

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

3 Allison E. Johnson^{1,*}, Joseph F. Welklin^{2,3,4}, Ian R. Hoppe⁵, and Daizaburo Shizuka⁶

4 1. School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE 68588,
5 USA; email: ajohnson165@unl.edu

6 2. Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14850, USA

7 3. Macaulay Library, Cornell Lab of Ornithology, Ithaca, NY 14850, USA

8 4. Department of Biology, University of Nevada Reno, Reno, NV 89557, USA; email:
9 jwelklin@gmail.com

10 5. School of Natural Resources, University of Nebraska-Lincoln, Lincoln, NE 68583, USA;
11 email: ianr.hoppe@gmail.com

12 6. School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE 68588,
13 USA; email: dshizuka2@unl.edu

14 *Corresponding author: School of Biological Sciences, University of Nebraska-Lincoln,

15 1104 T. St., Lincoln, Nebraska 68588; Phone: 308-631-6644; Email: ajohnson165@unl.edu;

16 Twitter: @FairywrenProj

17

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

19

20 **Keywords:** Cooperative breeding, ecological gradient, dual-benefits, ecological constraints,

21 social benefits, fairywrens

22 **Abstract:**

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

36 **Introduction**

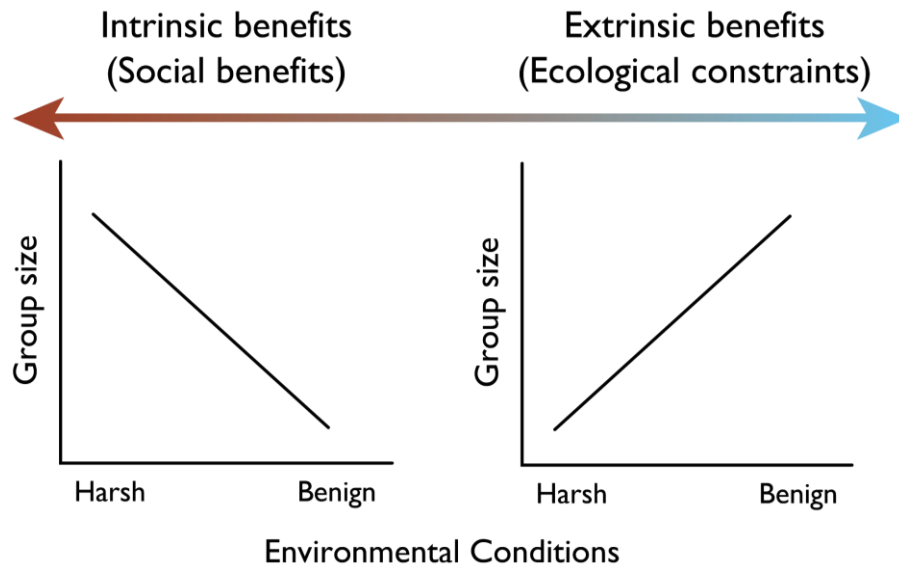
37 Social structure is shaped in part by evolutionary adaptations of organisms to their environment
38 (e.g., Crook & Gartlan 1966; Orians 1969; Emlen & Oring 1977; Hennessy et al. 2009; Guindre-
39 Parker & Rubenstein 2020, among others), but the links between environmental conditions and
40 social systems are complex due to their combined effects on resource acquisition, survival, and
41 reproduction. This complexity is exemplified by cooperative breeding systems, in which one or
42 more breeding pairs are joined by auxiliary members which provide care for offspring (Brown
43 1987). The evolution of cooperative social systems is thought to be driven by a combination of
44 kin-selection benefits, social benefits of group living, and constraints on breeding opportunities
45 (Hamilton 1964; Emlen 1982; Koenig et al. 1992; Covas & Griesser 2007; Riehl 2013). These
46 factors interact with environmental variation in different ways, and have led to the evolution of a
47 spectrum of social behaviors that are often collectively referred to as cooperative breeding
48 systems (Lin et al. 2019). For example, both breeders and auxiliary members may gain intrinsic
49 benefits from sociality (also known as collective action benefits and benefits of philopatry [sensu
50 Stacy & Ligon 1991]) when auxiliary members buffer group reproduction and survival against
51 temporally variable and harsh environments (true cooperative breeding; Emlen 1982; Koenig et
52 al. 1992; Koenig et al. 2011; Shen et al. 2017). In contrast, extrinsic benefits or ecological
53 constraints (or resource defense/access benefits) may be more likely to promote social groups in
54 benign environments where breeders may pay little costs for prolonged associations with
55 juveniles that stay in the natal territory. Such auxiliary individuals benefit by remaining with
56 their parents past maturity, potentially gaining access to resources, queueing for breeding
57 opportunities, or training for parental care, among other benefits (Emlen 1982; Koenig et al.
58 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.



104

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

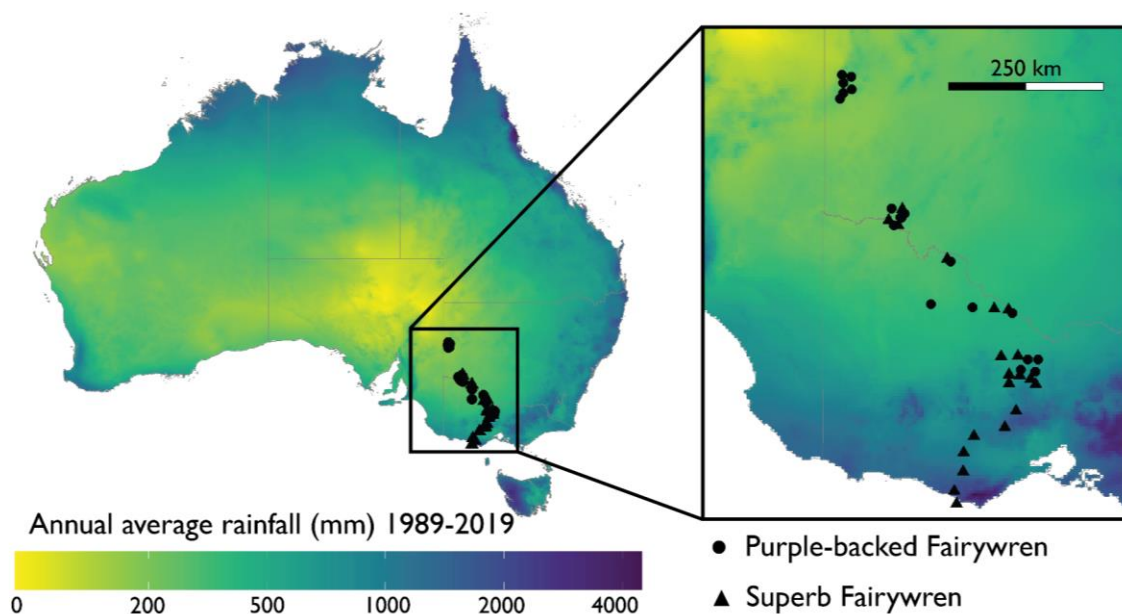
119

120 Fairywrens present an ideal system for examining intraspecific variation in group size because
 121 all species are cooperative to some degree (Rowley & Russell 1997), they are well studied and
 122 thus we have a good understanding of the benefits of cooperation, and many species range over a
 123 variety of climates. Further, climate has been tied to reproductive success in this family, with
 124 rainfall positively predicting nest initiation, clutch size, and reproductive success (Tidemann &
 125 Marples 1986; Nias & Ford 1992; Cockburn et al. 2008b; van de Pol et al. 2013; Hidalgo
 126 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.



158

159

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*

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 , $p = 0.69$).

305

306 *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 \pm 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 \pm 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).

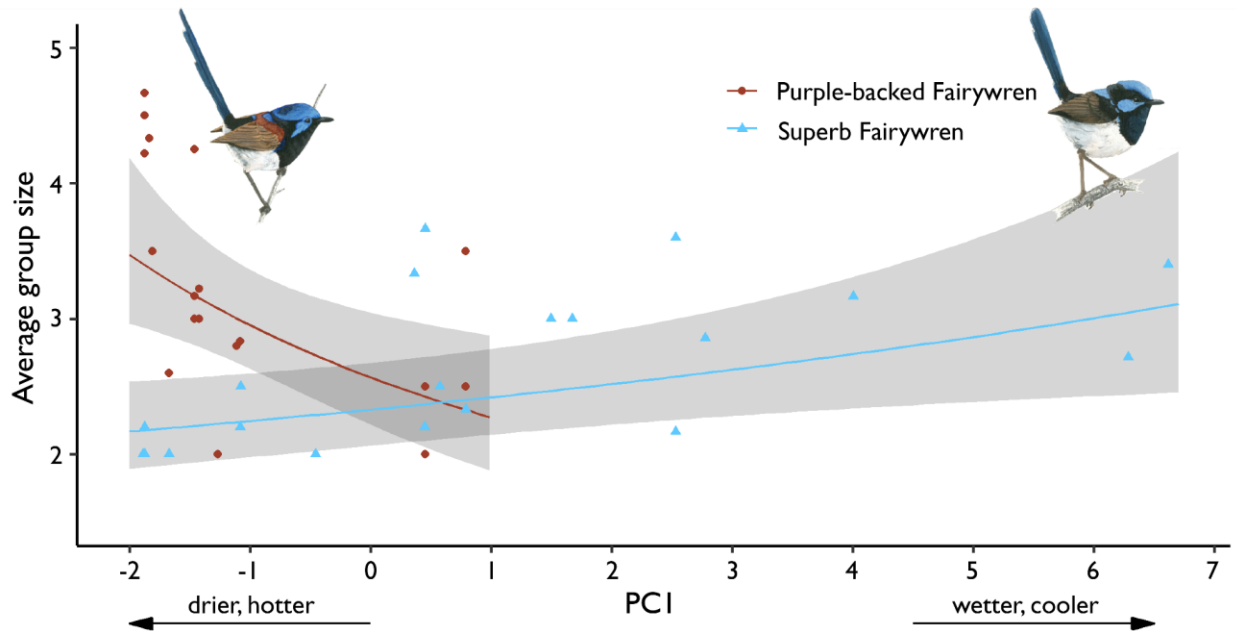
327

328 **Table 1. Full description of gamma distributed GLM describing the relationship between**
 329 **group size, species, year, and climate.**
 330

	Estimate	Std. Error	<i>t</i> value	<i>P</i> -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

331

332



333

334 **Figure 3. Average group size in relation to PC1**

335 Purple-backed Fairywrens (red dots and line) and Superb Fairywrens (blue triangles and line)
 336 show opposing patterns of intraspecific variation in average group size along the environmental
 337 gradient, described by PC1 (GLM; species × PC1 interaction: $P = 0.001$). Points are raw data,
 338 lines and 95% confidence intervals are predicted from the model and back-transformed for ease
 339 of interpretation. See Table 1 for full model description. Left illustration is a male Purple-backed
 340 Fairywren, right illustration is a male Superb Fairywren; illustrations by A.E.J.
 341

342

343 **Discussion**

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

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

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

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 (*Gymnorhina 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

431 **Author Contributions:** A.E.J. and J.F.W. conceived the study; A.E.J, J.F.W., and I.R.H
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

441 **Acknowledgements**

442 We acknowledge the Traditional Owners of country throughout Australia and pay our respects to
443 the Elders past and present. We thank T. Peacock and K. Davies for support in Australia while in
444 and out of the field. This research was supported by an American Ornithological Society
445 Research Award and Kessel Fellowship to A.E.J., UNL Layman Award (26-0506-0236-001) to
446 D.S., and NSF (IOS-1750606 and IOS-2024823) to D.S. This work was entirely observational,
447 and data were collected while birdwatching across south-eastern Australia. We thank the
448 Pravosudov lab at the University of Nevada Reno and the animal behavior journal club at the
449 University of Nebraska-Lincoln for helpful comments on the manuscript.

450

451

452

453 **References:**

- 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-](https://CRAN.R-project.org/package=DHARMA)
507 [project.org/package=DHARMA](https://CRAN.R-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. Neuroendocrin.*, **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.