correlation (e.g. Barber et  
91 al. 1996; Verboven and Mateman 1997; Moore et al. 1999; Václav and Hoi  
92 2002) or no relationship (e.g. Rätti et al. 2001).

93         Another factor hypothesized to influence EPP is breeding synchrony, i.e.  
94 the overlap of female fertility within a population. The male assessment  
95 hypothesis predicts that breeding synchrony increases EPP by enabling  
96 females to compare potential mates more effectively (Stutchbury and Morton  
97 1995). In contrast, the male trade-off hypothesis expects higher synchrony to  
98 decrease EPP because males will face a higher trade-off between mate-  
99 guarding and seeking copulations with extra-pair females (Westneat 1990).  
100 Studies addressing the relationship between breeding synchrony and EPP have  
101 provided mixed evidence so far (positive relationship: e.g. Stutchbury et al.  
102 1997; Stutchbury et al. 1998; negative relationship: e.g. Saino et al. 1999; van  
103 Dongen & Mulder 2009; no relationship: e.g. Kempnaers et al. 1997; Hoi-  
104 Leitner et al. 1999; Richardson and Burke 2001; Arlt et al. 2004; Brouwer et al.  
105 2017).

106         In group-breeding taxa, characteristics of the social group have also  
107 been predicted to influence genetic promiscuity. In cooperative breeders in  
108 which groups consist of a dominant pair and non-reproducing helpers, the  
109 proportion of EPP may increase when more helpers are present. Helpers may  
110 liberate females from their dependency on their social males, i.e. by mitigating  
111 the impact of those males reducing their parental care if they lose (confidence

112 in) paternity (Mulder et al. 1994). For example, in many *Maluridae* species, EPP  
113 frequency was shown to increase with the number of helpers (Mulder et al.  
114 1994; Webster et al. 2004; Brouwer et al. 2017; Hajduk et al. 2018; but see:  
115 Johnson and Pruett-Jones 2018). In some species, within-group EPP may  
116 occur because it leads to increased overall care to the brood and thus load-  
117 lightening for the dominant individuals, as a result of investment by those  
118 subordinates gaining paternity (Davies 1992). Evidence for this exists in several  
119 species, including dunnocks, *Prunella modularis* (Davies et al. 1996), and  
120 cichlids, *Neolamprologus pulcher* (Bruitjes et al. 2011).

121 In taxa in which social groups include multiple breeding males and  
122 females, genetic promiscuity can be considered in terms of extra-group  
123 paternity (EGP), resulting from the fertilization of females by males outside the  
124 social group. Group size has been predicted to increase the EGP frequency in  
125 such taxa, via a reduction in a male's ability to monopolize females (Van  
126 Noordwijk and Van Schaik 2004). In particular, it has been predicted that when  
127 there are more females in a group, males will be less effective in controlling or  
128 defending individual females (Isvaran and Clutton-Brock 2007). On the other  
129 hand, male group size has been expected to reduce the proportion of EGP,  
130 because of increased male monopolization of females (Van Noordwijk and Van  
131 Schaik 2004). To date, the relationship between EGP and group  
132 size/composition has not been resolved (see e.g. Van Noordwijk and Van  
133 Schaik 2004; Isvaran and Clutton-Brock 2007; Rubenstein 2007; Ruiz-  
134 Lambides et al. 2017).

135           The relatedness of the male and female in a pair has also been predicted  
136 to influence patterns of EPP. According to the inbreeding avoidance hypothesis  
137 females should seek extra-pair fertilizations when they are closely related to  
138 their social males in order to increase offspring heterozygosity and fitness  
139 (Brooker et al. 1990; Blomqvist et al. 2002). Evidence for this hypothesis is  
140 mixed, with some studies showing a positive relationship between pair  
141 relatedness and EPP (e.g. Blomqvist et al. 2002; Eimes et al. 2005; Arct et al.  
142 2015) and others finding no such relationship (e.g. Schmoll et al. 2005; Ackay  
143 and Roughgarden 2007; Edly-Wright et al. 2007; Barati et al. 2018).

144           Here, we simultaneously assess the relationship between multiple socio-  
145 ecological factors and female infidelity using data from a long-term study of an  
146 isolated population of Seychelles warblers, *Acrocephalus sechellensis* (see  
147 Table 1 for details). The Seychelles warbler is a socially monogamous, yet  
148 genetically promiscuous species, in which extra-pair fertilizations are common;  
149 ca 44% of offspring are sired by males other than the social male (Richardson  
150 et al. 2001; Hadfield et al. 2006). Individuals are territorial and live either in pairs  
151 or in groups consisting of a dominant pair and subordinate birds (helpers and  
152 non-helpers; Komdeur 1992; Richardson et al. 2002; Richardson et al. 2007).  
153 Subordinate females sometimes lay eggs in the dominant females' nest,  
154 accounting for ca 15% of offspring in the population (Richardson et al. 2001;  
155 Hadfield et al. 2006). Almost all paternity is gained by dominant males, with just  
156 2% of offspring being sired by subordinate males within the group (Richardson  
157 et al. 2001; Hadfield et al. 2006), usually those transitioning towards dominant  
158 status (H. Dugdale, unpublished data), while there are no recorded cases of

159 extra-group paternity (EGP) gained by subordinates (Richardson et al. 2001).  
160 Hence, EPP in this species is almost completely EGP, i.e. the result of  
161 fertilizations by males outside the group.

162 Our study population of the Seychelles warbler is confined to a single  
163 small island (Cousin, Seychelles) and displays virtually no inter-island dispersal  
164 (Komdeur et al. 2004; Komdeur et al. 2017). Since 1997, > 96% of Seychelles  
165 warblers on this island have been individually color-ringed and blood-sampled  
166 for sexing and parentage assignment (Brouwer et al. 2010). These features of  
167 our study population enable accurate parentage, reproductive output and  
168 survival estimates, unconfounded by migration in or out of the population. The  
169 long-term nature of the monitoring also enables us to capture changes in socio-  
170 ecological conditions across the lifetime of individual birds. The simultaneous  
171 assessment of multiple socio-ecological conditions in this study system  
172 therefore provides a powerful approach to reveal the factors influencing EGP.

173

## 174 Methods

### 175 *Study system*

176 The Seychelles warbler is an insectivorous passerine endemic to the  
177 Seychelles archipelago. The population on Cousin Island (29 ha, 04°20'S,  
178 55°40'E) has been monitored since 1981 (Komdeur 1992; Richardson et al.  
179 2002; Wright et al. 2014; Bebbington et al. 2017). Monitoring efforts were  
180 intensified since 1997: virtually all breeding attempts have been followed every



181 year during the major breeding season (June-September) and, often, during the  
182 minor breeding season (January-March, Richardson et al. 2002; Richardson et  
183 al. 2010). Every year, as many individuals as possible were caught with mist-  
184 nets, blood sampled (ca. 25  $\mu$ l) and, if caught for the first time, given a unique  
185 ring combination (a British Trust for Ornithology metal ring and three color  
186 rings). As inter-island dispersal is virtually absent ( $< 0.1\%$ ; Komdeur et al. 2004;  
187 Komdeur et al. 2017) and re-sighting probability is very high (ca 92% for  
188 individuals up to 2 years old and 98% for older birds), individuals that were not  
189 observed over two consecutive seasons could be confidently assumed to be  
190 dead (Brouwer et al. 2006; Brouwer et al. 2010).

191 Blood samples were used for molecular sexing, following Griffiths et al.  
192 (1998), and genotyping using 30 microsatellites (Richardson et al. 2001;  
193 Spurgin et al. 2014). Parentage assignment was completed using MasterBayes  
194 2.52 (for details see: Edwards et al. 2018). Pairwise genetic relatedness  
195 between each mother (dominant or subordinate) and the dominant male in her  
196 group was calculated based on the microsatellite data by implementing Queller  
197 and Goodnight's (1989) estimation of relatedness with the R package 'related'  
198 v. 0.8 (Pew et al. 2015).

199 Seychelles warblers are territorial: individuals normally pair up, reside in  
200 and defend the same territory for life (Komdeur 1992; Richardson et al. 2007).  
201 In about 30% (1997-1999) or 50% (2003-2014) of territories, the dominant pair  
202 is joined by one or more subordinates of either sex (Komdeur 1992; Richardson  
203 et al. 2002; Richardson et al. 2007; Kingma et al. 2016). Subordinates are often,  
204 but not always, offspring that delay dispersal from their natal territory (Kingma et

205 al. 2016). Throughout each breeding season, censuses were performed in all  
206 territories to assign group membership and determine individual status. Groups  
207 were identified based on foraging location, proximity and non-aggressive  
208 interactions between individuals. Within groups, dominant breeders were  
209 identified via clear courtship and pair behavior and subordinates were assigned  
210 helper or non-helper status, based on whether they contributed to raising young  
211 in the territory (Komdeur 1992; Richardson et al. 2002).

212         Seychelles warblers feed on arthropods, 98% of which are taken from  
213 the underside of leaves (Komdeur 1991). Hence, territory quality was calculated  
214 in terms of arthropod availability, estimated using a combination of arthropod  
215 counts, vegetation cover and territory size (Brouwer, Tinbergen, et al. 2009).  
216 Reproduction is seasonally limited by arthropod availability and is energetically  
217 expensive, as both sexes feed young for four months after hatching (Komdeur  
218 1996; Komdeur et al. 2017).

219

#### 220 *Dataset and parameter estimation*

221 We assessed the relationship between nine different socio-ecological  
222 parameters and the probability that young are sired by extra-group males (EGP  
223 likelihood). We obtained parentage data from previous work (Richardson et al.  
224 2001; Hadfield et al. 2006; Spurgin et al. 2014; Edwards et al. 2017) for  
225 individuals born on Cousin during major breeding seasons between 1997 and  
226 2014. A dataset consisting of offspring and the socio-ecological factors  
227 associated with each offspring's natal group during the individual's hatching

228 season was compiled (summarized in Table 1). We excluded offspring sired by  
229 within-group subordinate males (i.e. cases of within-group EPP) and young  
230 produced by extra-group subordinate males, as these were both very rare (9  
231 and 16 out of 990 offspring, respectively).

232

### 233 *Statistical analyses*

234 We separately assessed the effect of socio-ecological parameters on EGP  
235 likelihood of offspring from dominant ( $n = 861$ ) and subordinate ( $n = 104$ )  
236 females, as these may differ in terms of the most influential factors and their  
237 interactions. For simplicity, we refer to the EGP of offspring from dominant or  
238 subordinate females as ‘dominant female EGP’ or ‘subordinate female EGP’,  
239 respectively (EGP of offspring is the result of female infidelity). Information on  
240 all parameters was not available for all offspring, so we subdivided the dominant  
241 female dataset into three subsets with no missing values. Subset A ( $n = 816$ )  
242 was created by including all socio-ecological factors except breeding synchrony  
243 and clutch size, as these could be estimated only for a smaller number (see  
244 below) of offspring with the relevant nest information available. Territory quality  
245 data was unavailable for  $< 25\%$  of offspring (due to shorter fieldwork periods in  
246 a couple of years), but was included in subset A with missing data points  
247 extrapolated from adjacent seasons (mean territory quality value of the previous  
248 and the following main breeding season, following Brouwer et al. 2006). To test  
249 that this extrapolation did not affect results, we compiled a second subset (B,  $n$   
250 = 636), consisting of cases with complete territory quality (non-extrapolated)

251 data and all other data, except breeding synchrony and clutch size. We then  
252 created a third subset (C,  $n = 356$ ) with all available nest information, to address  
253 the effect of breeding synchrony and to control for a potential effect of clutch  
254 size. We did not subset the subordinate female dataset due to sample size  
255 limitations.

256 We analyzed each subset/dataset with an information-theoretic approach  
257 (model averaging) using R (v.3.4.0), based on the construction of global  
258 generalized mixed effect models (GLMMs) containing all non-collinear ( $VIF \leq 3$ )  
259 variables of interest as fixed effects (package *lme4* 1.1-12; Bates et al. 2015).  
260 To assess the effect of group size (which included immature birds) and of just  
261 the number of reproductively mature subordinates (which were correlated), we  
262 built two sets of models, each including one of these predictors with all other  
263 fixed effects and ran separate analyses. It was possible to model the number of  
264 helpers alongside group size or the number of mature subordinates because  
265 the number of helpers was not collinear with either of the latter two variables  
266 ( $VIF \leq 3$ ). Even though the number of mature subordinates included helpers  
267 and non-helpers, we modelled the number of helpers alongside that of all  
268 mature subordinates, rather than with the number of non-helping subordinates.  
269 We did this because we had specific predictions on the effect that helpers and  
270 mature subordinates may have on EGP (see Table 1), while we had no  
271 predictions for non-helping subordinates. Global GLMMs were built with a  
272 binomial error structure, standardization (scaling and centering) of continuous  
273 predictors and the '*Bobyqa*' non-linear optimization (Powell 2009) for model  
274 convergence. To eliminate pseudo-replication, we included the following

275 random effects: year, mother identity and social male identity. In analyses of the  
276 subordinate dataset featuring group size/helpers/mature subordinates split by  
277 sex, we combined mother identity and social male identity in one random effect  
278 (social pair identity), to avoid model overfitting. We used this combined random  
279 effect also when analyzing subset C, to aid model convergence. Here, we also  
280 included nest identity, since nest information was available, and found that this  
281 random effect explained zero variance (see Results section). From each global  
282 model, we built competing models based on all possible fixed effect  
283 combinations, ranked these models by AICc scores and assigned them Akaike  
284 weights ( $\omega_m$ ) based on such scores (package *MuMIn* 1.40.0, Barton 2017). All  
285 models with AICc within 2 of the best model AICc ( $\Delta AICc \leq 2$ ) were included in  
286 the top model set. We calculated full averaged estimates for each variable, i.e.  
287 model-weighted averages of predictor estimates over all top set models,  
288 including models that did not contain the predictor (in such models the estimate  
289 was zero). We also calculated the relative importance ( $\omega_p$ ) of explanatory  
290 variables, i.e. the sum of Akaike weights of all top set models containing the  
291 variable. Since models where  $\Delta AICc$  ranges 2-7 may have some support  
292 (Burnham et al. 2011), we re-analyzed our data using a top model set cut-off of  
293 7  $\Delta AICc$  and found results to be consistent. As the subordinate mother dataset  
294 was smaller – 101 offspring with no missing data (ignoring nest information) –  
295 and nest-related data was available only for 49 offspring, we analyzed all  
296 variables of interest, except breeding synchrony and clutch size, in relation to  
297 subordinate female EGP likelihood (Table 3).

298

## Results

299

300 We obtained parentage data for 990 offspring: 884 produced by dominant  
301 females and 106 by subordinate females. Out of all 990 offspring, 965 were  
302 sired by dominant males and 25 by subordinate males. Since cases of within-  
303 group and extra-group subordinate paternity were both very rare (9 and 16  
304 offspring, respectively), we excluded these from our analyses of EGP. The  
305 overall frequency of EGP was 41% (395/965). There was a tendency for  
306 subordinate mothers to have a higher proportion of offspring with EGP, 51%  
307 (53/104), than dominant mothers, 40% (341/861), but this did not reach  
308 statistical significance (GLMM:  $\beta_{Mother\ status} = 0.46 \pm 0.26$ ,  $p = 0.07$ ; Table S2).  
309 Dominant females produced 89% of all offspring and subordinate females 11%.  
310 However, only 32% of territories included  $\geq 1$  reproductively mature (i.e.  $\geq 8$   
311 months old) female subordinate. In these territories, 66% of all offspring had a  
312 dominant mother and 34% a subordinate mother. The genetic relatedness ( $R$ )  
313 between a female and the dominant male in her territory did not differ with  
314 respect to female status (LM:  $\beta_{Mother\ status} = 0.02 \pm 0.03$ ,  $p = 0.64$ ).

315

### 316 *Dominant female EGP*

317 Dominant female EGP increased in larger groups (Fig. 1, Table 2) and both  
318 male and female group size had similar (positive) effects (Table S3). Dominant  
319 female EGP was also higher in territories with more mature subordinates (Table  
320 S4), though group size was a better predictor of EGP than the number of

321 mature subordinates (the AICc score of the best overall model containing group  
322 size was six units lower than the AICc of the best overall model including the  
323 number of mature subordinates, Tables S13, S15). Male and female mature  
324 subordinates both had positive effects on dominant female EGP (Table S5); the  
325 analysis including these as two separate predictors gave a best overall model  
326 with a slightly weaker AICc than the best overall model from the analysis of all  
327 subordinates combined (Table S15, S16).

328         Dominant female EGP was not related to the number of helpers (or  
329 whether male and female helpers were present) or any of the other variables  
330 tested in subset A (population breeding density, local breeding density, territory  
331 quality and  $R$ ; Table 2, S6). The territory quality extrapolation did not affect  
332 results (see subset B analysis, Table S7), which were consistent across subsets  
333 with or without the extrapolated data. Population and local breeding synchrony,  
334 their interaction with population and local breeding density respectively, and  
335 clutch size also did not influence the likelihood of dominant female EGP (see  
336 subset C analysis, Table S8). Social male and social pair identity were the only  
337 random effects to explain variation in dominant female EGP with high  
338 confidence (i.e. with 95% CIs not overlapping zero, Table 2, S2-S6, S8) and  
339 explained *ca* 12-14% and 20%, respectively, of the total variance in dominant  
340 female EGP.

341

342 *Subordinate female EGP*

343 Subordinate female EGP was positively associated to both relatedness ( $R$ ) and  
344 group size (Table 3, Fig. 1, Fig. 2). Only  $R$  was conventionally significant (the  
345 95% CI of  $R$  did not overlap zero), but both group size and  $R$  had a  $\omega_p$  of 1.00  
346 (and the 90% CI of group size did not overlap zero). These results suggest that  
347 group size also influenced subordinate female EGP, but that power was limited  
348 in our much smaller sample of offspring from subordinate females. All other  
349 variables tested, including male and female group size, the number of mature  
350 subordinates and helpers (or whether male and female subordinates and  
351 helpers were present, respectively), had  $\omega_p < 0.90$  and CIs overlapping zero  
352 (see Table S9-S12). When testing for the effect of the number of mature  
353 subordinates (or whether male and female subordinates were present), the 95%  
354 CI of  $R$  overlapped zero and its  $\omega_p$  dropped below 1.00, possibly due to lack of  
355 power in the small sample. However,  $R$  was still a highly important factor in the  
356 models (Tables S10, S11). Overall, our results suggest that the likelihood of  
357 subordinate female EGP is related to  $R$ . Using the same microsatellite markers  
358 for the estimation of relatedness and the assignment of parentage could result  
359 in inadvertent bias, leading to the detection of a false positive association  
360 between relatedness and extra-pair paternity (see: Wetzel and Westneat 2009).  
361 However, we only found a positive  $R$ -EGP relationship in the small subset  
362 containing offspring of subordinate females, and not in the large subset with  
363 offspring of dominant females, even though the latter subset had much more  
364 power. Also, we know that the positive association between  $R$  and EGP in the  
365 subordinate subset was not caused by overall higher levels of female-male  
366 relatedness ( $R$  did not differ in relation to female status). Therefore, it is highly



367 unlikely that inadvertent bias influenced these results. All random effects tested  
368 had 95% CIs overlapping zero (Table 3, S9-S12).

369

370

## Discussion

371 In Seychelles warblers, 41% of offspring resulted from extra-group fertilizations,  
372 of which 96% were sired by dominant males. Here, we focused on analyzing the  
373 relationship between multiple social, demographic and ecological factors and  
374 female extra-group paternity (EGP). The proportion of EGP in offspring from  
375 dominant (40%) and subordinate (51%) females tended to differ, but this  
376 difference was not statistically significant. Both dominant and subordinate  
377 female EGP increased with group size. Importantly, the numbers of either male  
378 or female group members in a territory had similar positive effects on EGP.  
379 Furthermore, overall group size (including reproductively immature birds), was a  
380 better predictor of EGP than the number of mature subordinates in a territory.  
381 Although the relatedness of dominant and subordinate females to the dominant  
382 male did not differ significantly, female-dominant male relatedness was only a  
383 positive predictor of EGP likelihood for subordinate mothers. None of the other  
384 factors tested (i.e. breeding density, breeding synchrony, number of helpers,  
385 territory quality or clutch size) were found to influence EGP.

386

387 *Group features and EGP*

388 In group-breeding species, the number of adults within the group has been  
389 predicted to impair a male's ability to monopolize individual females and,  
390 consequently, to increase the proportion of EGP (Van Noordwijk and Van  
391 Schaik 2004). Past research addressing this hypothesis has often failed to  
392 provide clear supporting evidence (see e.g. Van Noordwijk and Van Schaik  
393 2004; Rubenstein 2007; Ruiz-Lambides et al. 2017). The same applies to  
394 studies specifically testing for an effect of the number of adult males in the  
395 group (e.g. Durrant and Hughes 2005; Isvaran and Clutton-Brock 2007; but see:  
396 Annavi et al. 2014), which may reduce EGP via improved control or defense of  
397 females (Van Noordwijk and Van Schaik 2004). Evidence that the number of  
398 adult females in the group leads to higher rates of EGP (because it impairs  
399 male monopolization of individual females; Van Noordwijk and Van Schaik  
400 2004) has perhaps found more support, though this was not always the case.  
401 For instance, a meta-analysis of group-living mammal species found a positive  
402 correlation between EGP frequency and the number of adult females per group  
403 (Isvaran and Clutton-Brock 2007), and a recent study on rhesus macaques,  
404 *Macaca mulatta*, found that EGP increased with the number of adult females,  
405 but only in large groups (Ruiz-Lambides et al. 2017). In contrast, work on  
406 European badgers, *Meles meles*, provided the opposite result (i.e. a negative  
407 relationship between adult female group size and EGP; Annavi et al. 2014).  
408 Studies on polygynous species have also provided mixed results relating to the  
409 effect of harem size on the proportion of extra-harem paternity (e.g. Cordero et  
410 al. 2003 vs Sousa and Westneat 2013).

411 As predicted (see Table 1), the number (or presence) of mature  
412 subordinates (of either sex) in a territory, had a similar positive effect on  
413 dominant female EGP. However, total group size, which also includes  
414 reproductively immature independent birds (old fledglings and sub-adults),  
415 better predicted dominant and subordinate female EGP than only the number of  
416 sexually mature subordinates. This, and the fact that the number of either male  
417 or female subordinates influenced EGP similarly, indicates that female EGP is  
418 increased by group size, rather than the group's composition acting via different  
419 mechanisms through male and female subordinates. One explanation for the  
420 group size–EGP relationship may be that, in territories with more residents,  
421 dominant males may be less effective at keeping track of, and closely mate-  
422 guarding, the fertile female(s). In the future it might be possible to test if group  
423 size influences mate-guarding rate.

424 Another plausible explanation for the positive effect of group size on EGP is  
425 that group size reflects the former reproductive success of the breeding  
426 female(s) and is used as a social cue by males seeking EGP. Studies have  
427 shown that reproductive success can be adopted by conspecifics as public  
428 information for mate and habitat selection (see e.g. Drullion and Dubois 2011;  
429 Pärt et al. 2011). If Seychelles warblers used group size as public information  
430 indicating breeder and/or territory productivity, males would preferentially seek  
431 extra-pair fertilizations with females living in larger groups, thus leading to  
432 higher EGP in larger groups. In Seychelles warblers, males were observed  
433 intruding into territories to seek extra-group copulations, but whether the

434 probability of this happening is linked to group size is unknown and needs  
435 investigating.

436 The effect of group size may be linked to the age and/or quality of female  
437 breeders, and a corresponding increase in the amount of young these females  
438 produce. Since offspring often delay dispersal from the natal group (Kingma et  
439 al. 2016), older and/or higher quality female breeders will more likely reside in  
440 larger groups (with a higher number of retained offspring). It is therefore  
441 possible that older (more experienced) and/or higher-quality females, which live  
442 in larger groups, are better at evading mate-guarding and at obtaining extra-  
443 group fertilizations. Also, EGP is likely modulated by social-male characteristics,  
444 as supported by the fact that social male and social pair identity explained 12-  
445 14% and 20% of the variation in EGP likelihood, respectively, at least for  
446 dominant females. This suggests that females paired with certain males are  
447 more unfaithful than others. Numerous studies have attempted to find individual  
448 traits related to the loss or gain of extra-pair paternity by males, but the  
449 evidence remains unclear (see reviews: Griffith et al. 2002; Ackay and  
450 Roughgarden 2007). A previous study in the Seychelles warbler showed that  
451 social males with low MHC diversity lost more paternity than those with higher  
452 MHC diversity (Richardson et al. 2005). Moreover, in a translocated Seychelles  
453 warbler population, where female choice was not constrained by territory  
454 availability, older and more heterozygous males were more likely to be paired  
455 (Wright et al. 2015). We also know that dominant Seychelles warbler males,  
456 which are on average older than subordinate males, gain most within and extra-  
457 group paternity (Richardson et al. 2001; Hadfield et al. 2006). Across many

458 species, it is generally true that older males obtain most of the paternity  
459 (Richardson and Burke 1999; Ackay and Roughgarden 2007; Hsu et al. 2015).  
460 To understand this further in Seychelles warblers, it would be helpful to assess  
461 any potential relationship between EGP and maternal or paternal traits,  
462 including age and features associated with individual fitness, as well as with the  
463 pairwise combination of such traits.

464 Several studies on cooperative species have shown that helpers provide  
465 load-lightening for dominants, i.e. allowing them to reduce their work rate and  
466 investment into young (e.g. MacColl and Hatchwell 2003; Clutton-Brock et al.  
467 2004; Russell et al. 2008; Brintjes et al. 2013; Zöttl et al. 2013). Having helpers  
468 who provide parental care may liberate females from the constraints imposed  
469 on them by reduced parental care from pair males who lose (certainty of)  
470 paternity (Mulder et al. 1994). Evidence supporting this prediction comes from  
471 studies of fairy wren species, showing that EPP increased with the number of  
472 helpers in the group (Mulder et al. 1994; Webster et al. 2004; Brouwer et al.  
473 2017; Hajduk et al. 2018; but see: Johnson and Pruett-Jones 2018). In  
474 Seychelles warblers, helpers facilitate the load-lightening of dominant females  
475 (van Boheemen et al. 2019) and increase offspring survival (Brouwer et al.  
476 2012). However, we found that the number (or presence) of helpers (of either  
477 sex) had no effect on EGP in either dominant or subordinate females. A  
478 possible explanation for this null result is the absence of male retaliation in  
479 Seychelles warblers. In this scenario, females are not constrained by social  
480 males and therefore do not need to be liberated by helpers. Comparisons of

481 parental care (e.g. feeding rates to nestlings) undertaken by cuckolded and  
482 non-cuckolded males would be necessary to confirm this.

483

#### 484 *Inbreeding avoidance via EGP*

485 Our results provide limited support for the idea that EGP may be part of an  
486 inbreeding avoidance mechanism, i.e. that females who are closely related to  
487 their social male avoid inbreeding by mating with extra-group males. While  
488 some studies have found a positive effect of pair relatedness on EPP (e.g.  
489 Blomqvist et al. 2002; Cohas et al. 2006; Freeman-Gallant et al. 2006; Leclaire  
490 et al. 2013), others have shown no effect (e.g. Schmoll et al. 2005; Edly-Wright  
491 et al. 2007; Barati et al. 2018). Mixed evidence has resulted also from meta-  
492 analyses (in favor: Arct et al. 2015; against: Ackay and Roughgarden 2007) and  
493 from research on polygynandrous species, which addressed the effect of  
494 female-male relatedness (within a group) on EGP levels (e.g. Nichols et al.  
495 2015 vs Ruiz-Lambides et al. 2018). In the Seychelles warbler we only detected  
496 a positive relationship between genetic relatedness and EGP likelihood for  
497 subordinate mothers. This result concurs with a previous, smaller study in  
498 Seychelles warblers that did not find an effect of relatedness on EGP across all  
499 females, but did show that extra-group young of subordinate mothers were less  
500 inbred than their within-group offspring (Richardson et al. 2004). This study also  
501 found that inbreeding had a negative inter-generational impact on offspring  
502 survival via maternal effects (Richardson et al. 2004), a result confirmed using  
503 telomeres as biomarkers in a much larger recent study (Bebbington et al. 2016).

504 A possible explanation as to why only subordinate, but not dominant, females  
505 may avoid inbreeding via EGP, is that dominant females are the primary focus  
506 of mate-guarding (Komdeur et al. 1999). Hence, subordinates may have more  
507 freedom to pursue extra-group fertilizations, which they may be more likely to  
508 seek when they are highly related to the dominant male in the territory.  
509 However, given that close inbreeding does occur in Seychelles warblers  
510 (Richardson et al 2004) and 40% of offspring from dominant females have EGP,  
511 there must be other reasons why dominant females do not avoid inbreeding.

512         Richardson et al. (2004) showed that subordinate mothers were more  
513 related to the dominant male than were dominant mothers and that the  
514 proportion of EGP for subordinate females was higher than for dominant  
515 females. However, we detected no difference in female–social male relatedness  
516 in the present study. This is possibly due to the high frequency of EGP in  
517 Seychelles warblers. Even if subordinate females are offspring that have  
518 remained in their natal territory, which is not always the case (Kingma et al.  
519 2016; Groenewoud et al. 2018), they have a 41% chance of having being sired  
520 by an extra-group male. Moreover, mortality and the replacement of dominant  
521 individuals does occur over time, thus further decreasing the chance of  
522 dominant males being the fathers of co-breeding subordinates (see Kingma et  
523 al, in prep.). Also, dominant females can be highly related to the social male if  
524 they have inherited dominance in their natal territory and have ended up being  
525 paired with their own father (Eikenaar et al. 2008).

526

527 *Territory quality, demographic factors and EGP*

528 Territory quality has been predicted to influence EPP positively – high territory  
529 quality may promote infidelity by compensating for costs (reduced paternal  
530 care) imposed by male retaliation against unfaithful females (Gowaty 1996) – or  
531 negatively – low territory quality may increase EPP if females can gain extra  
532 resources from extra-pair males (Gray 1997). Low territory quality may also  
533 result in females moving further afield while seeking resources, therefore  
534 increasing encounters with extra-pair males and, consequently, EPP levels. The  
535 relationship between territory quality and EPP, however, is far from being  
536 resolved, with studies showing either a positive (e.g. Hoi-Leitner et al. 1999;  
537 Charmantier and Blondel 2003) or a negative relationship (e.g. Vaclav et al.  
538 2003; Rubenstein 2007). In our study, territory quality does not seem to  
539 influence EGP likelihood. It is possible that male Seychelles warblers do not  
540 retaliate (i.e. reduce parental care) when they lose (confidence in) paternity and  
541 that infidelity does not cause females significant energetic costs, which would  
542 be compensated for by high habitat quality.

543 Breeding density has been predicted to promote EPP by increasing mate  
544 encounter rate (Alexander 1974; Birkhead 1978; Gladstone 1979; Moller &  
545 Birkhead 1993). Comparisons across species have provided little evidence for  
546 any such a correlation (Westneat and Sherman 1997; Griffith et al. 2002).  
547 However, the relationship seems to hold in various correlative studies focusing  
548 on individual species (e.g. Moller 1991; Richardson and Burke 2001; Soucy and  
549 Travis 2003; Mayer and Pasinelli 2013; Annavi et al. 2014; but see e.g. Barber  
550 et al. 1996; Verboven and Mateman 1997; Tarof and Stutchbury 1998; Moore et



551 al. 1999). The few studies which have experimentally manipulated breeding  
552 density also provided mixed evidence, finding either a positive breeding  
553 density–EPP correlation (Gowaty and Bridges 1991; Charmantier and Perret  
554 2004; Stewart et al. 2010), no relationship (Rätti et al. 2001) or a negative  
555 correlation (Dunn et al. 1994; Václav and Hoi 2002). Male Seychelles warblers  
556 have been shown to adjust their reproductive physiology (van de  
557 Crommenacker et al. 2004) and mate-guarding behavior in relation to local  
558 conspecific density (Komdeur 2001; Komdeur et al. 2007), which suggests that  
559 breeding density may affect EGP. However, our study does not show a  
560 relationship between EGP likelihood and neither local nor population-wide  
561 breeding density. As population density on Cousin has been relatively stable  
562 since carrying capacity was reached in 1982 (Brouwer, Tinbergen, et al. 2009;  
563 Komdeur et al. 2017), it may be that population breeding density is not variable  
564 enough to generate any observable effect on EGP in our study (see Table S1).  
565 Local breeding density, on the other hand, does display considerably more  
566 variation (Table S1). In fact, even though territory boundaries are relatively  
567 stable in time, new territories can form and old ones disappear/merge with  
568 others across years, and our long data period spans enough years (18) to  
569 capture any such changes. Considerable variation in local breeding density is  
570 present also within years, due to the location of different territories on the island.  
571 For example, central territories have many more adjacent territories compared  
572 to those bordering the coast, or next to the rocky uninhabited areas. Also,  
573 territories in invertebrate-rich areas (where territory density is higher) have more  
574 adjacent territories than those in low-quality areas. Despite this variation, local

575 breeding density did not influence EGP. It is possible that reasons other than  
576 local (and population) breeding density drive EGP in Seychelles warblers.  
577 Alternatively, local breeding density may not be a very good predictor of EGP  
578 likelihood, as individuals may move across several territories to obtain EGP. A  
579 previous study showed that although *ca* 59% of extra-group fertilizations  
580 occurred with males from within two territories away from a female's territory,  
581 the rest was shown to occur with males up to six territories away (see  
582 Richardson et al. 2001).

583 Breeding synchrony has been suggested as a factor either increasing  
584 EPP – by enabling females to compare potential mates more effectively  
585 (Stutchbury and Morton 1995) – or reducing EPP – by increasing the trade-off  
586 males face between mate-guarding and seeking extra-pair copulations  
587 (Westneat 1990). However, while some have found a positive (Stutchbury et al.  
588 1997; Stutchbury et al. 1998) or a negative correlation (Saino et al. 1999; van  
589 Dongen & Mulder 2009) between breeding synchrony and EPP, most studies  
590 have failed to find any relationship (e.g. Kempenaers et al. 1997; Hoi-Leitner et  
591 al. 1999; Richardson and Burke 2001; Arlt et al. 2004; Brouwer et al. 2017).  
592 Seychelles warbler males closely mate-guard their social female during her  
593 fertile period to prevent cuckoldry (Komdeur et al. 2007) and face a trade-off  
594 between mate-guarding and the pursuit of extra-pair fertilizations (Eikenaar  
595 2006). In this species EGP should, therefore, decrease with breeding  
596 synchrony. However, an earlier study found no such relationship (Eikenaar  
597 2006). This was suggested to be the case because there were always plenty of  
598 non-guarding extra-group males available, due to the low local breeding

599 synchrony and high local breeding density during the three years of that study  
600 (Eikenaar 2006). Despite our improved sample size (spanning 17 years), and  
601 more variation in breeding synchrony (Table S1), we detected no effect of this  
602 demographic factor on EGP neither at the local nor at the population level.

603

## 604 Conclusions

605 Our study investigated the effect of multiple socio-ecological conditions on  
606 extra-group paternity (EGP) likelihood in a wild population. Our finding that  
607 group size was positively correlated with EGP for both dominant and  
608 subordinate females suggests that larger groups may enable females to be less  
609 faithful, though why that is remains unclear. We also found some support for the  
610 idea that infidelity functions to reduce inbreeding (inbreeding avoidance  
611 hypothesis) but only for subordinate females, who may have more opportunity  
612 to obtain EGP than dominant females. The other social, demographic and  
613 ecological parameters tested (the number of helpers in a group, local and  
614 population breeding density, local and population breeding synchrony, territory  
615 quality) did not appear to affect EGP in the Seychelles warbler. Our study  
616 suggests that, at least in this system, other factors, possibly linked to individual  
617 traits and/or quality, may be the major determinants of EGP.

618

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636

637

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1062 Figure legends

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1064 **Figure 1. The proportion of extra-group paternity (EGP) of offspring with**  
1065 **dominant (top graph) and subordinate (bottom graph) mothers in relation**  
1066 **to group size in the Seychelles warbler.** The proportion of extra-group  
1067 offspring produced by dominant (top graph) and subordinate (bottom graph)  
1068 females is higher in larger groups. Clutch size is usually one (but *ca* 33% of  
1069 nests have 2 or 3 eggs, usually as a result of co-breeding) and most females  
1070 produce one offspring per nest.

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1072 **Figure 2. Extra-group paternity (EGP) likelihood in relation to pairwise**  
1073 **relatedness ( $R$ ) between each mother (dominant or subordinate) and the**  
1074 **dominant male in the territory (social male) in the Seychelles warbler.**  
1075 Likelihood of offspring being sired by extra-group males for dominant mothers  
1076 (in black,  $n = 861$ ) and subordinate mothers (in grey,  $n = 104$ ) in relation to the  
1077 genetic relatedness between the mother and the social male. The positive  
1078 relationship is significant for subordinate mothers but not for dominant mothers  
1079 (Table 2, 3).

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## Tables

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1086 **Table 1. List of socio-ecological parameters (1-9) and an additional control**1087 **factor (10), how these factors are estimated, and the predictions about**1088 **how they may influence extra-group paternity (EGP) in the Seychelles**1089 **warbler.**

| Parameter                              | Estimation   | Predicted effect on EGP   |
|--|--|---|
| 1. Territory quality                   | Invertebrate prey availability per territory (based on arthropod counts, vegetation cover and territory size)                                | Increase in EGP if resource abundance compensates for male retaliation (i.e. care reduction)  |
| 2. Local breeding density (males)      | Number of neighboring dominant males (i.e. in territories adjacent to the focal territory) <sup>a</sup>                                      | Increase in EGP via higher mate encounter rate  |
| 3. Population breeding density (males) | Number of dominant males on Cousin   | Increase in EGP via higher mate encounter rate  |
| 4. Local breeding synchrony            | Number of neighboring dominant females whose fertile period (6-0 days preceding egg laying (Eikenaar 2006) overlaps that of the focal female | Decrease in EGP due to male trade-off between mate-guarding and pursuit of EGP (a trade-off is present in Seychelles warblers; Eikenaar 2006) |

|                                       |  |   |
|---------------------------------------|--|---|
| 5. Population breeding synchrony      | Number of dominant females in the population whose fertile period overlaps that of the focal female                      | Reduction in EGP due to male trade-off between mate-guarding and EGP pursuit  |
| 6. Group size                         | Number of independent birds ( $\geq 3$ months old) in the focal territory  | Increase in EGP due to a reduction in mate-guarding (via a 'confusion effect')  |
| 7. Reproductively mature subordinates | All: Number of subordinates (helpers and non-helpers) $\geq 8$ months old (other than the mother) in the focal territory | Increase in EGP due to a reduction in mate-guarding effectiveness (via different mechanisms for mature males vs females, see below).  |
|                                       | Males: Presence of male subordinates $\geq 8$ months old   | Males: increase in EGP due to a trade-off between subordinate male suppression and mate-guarding (dominant males physiologically suppress subordinate males; Brouwer, Groothuis, et al. 2009) |
|                                       | Females: Presence of female subordinates $\geq 8$ months old (other than the mother)                                     | Females: increase in EGP via difficulty in controlling individual females when $> 1$ are present  |
| 8. Helpers                            | Number of helpers in the focal territory (other than   | Increase in EGP if helpers compensate for male retaliation  |

the mother)

(helpers provide load-lightning in Seychelles warblers; van Boheemen et al. 2019)

|   |   |  |
|---|---|--|
| 9. Pairwise genetic relatedness ( $R$ ) | Mother-social (dominant) male genetic relatedness using the Queller and Goodnight (1989) estimation | Increase in EGP via inbreeding avoidance                               |
| 10. Clutch size (per female)            | Presence/absence of >1 offspring produced by the same female in the same nest                       | Increase via higher chance of at least one offspring being extra-group |

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1090 <sup>a</sup> Territories are inhabited by a dominant male and a dominant female and, in  
1091 30-50% of cases, also by subordinate individuals of either sex. Extra-group  
1092 offspring are almost always sired by dominant males, which are often from  
1093 adjacent territories (Richardson et al. 2001; Hadfield et al. 2006).

1094 See Table S1 for details on the distribution of each socio-ecological variable.

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1101 **Table 2. Model-averaged parameters: the effect of socio-ecological**  
 1102 **predictors – including group size – on the likelihood of extra-group**  
 1103 **paternity (EGP) in offspring from dominant females in the Seychelles**  
 1104 **warbler (subset A).**

| <b>Fixed term</b>           | <b><math>\beta</math></b>    | <b>95% CI</b>     | <b><math>\omega_p</math></b> |
|-----------------------------|------------------------------|-------------------|------------------------------|
| (Intercept)                 | -0.47                        | -0.66, -0.27      | -                            |
| <b>Group size</b>           | <b>0.35</b>                  | <b>0.17, 0.53</b> | <b>1.00</b>                  |
| Population breeding density | -0.07                        | -0.24, 0.11       | 0.53                         |
| Pairwise relatedness        | 0.06                         | -0.12, 0.24       | 0.46                         |
| Territory quality           | 0.01                         | -0.09, 0.11       | 0.25                         |
| Number of helpers           | -0.01                        | -0.11, 0.09       | 0.19                         |
| Local breeding density      | -                            | -                 | -                            |
| <b>Random term</b>          | <b><math>\sigma^2</math></b> | <b>95% CI</b>     | <b>n</b>                     |
| Mother ID                   | 0.15                         | 0.00, 0.86        | 313                          |
| <b>Social male ID</b>       | <b>0.58</b>                  | <b>0.31, 1.10</b> | <b>311</b>                   |
| Year                        | 0.00                         | 0.00, 0.25        | 17                           |

**Response: Dominant female EGP likelihood ( $n = 816$  offspring).**

Candidate models: 64. Top set models: 11 (see Table S13 for details).

1105 Full model-averaged estimates ( $\beta$ ), 95% confidence intervals (CIs) and relative  
 1106 importance ( $\omega_p$ ) are shown for all socio-ecological predictors featuring in the top  
 1107 model set ( $\Delta AIC_c \leq 2$ ). Random effect variances ( $\sigma^2$ ) and their 95% CIs in the  
 1108 best model are also shown. Predictors whose CIs do not overlap with zero are  
 1109 given in bold.

1110

1111 **Table 3. Model-averaged parameters: the effect of socio-ecological**  
 1112 **predictors – including group size – on the likelihood of extra-group**  
 1113 **paternity (EGP) in offspring from subordinate mothers in the Seychelles**  
 1114 **warbler.**

| Fixed term                  | $\beta$     | 95% CI            | $\omega_p$  |
|-----------------------------|-------------|-------------------|-------------|
| (Intercept)                 | 0.10        | -0.52, 0.73       | -           |
| Group Size                  | 0.71        | -0.04, 1.46       | 1.00        |
| <b>Pairwise relatedness</b> | <b>0.71</b> | <b>0.05, 1.36</b> | <b>1.00</b> |
| Number of helpers           | -0.10       | -0.57, 0.37       | 0.28        |
| Territory quality           | 0.05        | -0.34, 0.45       | 0.21        |
| Population breeding density | -           | -                 | -           |
| Local breeding density      | -           | -                 | -           |
| Random term                 | $\sigma^2$  | 95% CI            | n           |
| Mother ID                   | 1.59        | 0.00, 2.21        | 53          |
| Social male ID              | 0.00        | 0.00, 2.91        | 58          |
| Year                        | 0.00        | 0.00, 0.97        | 16          |

**Response: subordinate female EGP likelihood ( $n = 101$  offspring).**

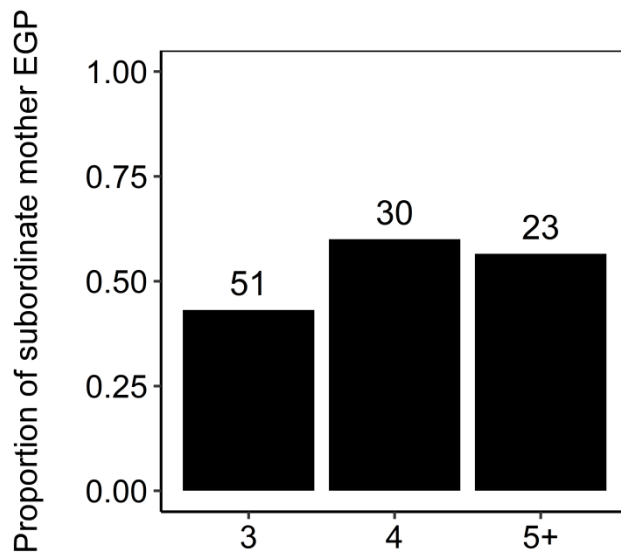
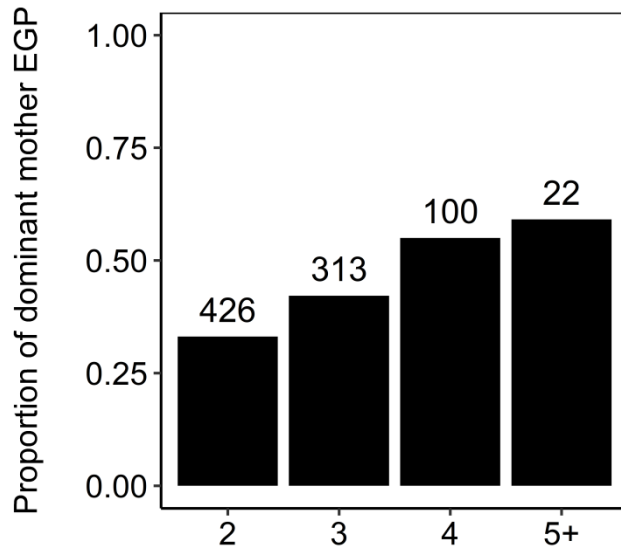
Candidate models: 64. Top set models: 3 (see Table S20 for details).

1115 Full model-averaged estimates ( $\beta$ ), 95% confidence intervals (CIs) and relative  
 1116 importance ( $\omega_p$ ) are shown for all socio-ecological predictors featuring in the top  
 1117 model set ( $\Delta AIC_c \leq 2$ ). Random effect variances ( $\sigma^2$ ) and their 95% CIs in the  
 1118 best model are also shown. Predictors whose CIs do not overlap with zero are  
 1119 given in bold.

1120

1121 Figures

1122 Figure 1



Group size

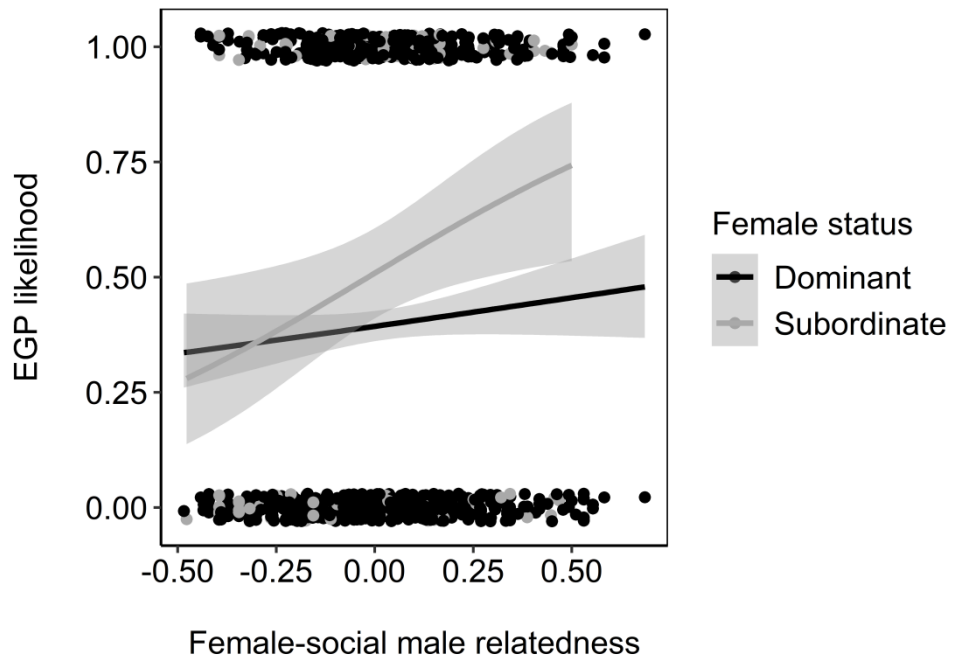
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1127 Figure 2



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