1 **Ecogeography of group size suggests differences in drivers of sociality among cooperatively**

2 **breeding fairywrens**

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18 **Running title:** Ecogeography of social group size

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Abstract:

Cooperatively breeding species exhibit a range of social behaviors associated with different costs and benefits to group-living, often in association with different environmental conditions. For example, species in which collective-care of offspring reduces the cost of reproduction are more common in harsh environments (true cooperative breeding), while species that collectively defend resources are present in benign environments (family-living). Here, we examine whether environment also shapes sociality within cooperatively-breeding species. We illustrate that Purple-backed Fairywrens, which primarily gain intrinsic, or collective-care benefits, have larger groups in hot, dry environments and smaller groups in cool, wet environments, whereas Superb Fairywrens which primarily gain extrinsic, or resource defense benefits, exhibit the opposite trend. We suggest differences in the costs and benefits of sociality contribute to these opposing ecogeographic patterns, demonstrating that comparisons of intraspecific patterns of social variation across species can provide insight into how ecology shapes transitions between social systems.

Introduction

Social structure is shaped in part by evolutionary adaptations of organisms to their environment (e.g., Crook & Gartlan 1966; Orians 1969; Emlen & Oring 1977; Hennessy et al. 2009; Guindre-Parker & Rubenstein 2020, among others), but the links between environmental conditions and social systems are complex due to their combined effects on resource acquisition, survival, and reproduction. This complexity is exemplified by cooperative breeding systems, in which one or more breeding pairs are joined by auxiliary members which provide care for offspring (Brown 1987). The evolution of cooperative social systems is thought to be driven by a combination of kin-selection benefits, social benefits of group living, and constraints on breeding opportunities (Hamilton 1964; Emlen 1982; Koenig et al. 1992; Covas & Griesser 2007; Riehl 2013). These factors interact with environmental variation in different ways, and have led to the evolution of a spectrum of social behaviors that are often collectively referred to as cooperative breeding systems (Lin et al. 2019). For example, both breeders and auxiliary members may gain intrinsic benefits from sociality (also known as collective action benefits and benefits of philopatry [sensu Stacy & Ligon 1991]) when auxiliary members buffer group reproduction and survival against temporally variable and harsh environments (true cooperative breeding; Emlen 1982; Koenig et al. 1992; Koenig et al. 2011; Shen et al. 2017). In contrast, extrinsic benefits or ecological constraints (or resource defense/access benefits) may be more likely to promote social groups in benign environments where breeders may pay little costs for prolonged associations with juveniles that stay in the natal territory. Such auxiliary individuals benefit by remaining with their parents past maturity, potentially gaining access to resources, queueing for breeding opportunities, or training for parental care, among other benefits (Emlen 1982; Koenig et al. 1992; Gonzalez et al. 2013; Shen et al. 2017). These types of constraint-driven systems have

59 been classified in the last few decades as family-living systems rather than true cooperative

60 breeding, particularly when helping behaviors often associated with cooperative breeding are

61 entirely absent (Griesser et al. 2017). Together, intrinsically and extrinsically driven systems

62 form a spectrum of cooperative social systems with true cooperative breeders on one side and

63 family-living species on the other (Covas & Griesser 2007; Griesser et al. 2017).

64   Recent analyses of the ecogeographical distribution of cooperative breeding systems

65 support the view that different sources of benefit are influenced by environmental conditions in

66 different ways. For example, harsh environments favor cooperative breeding in a clade where

67 subordinates can increase the reproductive output of breeders (African starlings: Rubenstein &

68 Lovette 2007), whereas harsh environments inhibit cooperative breeding in a clade where groups

69 primarily accrue only resource defense benefits (hornbills: Gonzalez et al. 2013; Lin et al. 2019).

70 Likewise, in broader comparisons, species demonstrating allocare (i.e., true cooperative

71 breeders) are more prevalent in habitats with high within-year environmental variability while

72 species without allocare (family-living) are more prevalent in less variable environments

73 (Griesser et al. 2017). Phylogenetic meta-analysis suggests that family-living is a frequent

74 steppingstone for transitions between pair-breeding and true cooperative breeding (Griesser et al.

75 2017), but what is still not understood are the mechanisms by which these transitions occur.

76 Further, it is unclear whether the same processes governing variation across species can apply to

77 populations within species exposed to different ecological conditions.

78   If the interplay between environment and sources of costs and benefits is key to the

79 evolution of cooperative groups, then the same interplay should regulate group size variation

80 along environmental gradients within species as well, providing variation for selection to act

81 upon to generate such evolutionary transitions to and away from cooperative breeding behavior.

82   Theoretical work using insider–outsider conflict theory has illustrated that species differences in

83   optimal group sizes under different environmental conditions can be explained by which end of

84   the cooperative social spectrum a species lies on (social benefits or resource defense; Shen et al.

85   2017). Applying this concept to within-species variation, we propose that environmental

86   gradients should generate different patterns of variation in group size based on a species'

87   position on this social spectrum. Species which gain intrinsic social benefits, where allocare

88   increases reproductive success of breeders and provides indirect fitness benefits to helpers,

89   should form the largest groups in harsh environments where the benefits of allocare are greatest.

90   In this context, breeders would be more tolerant of beneficial helpers despite potential costs of

91   sharing resources, and helpers would be less likely to succeed as independent breeders without

92   helpers. These species should have lower group sizes (or live in pairs) in more benign

93   environments where conditions might permit breeding pairs to raise young without assistance

94   (Fig. 1A). Species which only gain extrinsic, resource defense benefits should form social groups

95   only in benign environments when breeding vacancies are limited due to high reproductive

96   success and high survival (as suggested by the ecological constraints hypothesis; Emlen 1982;

97   Shen et al. 2017), and breeders can be more tolerant of auxiliary group members due to abundant

98   food resources in benign environments. Conversely, these species should live in pairs in

99   environments where helpers are able to disperse away from their natal territories into breeding

100   vacancies or where limited food resources make territory sharing more costly (Fig. 1B). We

101   sought to explicitly examine this hypothesis for intraspecific variation in group size by studying

102   populations of two species of Australian fairywrens (genus *Malurus*) along an ecological

103   gradient.

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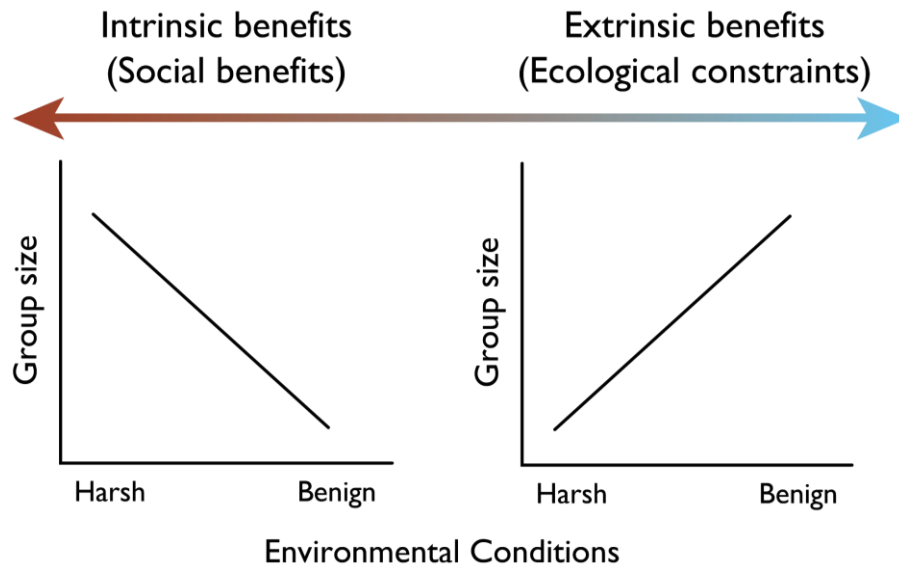
Figure 1. Conceptual illustration of the proposed relationship between group size and environmental conditions in cooperatively breeding species with different sources of benefit gained from sociality. True cooperatively breeding species in which individuals primarily gain intrinsic benefits from sociality are primarily found in harsh or variable environments, whereas family-living species in which individuals gain primarily extrinsic benefits are primarily found in benign or stable environments. We propose that this expectation can extend to social group size variation within species, generating opposing ecogeographic patterns in different species. Here we show expectations for the extreme ends of this social spectrum; species in which individuals gain only social benefits from behaviors such as allocare should form larger groups in harsh environments (left graph), where the potential productivity increase from help at the nest is highest, and should have smaller groups in benign environments, where pairs might be expected to successfully raise young on their own. However, we expect that species in which individuals gain only resource defense benefits should only form groups in benign environments where young individuals lack dispersal opportunities (right graph).

Fairywrens present an ideal system for examining intraspecific variation in group size because

all species are cooperative to some degree (Rowley & Russell 1997), they are well studied and

thus we have a good understanding of the benefits of cooperation, and many species range over a

variety of climates. Further, climate has been tied to reproductive success in this family, with

rainfall positively predicting nest initiation, clutch size, and reproductive success (Tidemann &

Marples 1986; Nias & Ford 1992; Cockburn et al. 2008b; van de Pol et al. 2013; Hidalgo

Aranzamendi et al., 2019, Lv et al., 2019), likely because higher rainfall is often associated with

127 higher insect abundance (Recher et al. 1996; Woinarski & Cullen 1984, Hidalgo Aranzamendi et

128 al., 2019). Thus, we suggest high rainfall environments are likely benign for these species, while

129 low rainfall environments are harsh. Specifically, we chose to examine the Purple-backed and

130 Superb fairywrens (*Malurus assimilis* and *M. cyaneus*) because while both are classified as

131 cooperative breeders, they appear to gain different benefits from group-living, and thus represent

132 different points on the cooperative breeding spectrum. Breeding Purple-backed Fairywrens in

133 social groups have higher reproductive output than those in pairs, suggesting Purple-backed

134 Fairywrens gain intrinsic benefits from the presence of helpers at the nest (Johnson 2016;

135 Johnson et al. 2018). Thus, we expect that Purple-backed Fairywrens should have larger group

136 sizes in arid, harsh environments where group living could buffer groups against the uncertainty

137 of resources. Correspondingly, we expect Purple-backed Fairywren group size to decline in

138 increasingly benign habitats where helpers might become unnecessary for successful

139 reproduction and where helpers would gain greater reproductive success from breeding on their

140 own. In contrast, the presence of auxiliary members in Superb Fairywren groups does not

141 provide increased reproductive output for breeders (Dunn et al. 1995; Cockburn et al. 2008b).

142 Instead, evidence suggests that group living in Superb Fairywrens is driven by juvenile males

143 that stay in their natal territory when breeding vacancies are lacking and thus benefit from

144 queueing or survival opportunities (Pruett-Jones & Lewis 1990; Cockburn et al. 2008a). Thus,

145 we expect that Superb Fairywrens should only have large group sizes in benign environments

146 where population density is high and young males are restricted from establishing independent

147 breeding territories, but where territory quality is high enough for such helpers to not impose a

148 resource cost on breeders, meaning they are likely to be tolerated in their natal territory. We

149 expect group size should decline in harsh environments where competition for resources is high

150   and the lack of benefit to helping behavior means helpers which delay dispersal should not be

151   tolerated.

152   We tested whether intraspecific group size variation is driven by environmental gradients

153   in both Purple-backed and Superb fairywrens by performing two observational transects along a

154   south-eastern portion of Australia where both species co-occur (Fig. 2). We show that these two

155   species indeed exhibit opposing patterns of social group size variation in the directions we

156   predicted, providing new evidence that responses of social systems to environmental variation is

157   dependent on the types of benefits and costs that group members can experience.
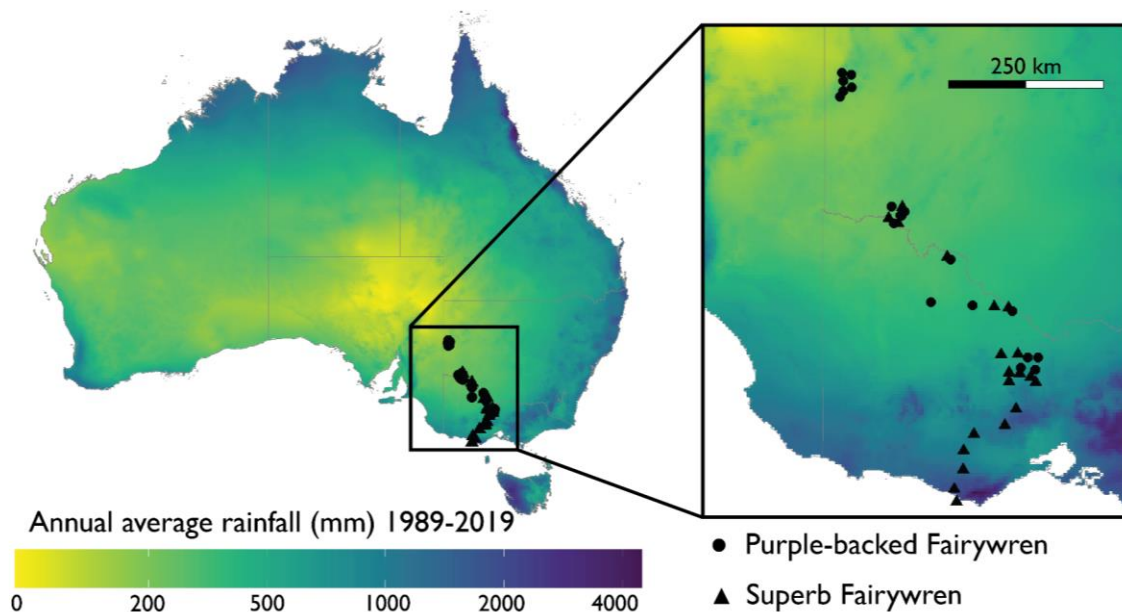
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160   **Figure 2. Fairywren populations observed along a steep climate gradient**
161   Fairywren group size was observed across a climate gradient in south-eastern Australia. Map
162   shows average annual rainfall, one aspect of climate variation, in Australia from 1989–2019 (the
163   time span covered by climate variables in the PCA), and points represent populations visited.
164   Inset is an enlargement of the region where populations were observed. Circles are Purple-
165   backed Fairywren populations and triangles are Superb Fairywren populations. Several sites had
166   populations of both species; points are jittered to assist visualization.
167

168   **Materials and Methods**

169   *Study system*

170   Purple-backed and Superb fairywrens are small, cooperatively breeding passerines native to

171   Australia (Rowley & Russell 1997). The Superb Fairywren is primarily found in south-eastern to

172   central-eastern Australia while the Purple-backed Fairywren (previously considered a subspecies

173   of the Variegated Fairywren as *M. lamberti assimilis* and recently given species status; Mclean et

174   al. 2012; Mclean et al. 2017; Gill & Donsker 2018) can be found throughout much of Australia

175   west of the Great Dividing Range. These two species co-occur over much of south-eastern

176   Australia.

177   While both species can breed in pairs, they often form cooperative-breeding groups that

178   are most frequently composed of one breeding pair and auxiliary group members or 'helpers'.

179   While both breed cooperatively, the social behavior of these species differs in several ways.

180   Superb Fairywren helpers are almost exclusively male offspring of one or both members of the

181   breeding pair from a previous breeding attempt; nearly all first-year males (87%; Mulder 1995)

182   remain in their natal territory, and many stay in their natal territories their whole lives. All

183   Superb Fairywren helpers provision young (Dunn and Cockburn 1996), and while the presence

184   of helpers is correlated with increased breeding female survival, they do not increase

185   reproductive output of the group (Cockburn 2008b). Extra-pair paternity is extremely high in

186   Superb Fairywrens, and rates of extra-pair paternity are higher in groups with helpers (Mulder et

187   al. 1994). As a result, helpers likely gain little inclusive fitness through kin selection while

188   remaining in their natal territory (Dunn et al. 1995; Cockburn et al. 2008b). Instead, Superb

189   Fairywren helper males likely stay due to a lack of available territories to disperse into; when

190   dispersal does occur, it is typically short in distance and in response to breeding vacancies

191 (Pruett-Jones & Lewis 1992; Mulder 1995; Cockburn et al. 2008a). Thus, despite exhibiting

192 allocare, Superb Fairywrens largely fit the criteria for "family-living" social systems in which

193 breeders will tolerate the presence of auxiliaries provided there are enough resources, and

194 auxiliaries stay because they may be able to survive longer, find alternative reproductive

195 opportunities as subordinates, such as extra-pair copulations, and potentially acquire life skills

196 while they wait for breeding vacancies (Cockburn et al. 2008a; Drobniak et al. 2015; Griesser et

197 al. 2017).

198　　　Purple-backed Fairywrens satisfy the criteria for true cooperative breeding in which

199 helpers contribute to increasing the productivity of breeders through collective care that increases

200 survival of the breeders' offspring (Johnson 2016; Johnson and Pruett-Jones 2018). While most

201 Purple-backed Fairywren helpers are males who are related to the breeding pair, 43% of helpers

202 are females who are typically unrelated (Johnson 2016). Of offspring with known age and origin

203 (N = 65 males and 17 females), 88.89% of males remain in their natal territory their first year,

204 and sometimes stay their whole lives, while only 11.76% of females remain in their natal

205 territory their first year (unpublished data collected by AEJ). Helpers of both sexes provision

206 young of the breeding pair, and unlike Superb Fairywrens extra-pair paternity rates decrease in

207 groups with helpers (Johnson & Pruett-Jones 2018), suggesting male helpers at least gain

208 inclusive fitness benefits through kin selection from remaining in their natal territory and rearing

209 related young. While male helpers are reluctant to disperse into experimentally made breeding

210 vacancies, female helpers readily disperse, suggesting that females may join unrelated groups in

211 order to queue for breeding vacancies and may "pay to stay" through provisioning young

212 (Johnson et al. unpublished data; Gaston 1978; Dunn et al. 1995).

213

214 *Population observation and group size estimation*

215 We performed two observational sampling transects (Fig. 2), one over ten days in mid-December

216 2018 (late breeding season) and the second over seven days in late August 2019 (early breeding

217 season). We visited local parks, conservation areas, and national parks, starting in coastal

218 Victoria and extending north to inland New South Wales, passively observing fairywren social

219 groups and recording their composition (group size and sex of individuals) at populations along

220 the transect. Fairywren social groups are gregarious, and group size can be easily and accurately

221 identified in a short period of time (Johnson & Welklin, person. exp.). Males of both species are

222 distinguished from females during the breeding season by bright blue and black plumage, while

223 females are generally brown. While some first-year males exhibit delayed plumage maturation,

224 they can be distinguished from females by black rather than brown bills. We distinguished

225 fledglings from females by behavior, presence of yellow gapes, and shorter tails, and did not

226 include fledglings in group size calculations. We observed each group until we were confident

227 all adult group members had been seen or we noted that the group was incompletely observed.

228 We recorded data using eBird (Sullivan et al. 2009), a community science-based bird observation

229 network, by adding notes to the species comments section describing the observed social groups

230 at each site. Separate checklists of groups observed in the same continuous park in the same year

231 were combined into one site. Only sites where we observed two or more complete social groups

232 of a focal species were included in subsequent analyses. After excluding incomplete groups and

233 sites where fewer than two social groups were observed, we sighted 81 Superb Fairywren social

234 groups in 20 populations, and 85 Purple-backed Fairywren social groups in 19 populations. Sizes

235 of groups observed at the same site and during the same year were averaged to generate a

236 population average group size that was used in subsequent analyses. Complete checklists are

237 available by request via eBird. Checklist identifiers, locations, and average group sizes can be

238 found in the supplemental data table.

239

240 ***Climate variables***

241 We obtained climate data from the Australian Bureau of Meteorology in April, 2021. We

242 downloaded two gridded datasets, monthly rainfall and monthly maximum temperature. Rainfall

243 grids have a resolution of 0.05 degrees (~5 km; Evans et al. 2020) and maximum temperature

244 grids have a resolution of 0.025 degrees (~2.5 km; Australian Bureau of Meteorology 2021).

245 Downloads spanned March 1988–February 2019. We chose a 30-year window to account for

246 variation at each site, as climate likely imposes selection pressures on group size, meaning group

247 size is a product of temporal variation. A single year's annual data was considered to span

248 March–February such that each year begins in the austral fall and ends with the austral summer.

249   Climate data was analyzed and prepared for further analysis in R 4.1.0 (R Core Team

250 2021). We generated one average annual value and two measures of variation in both rainfall and

251 temperature for each population (sensu Jetz & Rubenstein 2011). *Average annual rainfall* was

252 calculated by summing rainfall totals for each month in a year, then averaging rainfall across

253 years and log transforming the result. *Rainfall variation within years* was calculated by summing

254 seasonal rainfall totals (fall: March–May, winter: June–August, spring: September–November,

255 summer: December–February) and calculating standard deviation across seasons within each

256 year. We then averaged standard deviations across all years, providing an estimate of how

257 seasonal rainfall is at each grid location. *Rainfall variation across years* was determined by

258 calculating seasonal standard deviation of average seasonal rainfall across all years, then

259 averaging across all seasons.

260   Temperature metrics were determined similarly. *Average monthly maximum temperature*

261   was calculated by averaging the maximum monthly temperatures within a year, then averaging

262   across years. *Temperature variation within years* was determined by calculating the standard

263   deviation of average seasonal maximum temperatures within each year, then averaging the

264   standard deviations across all years. *Temperature variation across years* was determined by

265   calculating the seasonal standard deviation of average seasonal maximum temperatures across all

266   years, then averaging across all seasons.

267   Climate variables were extracted from each raster for the corresponding latitude and

268   longitude where each eBird checklist was made. In instances where two checklists made for the

269   same population were combined, the location of the first checklist was used. The calculated

270   climate variables are closely related, thus, we performed a principal components analysis to

271   reduce the dimension of climate variables used in subsequent analyses. All climate variables load

272   heavily onto PC1 and to a lesser extent PC2 (Table S1). PC1 explains 79.14% of the variance

273   and describes an inverse relationship between temperature and rainfall and can be interpreted as

274   encompassing a latent aspect of overall climate. Sites with high PC1 have relatively higher, more

275   variable rainfall, and lower, less variable temperatures and represent more benign environments

276   for fairywren reproduction, while sites with low PC1 are more arid and hot, representing harsher

277   environments. PC2 explains 14.78% of the total variance and is best described as an axis of

278   temperature and rainfall variability (Fig. S1). PC1 and PC2 together describe 93.92% of the

279   variance, so only PC1 and PC2 were used in model testing.

280

281   ***Analysis of the ecogeographic correlates of social group size***

13

282   We fit generalized linear models (using base R) with average group size as the response variable

283   to identify predictors of social group size. We tested ten models, each with a gamma error

284   distribution and inverse link function: 1) null (intercept only), 2) *species* only, 3) *year* only, 4)

285   *species* and *year*, 5) *species*, *year*, and *species by year* interaction, 6) *species*, *PC1*, *species by*

286   *PC1* interaction and *year* 7) *species*, *PC1*, *species by PC1* interaction, *year* and *species by year*

287   interaction, 8) *species*, *PC2*, *species by PC2* interaction and *year*, 9) *species*, *PC2*, *species by*

288   *PC2* interaction, *year* and *species by year* interaction, and 10) a global model which included

289   main effects of *species*, *year*, *PC1*, and *PC2* as well as *species by PC1* interaction, *species by*

290   *PC2* interaction, and *species by year* interaction. We included models with a species by year

291   interaction because the 2018 transect focused more heavily on Purple-backed Fairywrens while

292   the 2019 transect focused more heavily on Superb Fairywrens. The best-performing model was

293   selected based on lowest AIC_c, calculated using the package *MuMIn* (Table S2; Bartoń 2020).

294   We performed residual diagnostics to test residual fit and to test for overdispersion on the best

295   fitting model using the package *DHARMa* (Hartig 2021) and detected no significant issues.

296

297   **Results**

298   *Climate variables*

299   Sites with high PC1 had a wet, cool climate, whereas sites with a low PC1 had an arid, hot

300   climate. Sites with high PC2 had less variability in rainfall and temperature as well as hotter

301   climates, whereas sites with low PC2 had more variability and cooler climates (Fig. S1). PC1

302   strongly correlates with latitude (Spearman rank correlation: r_s = -0.89, $p \leq 0.001$), with northern

303   sites becoming increasingly arid and hot, while PC2 does not (Spearman rank correlation: r_s = -

304   0.07, $p = 0.69$).

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305

Ecogeographic correlates of group size

307   The best fitting model, as determined by AIC$_c$, had *species*, *PC1*, *species by PC1*

308   *interaction* and *year* as fixed effects (see Table 1 for top model estimates; see Table S2 for

309   model comparisons). The AIC$_c$ of this model was 2.59 lower than the next best performing

310   model (which also included *species by year* interaction).

311   Purple-backed and Superb fairywrens showed opposing patterns of group size variation

312   along the same climate gradient, as described by PC1 (GLM, fixed effect *species by PC1*: $p =$

313   0.001; Table 1, Fig. 3). Purple-backed Fairywrens exhibited larger group sizes in drier, hotter

314   climates (higher PC1), and smaller groups sizes in wetter, cooler climates (Purple-backed

315   Fairywren slope estimate ± SE: 0.05 ± 0.02), whereas Superb Fairywrens exhibited the opposite

316   trend with larger group sizes in wetter, cooler climates (lower PC1) and smaller group sizes in

317   drier, hotter climate (Superb Fairywren slope estimate ± SE: -0.02 ± 0.01). The Purple-backed

318   Fairywren population with the highest PC1 value (PC1 = 0.79; latitude: -36.65; average annual

319   rainfall = 480.56 mm; average maximum temperature = 21.40 °C) had an average group size of

320   2.5 (N = 6) while the population with the lowest PC1 value (PC1= -1.88; latitude: -34.15;

321   average rainfall = 269.11 mm; average maximum temperature = 24.95 °C) had an average group

322   size of 4.67 (N = 6). For Superb Fairywrens, the population with the highest PC1 value (PC1 =

323   6.62; latitude: -38.66; average rainfall = 948.48 mm; average maximum temperature = 18.40 °C)

324   had an average group size of 3.4 (N = 5), while the population with the lowest PC1 value (PC1 =

325   -1.89; latitude: -34.17; average rainfall = 269.85 mm; average maximum temperature = 24.99

326   °C) had an average group size of 2 (N = 2).

327

15

Table 1. Full description of gamma distributed GLM describing the relationship between group size, species, year, and climate.

	Estimate	Std. Error	*t* value	*P*-value
Intercept	0.390	0.030	12.920	<0.001
Species(Superb)	0.040	0.034	1.157	0.255
PC1	0.051	0.018	2.778	0.009
Year(2019)	-0.036	0.024	-1.481	0.148
Species(Superb) * PC1	-0.067	0.019	-3.458	0.001
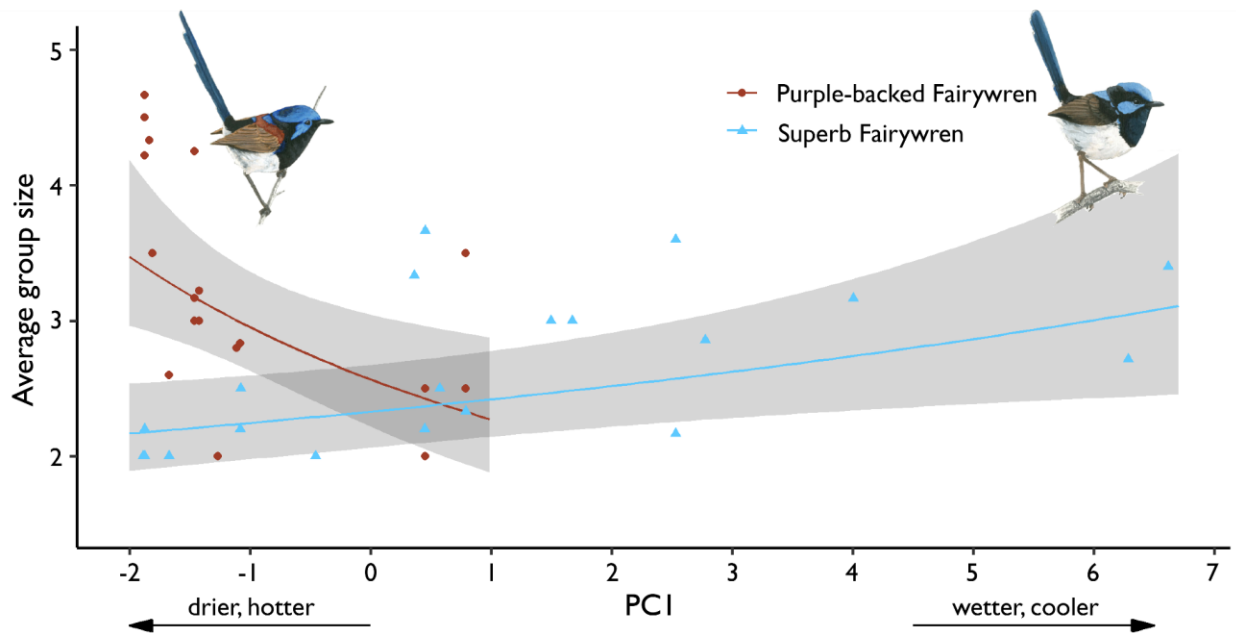
Figure 3. Average group size in relation to PC1
Purple-backed Fairywrens (red dots and line) and Superb Fairywrens (blue triangles and line) show opposing patterns of intraspecific variation in average group size along the environmental gradient, described by PC1 (GLM; species × PC1 interaction: P = 0.001). Points are raw data, lines and 95% confidence intervals are predicted from the model and back-transformed for ease of interpretation. See Table 1 for full model description. Left illustration is a male Purple-backed Fairywren, right illustration is a male Superb Fairywren; illustrations by A.E.J.

Discussion

Recent documentation of ecogeographic patterns across species has helped reveal that accounting for the continuum of cooperative behavior within cooperatively breeding systems (i.e., the 'family-living' to 'true cooperative breeding' continuum, sensu Griesser et al. 2017 and Lin et al. 2019) is key to understanding variation in cooperative behavior. Combined with work on insider–outsider group theory (Shen et al. 2017), these studies have helped to resolve some of the evolutionary puzzle of cooperative breeding, specifically why species with different degrees of helping behavior and different benefits gained from cooperative breeding are more prevalent in different environments. Here, we extend this framework to intraspecific variation in group size and test the hypothesis that patterns of group size variation within species should be affected by the degree of intrinsic or extrinsic sources of benefits gained by sociality in different environmental conditions. Confirming our hypothesis, we show that group size increases with environmental harshness in a species which has higher group productivity in the presence of helping allocare (Purple-backed Fairywrens), but the opposite pattern is true in a species in which the presence of helpers does not increase group productivity (Superb Fairywrens).

We suggest that groups are formed in Purple-backed Fairywrens in hot, arid climates when breeders benefit from the presence of helpers that buffer the effects of the harsh environment on reproductive success, and helpers do not leave because they have little chance to successfully breed without a social group. We suggest that Purple-backed Fairywren group sizes decline in cooler, wet habitats when pair breeding is more successful. In contrast, Superb Fairywrens may only form social groups in wet, cool climates when overall productivity, reproduction, and survival is high and thus territory availability is low, causing helpers to queue for breeding opportunities within their natal territories. Such helpers are tolerated by breeders

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366   because helpers in resource-dense environments inflict little cost. However, because Superb

367   Fairywren auxiliary members do not increase the reproductive success of breeders, increasing

368   conflict over resources between breeders and auxiliary members in hot, arid environments likely

369   drives the decrease in group size.

370   The patterns we document here are consistent with recent hypotheses showing that the

371   environmental influence on group size is driven by opposing effects of social conflict within

372   groups under different environments. Shen et al. (2017) showed that cooperatively breeding

373   groups that gain collective benefits may perform better in harsh environments, while conflicts

374   will be exacerbated in groups with only resource defense benefits. Supporting this theory,

375   cooperative species are more common under harsh environments in an avian lineage with

376   intrinsic benefits while the opposite is true in a lineage where groups do not provide intrinsic

377   benefits (Lin et al. 2019). Similarly, Kao et al. (2020) suggest that groups in which additional

378   members increase the per-capita resources available to the group through their contributions to

379   resource acquisition (similar to the 'collective action' groups of Shen et al. 2017) will increase in

380   size under resource scarcity. Broader examination of group size variation along environmental

381   gradients in larger sets of cooperative breeding species may provide further opportunity for

382   empirical tests of these theories. Ideally, such empirical tests will also involve field experiments

383   to demonstrate the social mechanisms regulating group size in these systems—e.g., do conflicts

384   between breeders and potential helpers change across environmental conditions, or does helping

385   behavior and its impact on reproductive success change across environmental conditions?

386   Our study is the first to explicitly demonstrate intraspecific ecogeographic patterns in

387   cooperative social groups, but anecdotal evidence suggests that such intraspecific variation in

388   sociality may be common. For example, Acorn Woodpeckers (*Melanerpes formicivorous*) in

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389   central California, USA form large cooperatively breeding social groups that defend acorn

390   granaries which support their year-round territories (Koenig 1981) while populations in

391   southeastern Arizona, USA where acorns are insufficiently plentiful to support year-round

392   residency, primarily breed in pairs and migrate (Stacey & Bock 1978). Cooperative breeding is

393   recovered in South America in the Columbian Andes, where aseasonal food sources can again

394   support year-round residency (Kattan 1988). This pattern suggests territory quality and the

395   ability to defend a joint territory might be beneficial in environments with stable or defensible

396   resources in the Acorn Woodpecker system. In Grey-crowned Babblers (*Pomatostomus*

397   *temporalis*), a species in which individuals gain intrinsic benefits from cooperative breeding

398   (Blackmore & Heinsohn 2007), group size was shown to increase along a latitudinal gradient

399   from north to south in northern Australia, a relationship that could relate to increasing harshness

400   experienced by southern populations within this gradient (Edwards & Kot 1995) and the social

401   benefits of being in a group. Similarly, group size in Australian Magpies (*Gymnohrina tibicen*),

402   in which helper provisioning is additive to breeder provisioning (Pike et al. 2019) appears to be

403   larger in more arid, southern populations across Australia (Hughes & Mather 1991; Hughes et al.

404   1996; Shurcliffe & Shurcliffe 1974; Carrick 1972). Taken together, these observations suggest

405   that the type of benefit received by cooperative breeders could indeed generate different

406   relationships between group size and environmental quality in other systems.

407   Prior studies of the relationship between environmental conditions and social behavior

408   have tended to take one of two alternative approaches. Either they examine variation in social

409   behavior within species over time, or they compare social behavior among species. The former

410   approach typically involves focusing on single populations, overlooking variation in social

411   behavior between populations; the latter overlooks both temporal and geographic variation

412   within species by regarding sociality as a species-specific trait. However, it has long been

413   recognized that social systems can vary widely between populations within species (e.g. Carrion

414   Crow: Baglione et al. 2002, mole rats: Bishop et al. 2004, Prairie Voles: Streatfeild et al. 2011).

415   We argue that close examination of interspecific and intraspecific variation in social systems

416   provides important information about the ecological correlates of the evolution of social

417   behavior. Those few studies that have examined both levels of variation have provided insight

418   into ecological and evolutionary processes that differ between species (e.g. *Polistes* wasps;

419   Sheehan et al. 2015; Tumulty et al. 2021). The *Malurus* systems are ideal for asking how

420   benefits of sociality might alter the relationship between ecogeography and sociality, as the

421   species in this clade are well known and their social behavior is relatively easy to quantify. We

422   show here that related species with similar social systems can exhibit opposite patterns of social

423   group size variation across the same environmental gradient. Such variation in ecogeographic

424   patterns can suggest generalizable biological principles that underlie adaptations to

425   environmental conditions. Our finding motivates further behavioral experiments along such

426   social and ecological gradients to test hypotheses regarding the mechanisms underlying

427   ecogeographic patterns in social systems. More generally, we suggest that replicated studies

428   along ecological gradients can enrich our understanding of the environmental contexts

429   underlying the evolution of cooperative behavior.

430

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432   collected and analyzed the data; A.E.J., J.F.W., I.R.H. and D.S. developed the conceptual figure;

433   A.E.J drafted the first version of the manuscript, A.E.J., J.F.W., I.R.H., and D.S. revised and

434   improved all parts of the manuscript and all authors contributed to the final version.

435

436 **Data Statement:** Raw social group size data will be deposited to OSF data repository pending

437 manuscript acceptance. Climate rasters can be acquired from the Australian Bureau of

438 Meteorology (http://www.bom.gov.au/climate/). Any additional information required to

439 reanalyze the data reported in the paper is available from the lead contact upon request.

440

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454   Australian Bureau of Meteorology. (2021). *Long range weather and climate*. Available at:

455   [http://www.bom.gov.au/climate/]. Last accessed 7 Dec 2021.

456   Baglione, V., Marcos, J.M. & Canestrari, D. (2002). Cooperatively Breeding Groups of Carrion

457   Crow (*Corvus corone corone*) in Northern Spain. *Auk,* **119**, 790–799.

458   Bartoń, K. (2020). *MuMIn: multi-model inference*. R package version 1.43.17. Available at:

459   [https://cran.r-project.org/web/packages/MuMIn/index.html]. Last accessed 23 Dec 2021.

460   Bishop, J.M., Jarvis, J.U.M., Spinks, A.C., Bennett, N.C. & O'Ryan, C. (2004). Molecular

461   insight into patterns of colony composition and paternity in the common mole-rat

462   Cryptomys hottentotus hottentotus. *Mol. Ecol.*, **13**, 1217–1229.

463   Blackmore, C.J. & Heinsohn, R. (2007). Reproductive success and helper effects in the

464   cooperatively breeding grey-crowned babbler. J. Zool., **273**, 326–332.

465   Brown, J.L. (1987). Helping and Communal Breeding in Birds: Ecology and Evolution.

466   Princeton University Press, Princeton, NJ.

467   Carrick, R. (1972). Population ecology of the Australian Black-backed Magpie, the Royal

468   Penguin and Silver Gull`. *U. S. Dep. Inter. Wildl. Res. Rep.*, **2**, 41–99.

469   Cockburn, A., Osmond, H.L., Mulder, R.A., Double, M.C. & Green, D.J. (2008a). Demography

470   of Male Reproductive Queues in Cooperatively Breeding Superb Fairy-Wrens *Malurus*

471   *cyaneus*. *J. Anim. Ecol.*, **77**, 297–304.

472   Cockburn, A., Sims, R.A., Osmond, H.L., Green, D.J., Double, M.C. & Mulder, R.A. (2008b).

473   Can we measure the benefits of help in cooperatively breeding birds: the case of superb

474   fairy-wrens *Malurus cyaneus*? *J. Anim. Ecol.*, **77**, 430–438.

475   Covas, R. & Griesser, M. (2007). Life history and the evolution of family living in birds. *Proc.*

476   *R. Soc. B.*, **274**, 1349-1357.

477   Crook, J.H., and Gartlan, J.S. (1966). Evolution of primate societies. *Nature*, **210**, 1200-1203.

478   Drobniak, S.M., Wagner, G., Mourocq, E. & Griesser, M. (2015). Family living: and overlooked

479   but pivotal social system to understand the evolution of cooperative breeding. *Behav.*

480   *Ecol.*, **26**, 805-811.

481   Dunn, P.O., Cockburn, A. & Mulder, R.A. (1995). Fairy-wren helpers often care for to which

482   they are unrelated. *Proc. R. Soc. Lond. B.,* **259**, 339-343.

483   Dunn, P.O. & Cockburn, A. (1996). Evolution of male parental care in a bird with almost

484   complete cuckoldry. *Evolution*, **50**, 2542-2548.

485   Edwards, S.V. & Kot, M. (1995). Comparative Methods at the Species Level: Geographic

486   Variation in Morphology and Group Size in Grey-Crowned Babblers (*Pomatostomus*

487   *temporalis*). *Evolution*, **49**, 1134.

488   Emlen, S.T. (1982). The Evolution of Helping. I. An Ecological Constraints Model. *Am. Nat.*,

489   *119*, 29–39.

490   Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating

491   systems. *Science*, 197, 215-223.

492   Evans, A., Jones, D., Smalley, R. & Lellyett, S. (2020). An enhanced gridded rainfall analysis

493   scheme for Australia. *Bureau of Meteorology Research Report. No.* 41.

494   Gaston, A.J. (1978). The evolution of group territorial behavior and cooperative breeding. *Am.*

495   *Nat.*, **112**, 1091-1100.

496   Gill F. & Donsker, D. (eds). (2018). IOC World Bird List (v 8.1). DOI:10.14344/IOC.ML8.1

497   Gonzalez, J.-C.T., Sheldon, B.C. & Tobias, J.A. (2013). Environmental stability and the

498   evolution of cooperative breeding in hornbills. *Proc. R. Soc. B.*, **280**, 20131297.

499   Griesser, M., Drobniak, S.M., Nakagawa, S. & Botero, C.A. (2017). Family living sets the stage

500   for cooperative breeding and ecological resilience in birds. *PLOS Biol.*, **15**, e2000483.

501   Guindre-Parker, S. & Rubenstein, D.R. (2020). Survival benefits of group living in a fluctuating

502   environment. *Am. Nat.*, **195**, 1027-1036.

503   Hamilton, W.D. (1964). The genetical evolution of social behaviour. I and II. *J. Theor. Biol.*, **7**,

504   1-52.

505   Hartig, F. (2021). DHARMa: residual diagnostics for hierarchical (multi-level / mixed)

506   regression models. R package version 0.4.3. Available at: [https://CRAN.R-

507   project.org/package=DHARMa]. Last accessed 23 Dec 2021.

508   Hennessy, M.B., Kaiser, S. & Sachser, N. (2009). Social buffering of the stress response:

509   diversity mechanisms, and functions. *Front. Neuroedocrin.*, **30**, 470-482.

510   Hidalgo Aranzamendi, N., Hall, M.L., Kingma, S.A., van de Pol, M. & Peters, A. (2019). Rapid

511   plastic breeding response to rain matches peak prey abundance in a tropical savanna bird.

512   J. Anim. Ecol., **88**, 1799–1811.

513   Hughes, J.M., Hesp, J.D.E., Kallioinen, R., Kempster, M., Lange, C.L., Hedstrom, K.E., Mather,

514   P.B., Robinson, A. & Wellbourn, M.J. (1996). Differences in Social Behaviour Between

515   Populations of the Australian Magpie *Gymnorhina tibicen*. *Emu*, **96**, 65–70.

516   Hughes, J.M. & Mather, P.B. (1991). Variation in the size of territorial groups in the Australian

517   Magpie Gymnorhina tibicen. *Proc. R. Soc. Qld.*, **101**, 13–19.

518   Jetz, W. & Rubenstein, D.R. (2011). Environmental Uncertainty and the Global Biogeography of

519   Cooperative Breeding in Birds. *Curr. Biol.*, **21**, 72–78.

520   Johnson, A.E. (2016) Thesis: *Evolution and Sociality in Fairy-wrens (Aves: Maluridae)*.

521   University of Chicago, Chicago, IL, USA.

522   Johnson, A.E. & Pruett-Jones, S. (2018). Reproductive promiscuity in the variegated fairy-wren:

523   an alternative reproductive strategy in the absence of helpers? *Anim. Behav.*, **139**, 171–

524   180.

525   Kattan, G. (1988). Food Habits and Social Organization of Acorn Woodpeckers in Colombia.

526   *Condor*, **90**, 100–106.

527   Kao, A.B., Hund, A.K., Santos, F.P., Young, J., Bhat, D., Garland, J., Oomen, R.A. & McCreery,

528   H.F. (2020). Changes in group size during resource shifts reveal drivers of sociality

529   across the tree of life. *bioRxiv*, 994343. https://doi.org/10.1101/2020.03.17.994343

530   Koenig, W.D. (1981). Reproductive Success, Group Size, and the Evolution of Cooperative

531   Breeding in the Acorn Woodpecker. *Am. Nat.*, **117**, 421–443.

532   Koenig, W.D., Pitelka, F.A., Carmen, W.J., Mumme, R.L. & Stanback, M.T. (1992). The

533   Evolution of Delayed Dispersal in Cooperative Breeders. *Q. Rev. Biol.*, **67**, 111–150.

534   Koenig, W.D., Walters, E.L. & Haydock, J. (2011). Variable helper effects, ecological

535   conditions, and the evolution of cooperative breeding in the acorn woodpecker. *Am. Nat.*,

536   **178**, 145-158.

537   Lin, Y.-H., Chan, S.-F., Rubenstein, D.R., Liu, M. & Shen, S.-F. (2019). Resolving the paradox

538   of environmental quality and sociality: the ecological causes and consequences of

539   cooperative breeding in two lineages of birds. *Am. Nat.*, **194**, 207-216.

540   Lv, L., Liu, Y., Osmond, H.L., Cockburn, A. & Kruuk, L.E.B. (2019). When to start and when to

541   stop: Effects of climate on breeding in a multi-brooded songbird. Glob. Change Biol., **26**,

542   443-457.

543 McLean, A.J., Toon, A., Schmidt, D.J., Joseph, L. & Hughes, J.M. (2012). Speciation in

544   chestnut-shouldered fairy-wrens (Malurus spp.) and rapid phenotypic divergence in

545   variegated fairy-wrens (Malurus lamberti): A multilocus approach. *Mol. Phylogenet.*

546   *Evol.* **63**, 668–678.

547 McLean, A.J., Toon, A., Schmidt, D.J., Hughes, J.M. & Joseph, L. (2017). Phylogeography and

548   geno-phenotypic discordance in a widespread Australian bird, the Variegated Fairy-wren,

549   Malurus lamberti (Aves: Maluridae). *Biol. J. Linn. Soc.*, **121**, 655–669.

550 Mulder, R.A. (1995). Natal and Breeding Dispersal in a Co-Operative, Extra-Group-Mating

551   Bird. *J. Avian Biol.*, **26**, 234–240.

552 Mulder, R.A., Dunn, P.O., Cockburn, A., Lazenby-Cohen, K.A. and Howell, M.J. (1994).

553   Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. *Proc. R.*

554   *Soc. Lond. B*., **255**, 223–229.

555 Nias, R.C. & Ford, H.A. (1992). The Influence of Group Size and Habitat on Reproductive

556   Success in the Superb Fairy-wren *Malurus cyaneus*. *Emu*, 92, 238–243.

557 Orians, G.H. (1969). On the evolution of mating systems in birds and mammals. *Am. Nat.*, **103**,

558   589-603.

559 Pike, K.N., Ashton, B.J., Morgan, K.V. & Ridley, A.R. (2019). Social and Individual Factors

560   Influence Variation in Offspring Care in the Cooperatively Breeding Western Australian

561   Magpie. *Front. Ecol. Evol.*, **7**, 92.

562 Pruett-Jones, S.G. & Lewis, M.J. (1990). Sex ratio and habitat limitation promote delayed

563   dispersal in superb fairy-wrens. *Nature*, **348**, 541–542.

564   R Core Team. (2021). R: A language and environment for statistical computing. R Foundation

565   for Statistical Computing, Vienna, Austria. Available at: [https://www.R-project.org/].

566   Last accessed 23 Dec 2021.

567   Recher, H.F., Majer, J.D. & Ganesh, S. (1996). Seasonality of canopy invertebrate communities

568   in eucalypt forests of eastern and western Australia. *Aust. J. Ecol.*, **21**, 64-80.

569   Riehl, C. (2013). Evolutionary routes to non-kin cooperative breeding in birds. *Proc. R. Soc. B.*,

570   **280**, 20132245.

571   Rowley, I., and Russell, E.M. (1997). Fairy-wrens and Grasswrens: Maluridae. Oxford

572   University Press, Oxford, UK.

573   Rubenstein, D.R. & Lovette, I.J. (2007). Temporal Environmental Variability Drives the

574   Evolution of Cooperative Breeding in Birds. *Curr. Biol.*, **17**, 1414–1419.

575   Sheehan, M.J., Botero, C.A., Hendry, T.A., Sedio, B.E., Jandt, J.M., Weiner, S., Toth, A.L. &

576   Tibbetts, E.A. (2015). Different axes of environmental variation explain the presence vs.

577   extent of cooperative nest founding associations in Polistes paper wasps. *Ecol. Lett.*, **18**,

578   1057–1067.

579   Shen, S.-F., Emlen, S.T., Koenig, W.D. & Rubenstein, D.R. (2017). The ecology of cooperative

580   breeding behaviour. *Ecol. Lett.*, **20**, 708–720.

581   Shurcliffe, A. & Shurcliffe, K. (1974). Territory in the Australian Magpie (Gymnorhina tibicen),

582   an analysis of its size and change. *South Aust. Ornithol.*, **26**, 127–132.

583   Stacey, P.B. & Bock, C.E. (1978). Social Plasticity in the Acorn Woodpecker. *Science*, **202**,

584   1298–1300.

585   Stacy, P.B. and Ligon, J.D. (1991). The benefits-of-philopatry hypothesis for the evolution of

586   cooperative breeding: variation in territory quality and group size effects. *Am. Nat.,* **137**,

587   831-846.

588   Streatfeild, C.A., Mabry, K.E., Keane, B., Crist, T.O. and Solomon, N.G. (2011). Intraspecific

589   variability in the social and genetic mating systems of prairie voles, Microtus

590   ochrogaster. *Anim. Behav.*, **82**, 1387–1398.

591   Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D. & Kelling, S. (2009). eBird: A

592   citizen-based bird observation network in the biological sciences. *Biol. Conserv.*, **142**,

593   2282–2292.

594   Tidemann, S.C. and Marples, T.G. (1986). Periodicity of breeding behaviour of three species of

595   Fairy-wrens (*Malurus* spp.). *Emu*, **87**, 73-77.

596   Tumulty, J.P., Miller, S.E., Belleghem, S.M.V., Weller, H.I., Jernigan, C.M., Vincent, S., et al.

597   (2021). Evidence for a selective link between cooperation and individual recognition.

598   *bioRxiv*, DOI:10.1101/2021.09.07.459327.

599   van de Pol, M., Brouwer, L., Brooker, L.C., Brooker, M.G., Colombeli-Négrel, D., Hall, M.L.,

600   Langmore, N.E., Peters, A., Pruett-Jones, P., Russell, E.M., Webster, M.S. & Cockburn,

601   A. (2013). Problems with using large-scale oceanic climate indices to compare climactic

602   sensitivities across populations and species. *Ecogeography,* **36**, 249-255.

603   Woinarski, J.C.Z. & Cullen, J.M. (1984). Distribution of invertebrates on foliage in forests of

604   south-eastern Australia. *Aust. J. Ecol.*, **9**, 207-232.