

1 Cooperation with nonfamily as a strategy for reproducing in variable climates in birds

2 Christina Hansen Wheat^{1,2}, Emily O'Connor¹, Philip A. Downing³, Ashleigh S. Griffin⁴ and
3 Charlie K. Cornwallis^{1*}

4 ¹ Lund University, Kontaktvägen 10, Lund, Sweden.

5 ² IFM Biology, Linköping University, 581 83 Linköping, Sweden.

6 ³ Ecology and Genetics Research Unit, University of Oulu, Oulu, Finland.

7 ⁴ Department of Biology, University of Oxford, United Kingdom.

8 * Corresponding author. Email: charlie.cornwallis@biol.lu.se

9

10 **Keywords:** cooperative breeding; nonfamily cooperation; climate variability; birds; phylogenetic
11 comparative analysis

12 Abstract

13 Climate change is making conditions more extreme and variable, threatening many species.
14 Cooperative breeding can be more common under such conditions, suggesting it may improve
15 resilience to climate change. However, it is unclear whether specific features of cooperative
16 breeding systems, such as how groups form and how large they become, evolved in response to
17 particular climate challenges. We test two predictions using phylogenetic analyses across birds.
18 First, cooperative breeding with unrelated individuals ('nonfamily') is an adaptation to variable
19 environments. Nonfamily groups can form relatively quickly when conditions deteriorate, in
20 contrast to family groups, which typically form when individuals remain in their natal areas over
21 multiple generations. Second, species with larger groups are able to breed in more extreme
22 environments. Nonfamily cooperative breeding was more frequent and group sizes were larger
23 ($n_{\text{species}}=39$) in hotter climates with more variable precipitation. Conversely, cooperative breeding
24 in family groups was more frequent in stable, hot environments and group sizes were not related
25 to climate ($n_{\text{species}}=128$). Both nonfamily and family cooperatively breeding species also had
26 broader climatic niches than phylogenetically matched pair breeders ($n_{\text{species}}=456$). These results
27 highlight that cooperation with unrelated individuals may enable species to live in hot
28 environments with variable rainfall, which are expected to become more common in the future.

29 Teaser

30 Nonfamily cooperation in birds is associated with hot climates and variable rainfall.

31 **Introduction**

32 Extreme and variable climates make it hard for organisms to survive and reproduce (1, 2). The
33 speed of recent climate change is thought to be outpacing that of genetic adaptation for many
34 species, such as long-lived vertebrates (3, 4). Cooperation can help buffer individuals against
35 adverse environmental conditions and this has led to an expectation that cooperative breeding
36 may mitigate the effects of climate change (5–9). However, cooperative groups vary in how they
37 are formed and maintained, their genetic structure and how large they become, and we lack an
38 understanding of whether this influences the resilience of species to different climatic conditions
39 (10–16).

40 Cooperative breeding groups can form and be maintained in different ways (15, 17). First,
41 nonfamily members can aggregate after dispersing from their natal territories. These groups
42 typically consist of unrelated individuals who all attempt to breed at some point during their life
43 and mutually benefit from cooperative care (10, 12, 18–25). Second, offspring can remain in their
44 natal territory to help their parents raise siblings, resulting in multi-generational family groups
45 (26, 27). Under these circumstances, individuals typically forego independent reproduction until
46 breeding opportunities arise, either through breeder turnover or by dispersing to compete for
47 vacant breeding positions (11–13, 28, 29).

48 The way groups are formed and maintained can also influence levels of relatedness (15), which
49 may indirectly affect the climatic conditions that species can tolerate. For example, nonfamily
50 groups can form relatively quickly in environments where high mortality erodes kinship among
51 potential group members (11, 21, 23, 24, 30–33). Nonfamily cooperative breeders are therefore
52 expected to be more common in variable climatic regions where independent breeding is difficult
53 and options for cooperating with kin are limited (34, 35). In contrast, family groups arise when
54 kin associations are maintained across multiple generations through limited dispersal and low
55 mortality rates, which are more likely in stable environments (26, 27). Family groups may also be
56 able to colonise and persist in challenging environments because indirect fitness benefits allow
57 helpers to pass on genes without reproducing themselves (13, 36, 37). Foregoing reproduction
58 allows individuals to devote more time to other activities, such as foraging and predator defence
59 (38, 39), which can be critical to successfully raising offspring under adverse conditions (6).

60 Group size may also influence the environments where species can occur (40, 41). Being in large
61 groups can be beneficial due to economies of scale and greater opportunities for the division of
62 labour (42). Partitioning tasks, such as foraging, predator vigilance and offspring care, among
63 more individuals may enable larger groups to provide offspring with more food and protection

64 under more extreme climatic conditions (7, 40). Larger groups can also be more robust to
65 demographic changes, reducing the costs of individuals switching between tasks (43), which can
66 occur when environments change.

67 Family and nonfamily cooperative breeders can differ in their group sizes (15, 21). In nonfamily
68 groups, reproductive competition among unrelated individuals can limit group size, whereas in
69 family groups, helpers often forego reproduction to aid relatives, relaxing this constraint. This
70 can result in family groups being larger (15), enabling them to potentially inhabit more extreme
71 environments (5). However, it is currently unclear whether the way groups form and are
72 maintained, as well as how large groups become, influences the climatic conditions species can
73 tolerate. This is primarily because the frequency of cooperation (e.g. % of cooperative breeding
74 nests in populations) and group sizes of species breeding in nonfamily and family groups have
75 not been analysed in relation to climatic conditions, or formally compared with the climatic
76 niches of phylogenetically matched pair-breeding species (44–48).

77 Here we use data across birds to test if species that breed in nonfamily and family groups live in
78 environments with different climatic conditions, using global climatological databases to
79 characterise the climatic niches of species during breeding months ([table S1](#); [table S2](#)). We first
80 test whether variation in the frequency of cooperative breeding (% nests with 2+ adults) and
81 group size are related to climate, and if this differs between nonfamily and family groups.
82 Second, we test if the environments that nonfamily and family cooperative breeders inhabit differ
83 from phylogenetically matched pair-breeding species (five most closely related species:
84 $n_{\text{species}}=456$). The breeding systems of cooperative species were classified using data on the
85 presence of cobreeders (pairs versus multiple breeders) and related and unrelated nonbreeding
86 adults at >10% of nests in the population (see Materials and Methods section ‘Classification of
87 breeding systems’. [Table 2](#)). Species were defined as nonfamily if groups had multiple co-
88 breeding individuals (2+) without related nonbreeding individuals, and family if groups consisted
89 of breeders assisted by one or more related nonbreeding helpers (15) ([Table 2](#)). We examined the
90 sensitivity of our results to different classifications of cooperative breeding based on the numbers
91 of breeders (pairs versus more than two breeders) and variation in the presence of related and
92 unrelated helpers at different percentages of nests in populations (>0% versus >30% of nests).

93 Data were analysed using multi-response (MR) Bayesian phylogenetic mixed models (BPMM)
94 where climate variables (median, within-year variation and between-year variation in temperature
95 and precipitation) were fitted as response variables to estimate phylogenetic correlations for
96 nonfamily, family and pair breeding systems. By fitting climate variables as response variables in
97 MR-BPMMs rather than as predictors in regression analysis, we avoid three key issues: (i)

98 collinearity, as climate variables can be highly correlated; (ii) the assumption that species'
99 climatic niches are independent of their phylogenetic history; and (iii) the assumption that climate
100 causally affects cooperative breeding and not the reverse (49–52).

101 **Results**

102 **Nonfamily cooperation increases with climatic variation**

103 Nonfamily cooperative breeders are broadly distributed across the globe, occurring in northern,
104 southern and equatorial regions ([Figure 1](#)). The frequency of cooperative breeding in nonfamily
105 groups was significantly higher in environments with more variable precipitation across breeding
106 seasons and higher average temperatures ([Figure 2](#), [fig. S3](#)). Variation in precipitation between
107 years (95% credible interval, CI) = 0.34 (0.13, 0.5), pMCMC = 0.001; temperature = 0.28 (0.1,
108 0.45), pMCMC = 0.001. [table S3](#)). Similarly, nonfamily cooperative breeding groups were larger
109 in hotter environments with more variable precipitation across breeding seasons ([Figure 2](#),
110 [fig. S4](#)). Variation in precipitation between years (CI) = 0.97 (0, 2.36), pMCMC = 0.058.
111 Temperature (CI) = 1.44 (0.04, 2.39), pMCMC = 0.046. [table S4](#)).

112 In contrast, the frequency of family cooperative breeding increased in hotter, more stable
113 environments ([Figure 2](#), [fig. S3](#)). Temperature (CI) 0.19 (0.03, 0.26), pMCMC = 0.012. Variation
114 in temperature between years (CI) -0.13 (-0.26, -0.02), pMCMC = 0.02. [table S3](#)). This is
115 reflected by the concentration of family cooperative breeders around equatorial regions
116 ([Figure 1](#)). Contrary to our findings for nonfamily cooperative breeders, the size of family groups
117 was not related to any climate variables ([Figure 2](#), [fig. S4](#), [table S4](#)).

118 **Cooperative breeders occupy more arid environments than pair breeders**

119 Compared to phylogenetically matched pair breeders, both nonfamily and family cooperative
120 breeders inhabit drier environments than pair-breeding species ([Figure 3](#) A, C, [fig. S2](#)). Pair vs
121 Nonfamily: Precipitation (CI) = 0.42 (0.05, 0.81), pMCMC = 0.034. Pair vs Family: Precipitation
122 (CI) = 0.28 (0.01, 0.58), pMCMC = 0.048. [Table 1](#), [table S5](#)). Cooperative species also inhabit
123 areas with less variable precipitation during the breeding season, indicating they occupy
124 consistently drier regions than pair breeders ([fig. S5](#)). Pair vs Nonfamily: Within-year variation in
125 precipitation (CI) = 0.7 (0.3, 1.11), pMCMC = 0.001. Pair vs Family: Within-year variation in
126 precipitation (CI) = 0.36 (0.12, 0.69), pMCMC = 0.004. [Table 1](#), [table S5](#)). The temperature of
127 the environments inhabited by nonfamily and family cooperative breeders were, however, similar
128 to pair breeders ([Figure 3](#) B, C, [Table 1](#)).

129 **Cooperative breeders show weaker climatic constraints than pair breeders**

130 The conditions species can cope with may depend on how climate variables covary. For example,
131 it may be more challenging to reproduce in dry areas when temperatures are high, as limits to
132 thermal tolerance may reduce the time animals can spend foraging (53). In this scenario,
133 precipitation and temperature will be negatively related, as species will only occur in dry areas
134 under cooler conditions and hotter areas under wetter conditions. Such climatic constraints may
135 be circumvented if cooperative breeding enables individuals to acquire sufficient resources to
136 raise offspring while reducing their workloads (33). In this case, cooperatively breeding species
137 are expected to occupy hot, dry regions, thereby weakening or eliminating any cross-species
138 correlation between precipitation and temperature.

139 We tested if the correlations between climate variables differed between pair breeders, nonfamily
140 and family cooperative breeders in two ways. First, we estimated phylogenetic covariance
141 matrices of climate variables for each breeding system using MR-BPMMs (Figure 4). Second, we
142 used eigenvector analysis to test if the overall structure of the climate covariance matrices
143 differed between breeding systems. This approach identifies independent axes of climate
144 variation (eigenvectors), where the amount of variation explained by each axis is given by its
145 eigenvalue. If the leading eigenvector for one breeding system, such as pair breeders, has a larger
146 eigenvalue than for other systems, such as nonfamily or family cooperative breeders, it suggests
147 that these species occupy environments where climatic variation is concentrated along a single
148 dominant axis (see [Statistical analyses](#) for more details).

149 Among the 15 possible phylogenetic correlations between climate variables, 12 were significant
150 for pair breeders, whereas only four were significant for family cooperative breeders, and none
151 were significant for nonfamily cooperative breeders (Figure 4). In particular, pair breeders occur
152 in environments where precipitation is negatively correlated with temperature variation, both
153 within and between years, which was not the case for nonfamily or family cooperative breeders
154 (Figure 4 A-C. Phylogenetic correlation between precipitation and temperature variation within-
155 years (CI): pair = -0.59 (-0.69, -0.33), pMCMC = 0.001; nonfamily = -0.14 (-0.48, 0.4), pMCMC
156 = 0.846; family = -0.27 (-0.58, 0.11), pMCMC = 0.236. [table S6](#)). Furthermore, across pair
157 breeders the leading eigenvector explained significantly more variation compared to the leading
158 eigenvector for nonfamily and family cooperative breeders (Figure 4 D).

159 It is possible that including more pair breeding species (456 versus 39 nonfamily and 128 family)
160 may bias variance and covariance estimates across climate variables. We therefore verified that
161 our phylogenetic variance-covariance estimates for pair breeders were not different from

162 cooperative breeders by down-sampling our data to the same number of species as family
163 cooperative breeders and re-running analyses, which recovered qualitatively and quantitatively
164 similar results ([table S7](#)). Together, these findings suggest that pair breeding is challenging in dry
165 environments with low temperature variability, conditions often associated with high
166 temperatures, and that cooperative breeding partially alleviates these constraints.

167 **Sensitivity of results to different classifications of cooperative breeding**

168 The group composition of family cooperative breeders varies. Some species have groups with a
169 pair of breeders while others have multiple breeders (>2), and these can be assisted by family
170 helpers or a mix of family and immigrant nonfamily helpers. Classifying species broadly as
171 ‘family’ misses this variation, which may be important in determining the environments where
172 species persist. Such variation does not occur in nonfamily cooperative breeders as they were
173 defined as nonfamily individuals forming groups after dispersal from their natal territories.

174 We examined the sensitivity of our results to more detailed classifications of family cooperative
175 breeding by defining species as pairs with family helpers (“Pair Family”), pairs with family and
176 nonfamily helpers (“Pair Mixed”) and multiple breeders with family helpers (“Multiple Family”).
177 Note that multiple breeders with nonfamily and family helpers is possible but did not occur in our
178 dataset. [Table 1](#); [Table 2](#)). Using these classifications, we repeated our analyses of the percentage
179 of cooperative nests in populations, group size and differences between pair, nonfamily
180 cooperative breeders and pair breeders ([Table 1](#)). In addition, we examined the sensitivity of our
181 results to classifying species using different thresholds of the % of nests in populations where at
182 least one family and nonfamily nonbreeder were present.

183 We found that the frequency of cooperation in populations increased with temperature in species
184 where all helpers were family members, irrespective of the number of breeders ([Table 1](#); [table](#)
185 [S10](#)). Groups with multiple breeders were also in environments with more stable temperatures
186 ([Table 1](#); [table S10](#)). These results are largely consistent with our broad classification of family
187 cooperative breeding ([Figure 2](#)). However, for groups with a mix of family and nonfamily
188 helpers, the frequency of cooperation was not significantly related to temperature or precipitation
189 ([Table 1](#)).

190 Consistent with our previous analyses, group sizes did not vary with climate across any of our
191 more detailed classifications of family groups ([Table 1](#); [table S11](#)). Furthermore, classifications
192 made using >0% and >30% of nests in populations showed similar patterns to the >10%
193 threshold, with pair breeders being in environments with higher precipitation and more variable
194 precipitation than cooperative breeders ([Table 1](#); [table S8](#); [table S9](#)). There were, however, a

195 number of results that became non-significant, for example, the difference in precipitation
196 between pair breeders and nonfamily cooperative breeders and lower between-year temperature
197 variation in family cooperative breeders ([Table 1](#); [fig. S5](#); [table S8](#); [table S9](#)). In addition, only
198 cooperative breeders where pairs were assisted by family helpers inhabited environments that
199 significantly differed from pair breeders ([Table 1](#)). Differences in statistical significance were
200 largely due to increased variation (wider CIs) around estimates, rather than differences in the
201 direction or magnitude of the relationships, and in some cases sample sizes were much smaller
202 ([Table 1](#); [fig. S5](#); [table S8](#); [table S9](#); [table S12](#)). It is therefore likely that differences across
203 analyses are due to the power to detect effects rather than biological differences

Table 1: Summary of the main analyses examining nonfamily cooperative breeding, family cooperative breeding and pair breeding in relation to climate (bolded analyses) and robustness tests assessing the sensitivity of results to breeding system classifications (unbolded analyses). Robustness tests included: (i) examining if variation within family groups in the number of breeders within groups (“Pair” versus more than two “Multiple”) and whether helpers were all family (“Family”) or a mix of family and nonfamily (“Mixed”) was related to the percentage of cooperative nests within the population (“% Cooperative nests detailed”) and group size (“Group size detailed”); (ii) comparing the climatic niches of species after reclassifying them according to presence of nonfamily and family nonbreeding individuals at >0% and >30% of nests, referred to as “0%” and “30%” respectively; (iii) comparing the climatic niches of species after reclassifying family groups according to the number of breeders within groups (“Pair” versus more than two “Multiple”) and whether helpers were all family (“Family”) or a mix of family and nonfamily (“Mixed”). Posterior modes with CIs are presented for significant relationships with blank cells indicating relationships were non-significant. Full details of analyses can be found in supplementary tables: [table S3](#); [table S10](#); [table S4](#); [table S11](#); [table S5](#); [table S8](#); [table S9](#); and [table S12](#).

Analysis	Comparison	Number of species	Precipitation	Precipitation within-year variation	Precipitation between-year variation	Temperature	Temperature within-year variation	Temperature between-year variation
% Cooperative nests	Nonfamily	37	0.17 (0.01, 0.39)	0.32 (0.11, 0.47)	0.34 (0.13, 0.5)	0.28 (0.1, 0.45)	-0.31 (-0.44, -0.09)	
	Family	125				0.19 (0.03, 0.26)		-0.13 (-0.26, -0.02)
% Cooperative nests detailed	Pair Family	65				0.15 (0.04, 0.35)		
	Pair Mixed	34						
	Multiple Family	26				0.19 (0.02, 0.56)	-0.41 (-0.65, -0.09)	
Group size	Nonfamily	35				1.44 (0.04, 2.39)		

	Family	119			
Group size detailed	Pair Family	60			
	Pair Mixed	33			
	Multiple Family	26			
Breeding system 10%	Pair vs Nonfamily	466 vs 27	0.42 (0.05, 0.81)	0.7 (0.3, 1.11)	
	Pair vs Family	466 vs 53	0.28 (0.01, 0.58)	0.36 (0.12, 0.69)	-0.27 (-0.58, -0.04)
	Nonfamily vs Family	53 vs 27			
Breeding system 0%	Pair vs Nonfamily	456 vs 39		0.5 (0.11, 0.75)	
	Pair vs Family ¹	456 vs 128	0.3 (0.08, 0.46)	0.34 (0.13, 0.51)	
	Nonfamily vs Family	128 vs 39			
Breeding system 30%	Pair vs Nonfamily	487 vs 21		0.47 (0.05, 0.93)	
	Pair vs Family	487 vs 35	0.4 (0.06, 0.75)	0.43 (0.08, 0.78)	
	Nonfamily vs Family	35 vs 21			
Breeding system detailed	Pair vs Pair Family	466 vs 23		0.71 (0.19, 1.06)	-0.46 (-0.85, -0.04)
	Pair vs Pair Mixed	466 vs 16			

Pair vs Multiple Family	466 vs 14		
Pair vs Nonfamily	466 vs 27	0.41 (0.05, 0.8)	0.67 (0.31, 1.11)
Pair Family vs Pair Mixed	23 vs 16		
Pair Family vs Multiple Family	23 vs 14		
Pair Family vs Nonfamily	23 vs 27		
Pair Mixed vs Multiple Family	16 vs 14		
Pair Mixed vs Nonfamily	16 vs 27		
Multiple Family vs Nonfamily	14 vs 27		

¹No helpers indicates all individuals breed i.e. are nonfamily cooperative breeders

206 **Discussion**

207 Our results show that cooperation with nonfamily is more common in hot climates with variable
208 precipitation, conditions that are also associated with larger nonfamily groups. In contrast,
209 cooperative breeding in family groups increases in stable hot environments and group sizes are
210 largely decoupled from climatic variation. Compared to pair breeders, both nonfamily and family
211 cooperative breeders occupy a wider range of environments, in particular more arid
212 environments. Together these results highlight the potential importance of social behaviour in
213 determining the resilience of species to climatic challenges.

214 Family and nonfamily cooperative breeding systems have evolved independently, with important
215 consequences for the reproductive division of labour (15, 17, 37, 55, 56). Our results suggest that
216 this evolutionary distinction also extends to the ecological niches of species breeding in
217 nonfamily versus family groups. In terrestrial vertebrates, cooperative breeding has been linked
218 to high temperatures and variable rainfall, yet previous studies either examined only family
219 groups or pooled family and nonfamily species (31, 57–62). Building on this work, we show that
220 cooperative breeding in both nonfamily and family groups becomes more common with
221 increasing temperature. Crucially, however, only nonfamily cooperative breeding is associated
222 with greater precipitation variability, whereas family cooperative breeding shows the reverse
223 pattern and is more prevalent in stable climates.

224 Several mechanisms may explain why nonfamily cooperative breeding is associated with more
225 variable precipitation across breeding seasons. First, fluctuating environmental conditions can
226 erode population genetic structure, limiting opportunities for cooperating with kin (5, 23, 63, 64).
227 Kin structure can be reduced by higher dispersal and mortality, which increase in cooperatively
228 breeding species during extreme rainfall years (24, 34, 65, 66), and by direct and indirect effects
229 of temperature and rainfall on adult and juvenile survival (3, 33, 64, 67–69). In variable
230 environments, weakened kin structure may create vacancies for unrelated immigrants, whereas in
231 stable environments with stronger kin structure, opportunities for unrelated individuals to join
232 groups may be limited (26, 27). Consistent with this, our sensitivity analyses show that species
233 with a mix of family and nonfamily helpers had climatic associations distinct from species with
234 exclusively family or nonfamily group members ([Table 1](#)), suggesting that immigration of
235 unrelated individuals and retention of related offspring are shaped by different ecological
236 pressures. Second, because nonfamily groups can form relatively quickly, individuals may adjust
237 cooperative behaviour in response to environmental change more readily than in family groups,
238 which take longer to establish. For example, in Taiwan yuhinas, *Yuhina brunneiceps*, females
239 increase cooperation with unrelated cobreeders in years when rainfall makes independent

240 breeding harder (34), whereas conflicts over reproduction can cause nonfamily groups to dissolve
241 when conditions improve. Nonfamily cooperative breeding may therefore be favoured where
242 variable climatic conditions both erode kin structure and select for rapid group formation and
243 breakdown. Disentangling these processes, requires tracking individual movement and group
244 composition in relation to environmental fluctuations over time, emphasising the value of long-
245 term longitudinal studies.

246 Nonfamily groups were larger in hotter climates with fluctuating precipitation, whereas family
247 group size varied independently of climate. The costs of reproductive competition amongst
248 unrelated individuals in nonfamily groups may mean that groups only become larger when
249 environmental conditions increase the benefits of cooperation, resulting in group size closely
250 tracking climatic variation (40, 41). For example, in nonfamily groups of the greater ani,
251 *Crotophaga major*, it has been shown that dry years favour small groups because of competition
252 over food, whereas larger groups are more successful in wet years because of better protection
253 against predators (40). In contrast, the consequences of living in different-sized family groups
254 does not appear to be associated with climate in birds (e.g. (33, 64, 70)). Instead, the effect of
255 group size on fitness in family groups may be determined by diminishing indirect fitness returns,
256 capped by the reproductive output of the breeding female (11, 71).

257 Nonfamily and family cooperative breeders occupied broader climatic niches than pair breeders,
258 particularly in more arid environments. Independent breeding in arid conditions is challenging:
259 extended foraging periods are required to fledge offspring successfully, and protection from
260 thermal stress and predators is essential (30, 33, 40, 72, 73). Cooperation may enable individuals
261 to overcome these challenges, especially where variation among group members in morphology
262 or behaviour allows more efficient resource acquisition and defence against enemies (38, 39, 73,
263 74). In regions with extreme or variable climates, the mutual benefits of cooperating with nonkin
264 and the indirect benefits of helping kin are therefore likely to be high (21), and may even be
265 necessary for colonising and persisting in such environments (8, 60, 75, 76). Cooperative
266 breeding may also be favoured in environments that are suitable for independent breeding when
267 habitat saturation limits breeding opportunities (77). Together, the combined ecological and
268 demographic constraints on independent breeding may explain why cooperatively breeding
269 species occupy more diverse environments than pair breeders (30, 77–79).

270 Extreme climatic conditions, where high temperatures are combined with periods of drought can
271 lead to reproductive failure and even the collapse of entire communities (3, 33, 64, 67).

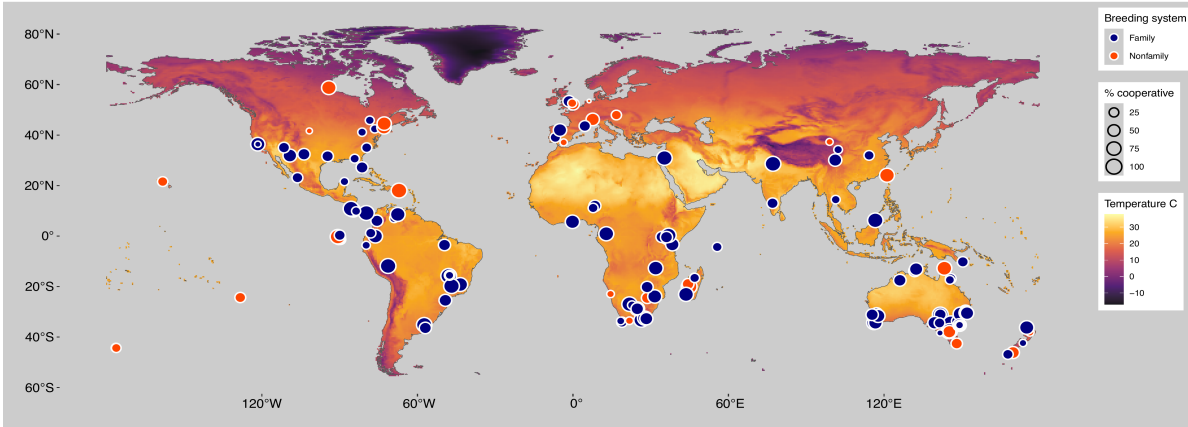
272 Cooperative breeding is one way species may cope with such adverse climates (6, 65, 80).

273 Climate change is expected to magnify environmental variation and it has been proposed that

274 cooperative breeding can help reduce the impact of such variation on reproductive success (81).
275 However, recent work shows that variable environments do not always select for cooperative
276 behaviour among relatives (16). In line with this, our results show that family cooperative
277 breeding is associated with hot, stable climates whereas cooperation with unrelated individuals is
278 associated with variable environments. Cooperation amongst unrelated individuals may therefore
279 be an important strategy that allows animals to cope with climatic conditions that are becoming
280 ever more frequent.

281

A



B

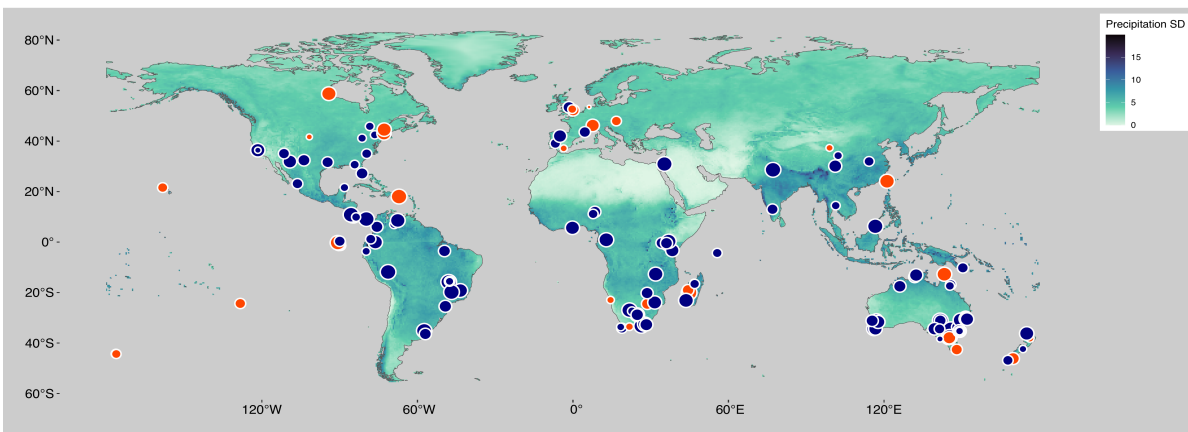


Fig. 1: The areas where family and nonfamily cooperative breeders occur in relation to (A) median temperature and (B) variation in precipitation across years. Points represent study sites, the colour of the circles represents the breeding system, and the size of the circle represents the % of cooperative nests in the population. Maps of all climatic variables with points labelled by species are presented in [fig. S1](#). Median temperature is measured in centigrade and precipitation variation is shown as the square-root-transformed standard deviation of monthly precipitation (mm/month) across years.

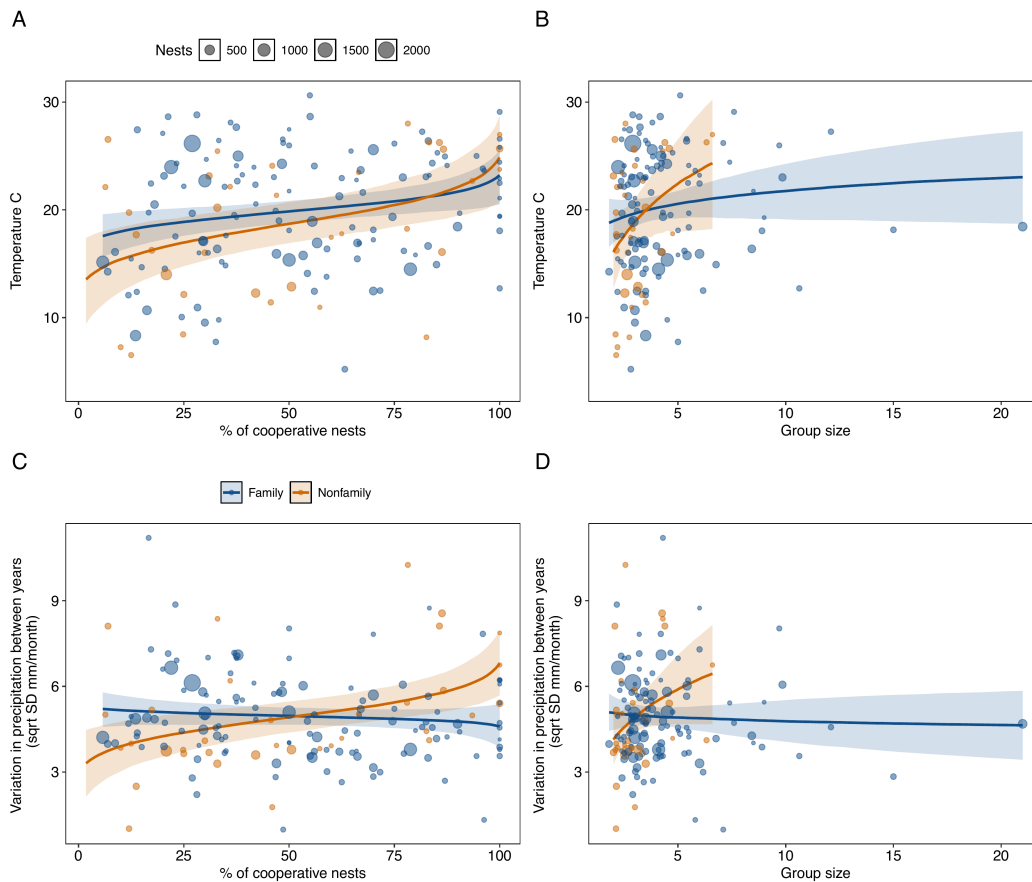


Fig. 2: Contrasting relationships between climate and the percentage of cooperative nests (>2 adults) and group sizes between family and nonfamily cooperative breeders. In nonfamily cooperative breeders, the percentage of cooperative nests and group sizes were greater in environments with higher temperatures (A-B) and variable precipitation across years (C-D). In family cooperative breeders, the percentage of cooperative nests only increased with median temperature (A) and group size was independent of climate (B, D). Points represent species with the size of circles proportional to the number of nests studied to ascertain % of cooperative nests and group sizes. Lines show posterior median fixed-effect predictions with shaded areas indicating 95% credible intervals from Bayesian phylogenetic mixed models. For relationships between all climatic variables and the % of cooperative nests and group sizes see [fig. S3](#) and [fig. S4](#). Median temperature is measured in centigrade and precipitation variation is measured as the square-root-transformed standard deviation of monthly precipitation (mm/month) across years.

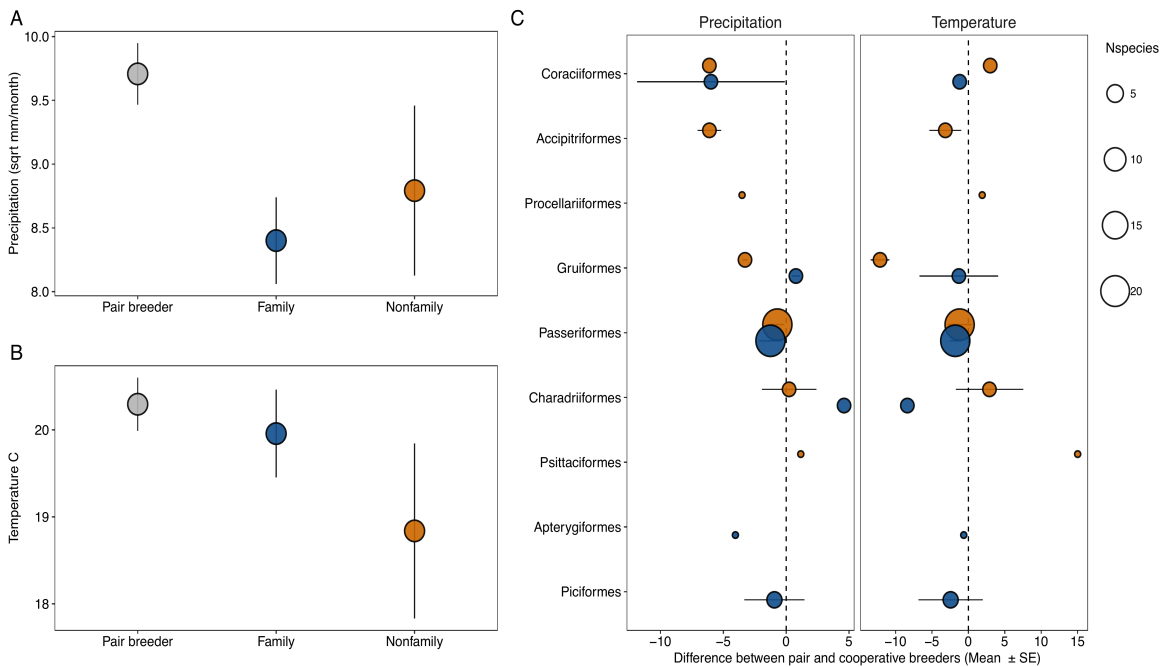


Fig. 3: The environments where nonfamily, family and pair-breeding species occur. Different breeding systems in relation to (A, C left) square-root-transformed median monthly precipitation (mm/month) and (B, C right) median temperature (Centigrade). Nonfamily and family cooperative breeders were in environments with significantly less precipitation but similar temperatures to closely related pair breeders. Points are means \pm SEs. (C) The differences in the climatic niches of breeding systems plotted across bird orders to give an indication of how patterns vary with phylogeny with the size of circles representative of the number of species. Orange dots show mean \pm SEs of pair - nonfamily species and blue dots show pair - family species for different bird orders. In five out of seven bird orders, nonfamily cooperative breeders were in environments with lower precipitation than pair breeders (left of dashed line, C left panel) and were also in a wide variety of thermal environments (C right panel). In contrast, family cooperative breeders occur in environments with similar temperatures to pair breeders (C right panel) and in three out of six bird orders environments had less precipitation (C left panel). For plots with more breeding system classifications that distinguish between species with multiple breeders and a combination of family and nonfamily members see [fig. S5](#).

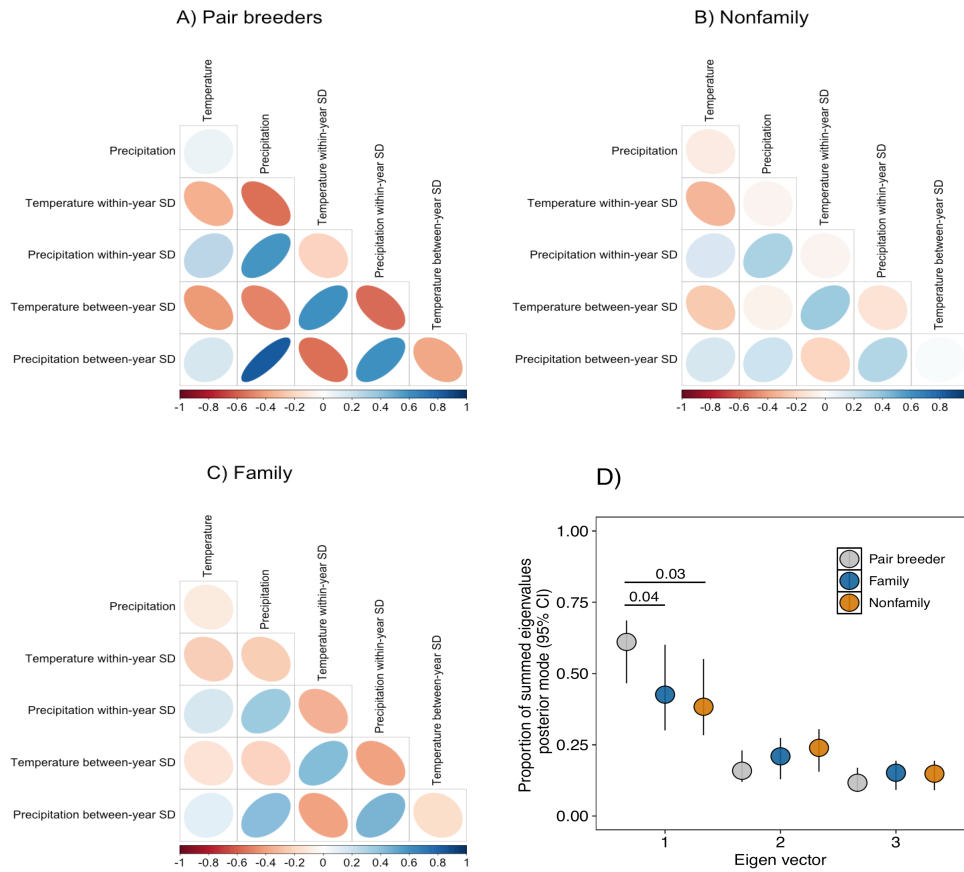


Fig. 4: Nonfamily and family cooperative breeders occupy a broader range of climates than pair breeding species. (A-C) The correlational structure of climate variables across the different breeding systems. Ellipses show the direction and strength of correlations (tighter ellipses represent stronger correlations) with more intense blue colours indicating stronger positive correlations and more intense red colours indicating stronger negative correlations. Temperature is measured in centigrade and precipitation variables are monthly totals or standard deviations in mm/month. D) The proportion of total eigenvalue variation (eigenvalue / sum of all eigenvalues) explained by each eigenvector across breeding systems. The leading eigenvector explained more variation than other eigenvalues across pair breeding species, indicating that more variation is aligned along a single axis of climatic variation than cooperative breeding species. Lines represent significant differences (95% CI of difference does not include 0) with pMCMC values (proportion of iterations greater or less than 0). Only the leading three eigenvectors are shown as the variation explained by eigenvectors four to six was less than 10% and were not significantly different between breeding systems.

286 **Methods**

287 We collected data from published papers on group formation, relatedness among group members,
288 presence of cobreeders, presence of nonbreeding adults assisting with offspring care, frequency
289 of group breeding nests in populations, and group size to quantify variation across cooperative
290 breeding systems. For each cooperative species, we selected the five most closely related pair-
291 breeding species using phylogenetic information (82). Five comparator species were chosen to
292 provide a robust estimate of the climatic niche occupied by pair breeders at each phylogenetic
293 position where cooperation has evolved. Results were qualitatively and quantitatively similar
294 when down-sampling to one pair-breeding species per cooperative breeder (table S7). Pair-
295 breeding species were initially identified using breeding system data from Cockburn 2006 (83)
296 and subsequently verified against current literature, including Birds of the World species
297 accounts (84), to confirm that each species is pair-breeding. We extracted climate data
298 (temperature and precipitation) for breeding and nonbreeding seasons from study sites and
299 species ranges for 1979–2018 using the ERA5 global bioclimatic indicators dataset (85). Data
300 were analysed using the R package *MCMCglmm* to fit Bayesian phylogenetic mixed models (86).

301 **Data collection**

302 We used the species list of cooperative breeders and corresponding literature from Downing et
303 al. 2020 (15), supplemented with additional literature (full list of references in table S1). To find
304 additional species the following search terms were used: “cooperative breeding” OR “helper” OR
305 “related” OR “unrelated” OR “kin” OR “nonkin” OR “nonfamily” OR “family” AND “bird” OR
306 “avian”. Where required data were missing for specific species, we also searched for references
307 using only the common and Latin names of the species as given by BirdLife and Handbook of
308 Birds of World. For our searches we used Google Scholar, PubMed and the library database at
309 Lund University. Because our data requirements are stringent (exact percentages of cooperative
310 nests, helper relatedness), the resulting dataset may be biased towards well-studied species.
311 However, our sensitivity analyses using relaxed classification criteria (see ‘Classification of
312 breeding systems’) produced qualitatively similar results, suggesting that the findings are not
313 driven by non-random sampling of species.

314 **Data on breeding systems, helpers and helper relatedness**

315 ***Classification of breeding systems***

316 Species were classified according to the presence of cobreeders in groups (pair or multiple
317 breeders) and the presence of related and/or unrelated individuals that help raise offspring

318 (Table 2). Pairs within cooperative species were socially monogamous pairs with one or more
 319 helpers. Multiple breeders were any species where more than two adults contribute offspring to
 320 the brood, ascertained using information on joint nesting females and rates of within-group
 321 multiple paternity. Classifications were based on species-specific articles and available
 322 information in review articles of avian breeding systems (table S1 and table S2) (15, 20, 60, 83).
 323 Data were compiled by two authors (CHW and PAD), with independent cross-checking of
 324 subsets by a third author (CKC). Data were only included if exact percentages of nests with
 325 cobreeders (pair versus multiple) and the presence of nonfamily and family helpers (yes versus
 326 no) were recorded (but see ‘Sensitivity to breeding system classifications’ for relaxation of this
 327 criteria). This reduced the number of species from 39 to 32 for nonfamily cooperative breeders
 328 and 128 to 58 for family cooperative breeders. Classifications of breeders and helpers were made
 329 at a threshold of >10% of nests, for example, species were recorded as having multiple breeders
 330 if there were more than two breeding adults at more than 10% of nests.

Table 2: Classification of different cooperative breeding systems.

Breeders¹	Family Helpers²	Nonfamily Helpers²	Group size³	Detailed Classification⁴	Broad Classification
Pair	Yes	No	>2	Pair Family	Family
Pair	Yes	Yes	>2	Pair Mixed	Family
Multiple	Yes	No	>2	Multiple Family	Family
Multiple	Yes	Yes	>2	Multiple Mixed	Family
Multiple	No	Yes	>2	Multiple Nonfamily	Nonfamily
Pair	No	No	2	Pair	Pair

¹Breeders = reproducing individuals

²Helpers = adult individuals foregoing reproduction

³Group size >2 = cooperative species

⁴Note there were no species with clear evidence of a pair of breeders with only nonfamily helpers.

331 **Classification of helpers and helper behaviour**

332 Helpers were defined as adult nonbreeding individuals that assisted with offspring care. Immature
 333 individuals were disregarded in this study and not included in any data or analyses. For example,
 334 if a species had helpers at 100% of nests but 50% of the helpers were juveniles, species were

335 recorded as having helpers at 50% of nests. If it was clear that both juvenile and adult helpers
336 were present at nests, but it was not possible to disentangle the exact percentage of helper
337 presence for each age group from any references, we assumed an estimate of 50% for each helper
338 age group. Although helping encompasses diverse behaviours (nest construction, incubation,
339 provisioning, defence), we recorded only verified accounts of incubation and/or chick or
340 fledgling provisioning. Studies including only other accounts of helping behaviour were
341 excluded. Studies in which observations of incubation or feeding were rare (i.e. only for one nest
342 or only observed on one occasion) were also excluded.

343 ***Relatedness of helpers to breeders***

344 The relatedness of helpers to the breeding pair and chicks they helped raise was assessed using
345 information on genetic markers and pedigrees constructed from ringing data. In cases of multiple
346 studies on the same species using different methods, we first used information from genetic
347 markers to assess relatedness, followed by pedigree data ([table S5](#)). For species with polygamous,
348 polyandrous or polygynandrous mating systems, we assumed that breeding/adult individuals
349 were unrelated unless genetic analyses of the population specifically state otherwise. If data on
350 relatedness was too sparse to assess if groups members were nonfamily or family, species were
351 excluded from analyses.

352 **Climate data**

353 Information on temperature and precipitation was extracted from the ERA5 global bioclimatic
354 indicators dataset (85). This dataset combines multiple sources of observational data with forecast
355 models to accurately reconstruct the global weather conditions between 1979 to 2018 at a
356 resolution of $0.5^\circ \times 0.5^\circ$. We extracted data on monthly mean air temperature at 2m above the
357 surface in units of Kelvin (converted to centigrade for analyses) and monthly mean precipitation
358 as accumulated liquid and frozen water, comprising rain and snow, falling onto the Earth's
359 surface in meters per second. Before calculating summary statistics, precipitation values were
360 converted to calendar-month totals (mm/month) using the number of days in each month.

361 ERA5 reanalysis data offers gap-free spatial and temporal coverage by integrating observational
362 weather data from multiple sources (satellites, weather stations) into a model that accounts for
363 climatic variable interactions, yielding highly reliable historical estimates (87). Station-based
364 precipitation data, such as CRU, which have been used in previous cooperative breeding studies
365 (59, 60, 88), can be sensitive to gauge biases and local topography (89). Reanalysis data is less
366 impacted by anomalies in single sources of observational data (87, 89, 90).

367 For all species we extracted information on temperature and precipitation for study sites for
368 cooperative breeding species and centroid coordinates for pair breeding species. We also
369 examined temperature and precipitation values across entire distributions by intersecting climate
370 data with range maps from BirdLife International (91) and Handbook of Birds of the World (84).
371 The map shapefiles contain information on the seasonal distribution of each species, allowing us
372 to separate breeding and wintering ranges. To extract the climatic data for the relevant
373 coordinates for each species from the gridded ERA5 dataset the R package ‘Raster’ was used
374 (92). This resulted in datasets containing monthly mean estimates of temperature and
375 precipitation for each species between 1979-2018. For the data extracted using species ranges we
376 calculated a median value across the range for each time point. From each of these datasets, we
377 selected only the breeding season months for each species (see ‘Breeding seasons’). Three
378 summary values were then calculated for each dataset for each species: (i) the median breeding
379 season temperature and precipitation across the full 40 year period (calculated from yearly
380 medians); (ii) the within breeding season variation in temperature and precipitation calculated as
381 the median of the standard deviation within years; and (iii) the between breeding season variation
382 in temperature and precipitation calculated as the standard deviation of the yearly medians.

383 There was strong correspondence between measurements at study sites/centroid values and
384 measurements across whole ranges (correlation coefficients across datasets (r): temperature
385 median and variation $r > 0.79$; precipitation median and variation $r > 0.73$). See R script
386 [‘data_nonfam.R’](#). Therefore, we analysed climate data from study sites/centroid values.

387 **Breeding seasons**

388 Cooperative species with widespread distributions show variable breeding seasons across sites, so
389 we used a two-step approach. First, we assessed the breeding season for each species at the study
390 sites given in references ([table S1](#)). In the few cases where a breeding season was not stated in the
391 reference, we used breeding seasons given for the same species at identical study sites, or sites
392 within reasonable proximity in different references, or lastly from Birds of the World or
393 Handbook of Birds of the World species accounts (84). In cases where breeding seasons given for
394 species at the same location did not match across references, we recorded all months where
395 breeding was reported across all references. For the breeding seasons of pair breeding species we
396 used Birds of the World or Handbook of Birds of the World species accounts ([table S2](#)). When
397 dated breeding records were sparse, we interpolated short gaps by coding one or two missing
398 months between recorded breeding months as breeding months, unless the source indicated
399 discontinuous breeding events. Breeding season data were used to select months from the
400 climatic database to ensure conditions during breeding were examined.

401 **Data compilation**

402 Raw data on cooperative breeding species is presented in [table S1](#) with references and details of
403 where information in primary papers was obtained. [table S1](#) contains multiple rows per species
404 when multiple studies, populations, or years were available. Species data were summarized as
405 follows: (i) cooperative and noncooperative nests were summed across years, studies, and
406 populations; (ii) group size estimates were weighted-averaged; (iii) the percentage of nests with
407 pair versus multiple (2+) breeders was calculated at >0%, 10%, and 30% thresholds; (iv) the
408 percentage of nests with family and/or nonfamily members was calculated at the same thresholds.
409 Datasets were compiled using the R script '[data_nonfam.R](#)' and data on breeding seasons and
410 climate data for all species, together with summarised information on cooperative breeders, is
411 presented in [table S2](#).

412 **Statistical analyses**

413 We conducted three sets of analyses using multi-response Bayesian phylogenetic mixed models
414 (MR-BPMM) with the R package *MCMCglmm* for MCMC estimation (86). First, we examined
415 whether cooperative breeding frequency and group size relate to climate across nonfamily and
416 family breeders. Second, we tested for climatic differences between cooperative and pair
417 breeders. Third, we assessed whether the relationships between climate variables differ across
418 breeding systems. See R script '[analyses_nonfam.R](#)'.

419 **Model settings**

420 For MR-BPMMs default priors were used for fixed effects (independent normal priors with zero
421 mean and large variance (10^{10})) and for random effects inverse-gamma priors were used ($V =$
422 $\text{diag}(n)$, $\nu = n - 1 + 0.002$, where ν is the degree of belief and n was equivalent to the number
423 of response traits). Phylogenetic relationships were modelled by fitting a variance-covariance
424 matrix constructed from the phylogeny as a random effect. To account for uncertainty in
425 phylogenetic relationships, we ran models across a sample of 1500 trees. Estimates from the last
426 iteration from tree i were used as starting values for tree $i+1$. Estimates from the last iteration of
427 each tree were saved, with samples from the first 500 trees being discarded as a burn-in. Each
428 tree was sampled for 2000 iterations with a burn-in of 1999 and a thinning interval of 1. Model
429 convergence was examined by repeating each analysis three times and examining the
430 correspondence between chains using the R package 'coda' for convergence checks (93) in the
431 following ways: (i) visually inspecting the traces of the MCMC posterior estimates and their
432 overlap; (ii) calculating the autocorrelation and effective sample size of the posterior distribution
433 of each chain; and (iii) using Gelman and Rubin's convergence diagnostic test that compares

434 within- and between- chain variance using a potential scale reduction factor (PSR). PSR values
435 substantially higher than 1.1 indicate chains with poor convergence properties.

436 ***Parameter estimation***

437 The global intercept was removed from MR-BPMMs to allow trait specific intercepts to be
438 estimated. Parameter estimates from models are presented as posterior modes (PM) with 95%
439 credible intervals (CIs). P values (pMCMC) were calculated as the number of posterior samples
440 above or below a specified value divided by the total number of posterior samples, corrected for
441 the finite number of MCMC samples. For correlations and fixed effects, the specified value was
442 0, and for testing differences between fixed effect levels (e.g. breeding systems) it was the
443 number of posterior samples where one level was greater than the other.

444 Phylogenetic and residual correlations between traits were calculated using the variance and
445 covariance estimates from the unstructured phylogenetic and residual variance-covariance
446 matrices. We estimated the amount of variation in response variables explained by random
447 effects (RE), including phylogenetic effects, as the intraclass correlation coefficient (ICC)
448 estimated as:

$$449 V_i / V_{RE} + V_e$$

450 where V_i is the focal random effect, V_{RE} is the sum of all random effects and V_e is the residual
451 variance on the latent scale (94, 95).

452 ***Specific analyses***

453 ***Differences in the % of cooperative nests and the number of individuals in groups in*** 454 ***relation to climate***

455 We tested whether cooperative breeding frequency relates to climate using MR-BPMM with six
456 climate response variables (median, within-year variation, and between-year variation for
457 temperature and precipitation). The percentage of nests with more than two individuals (logit
458 transformed) was fitted as a covariate interacted with each climate variable separately for
459 nonfamily and family cooperative breeders using the 'at.level' notation in MCMCglmm (Rcode
460 model mod_nests). Group size relationships with climate were examined using the same
461 approach but substituting group size for cooperative nest percentage (model mod_groupsize).

462 ***Median climatic differences across cooperative breeders and pair breeders***

463 We tested for climatic differences across breeding systems using MR-BPMM with six climate
464 response variables and breeding system as a fixed effect. The “at.level” notation was used to
465 estimate each climate variable at each breeding system level (model mod_bs10, [table S5](#)).

466 ***Differences in the relationships between climate variables across cooperative and pair***
467 ***breeders***

468 To examine if the correlations between climatic variables differed across breeding systems we re-
469 ran model mod_bs10 including separate phylogenetic variance-covariance matrices for each
470 breeding system (nonfamily cooperative breeders, family cooperative and pair breeders). This
471 was done using the “at.level” notation in MCMCglmm and variance-covariance estimates were
472 used to calculate phylogenetic correlations between all climate variables for each breeding
473 system (Rcode model mod_climcorr). To verify that differences in the covariance matrices
474 between breeding systems were not due to different number of species (456 versus 39 nonfamily
475 and 128 family), we re-ran this analysis on data where the number of pair breeding species was
476 down-sampled to the same number of family cooperatively breeding species (Rcode model
477 mod_climcorrdown. [table S7](#)).

478 We analysed covariance matrix structure by calculating eigenvectors and eigenvalues for each
479 posterior sample from model mod_climcorr using the R function ‘eigen’. The proportion of total
480 eigenvalue variation for each eigenvector was calculated as (eigenvalue / sum of all eigenvalues)
481 ([Figure 4](#)). Breeding systems were considered to differ in climatic niches when: (i) the 95% CI
482 for the difference in proportion of eigenvalue variation between systems did not include zero, and
483 (ii) fewer than 5% of iterations showed differences in the opposite direction.

484 ***Sensitivity to different breeding system classifications***

485 The level of detail on cooperative breeding varied across species. The main analyses used a
486 >10% nest threshold to assign species to ‘multiple versus pair breeding’ and ‘presence of related
487 nonbreeding individuals’ categories for consistency with previous studies (15, 60, 83). To assess
488 the sensitivity of our results to excluding species without data on the exact percentages of nests
489 with cobreeders and/or the presence of nonfamily and family members, we classified as many
490 species as possible using a summary of available information from all references for a given
491 species ([table S1](#)). In cases where there were discrepancies between references, we implemented
492 a hierarchical decision-making process with advantage given to information based genetic data,
493 then ringing data, then observational data and lastly anecdotal or referred to information

494 (i.e. information based on other studies, unpublished data, personal communication or references
495 of unclear origin). This is referred to as analyses using a >0% threshold of nests in a population.
496 We also examined the sensitivity of our results to classifying species at a higher threshold of
497 >30% of nests ([table S1](#)). For example, if a species had multiple breeders at 15% of nests,
498 nonfamily helpers at 20% of nests and family helpers at 40% of nests it would be classified at the
499 10% threshold as “multiple mixed” whereas it would be reclassified at a >30% threshold as “pair
500 family”. We examined sensitivity to classification choices across three analyses: (i) detailed
501 family group classifications (pair vs. multiple breeders; family vs. mixed helpers) and their
502 relationships with cooperative breeding frequency and group size; (ii) species reclassification at
503 >0% and >30% thresholds for family and nonfamily members; (iii) family groups reclassified by
504 breeder number and helper type (family vs. mixed).

505 **Data and code availability**

506 All code, data and analysis results are available at the Open Science Framework project
507 <https://doi.org/10.17605/OSF.IO/QHVS5>.

508 **Acknowledgments**

509 **Funding:** We are grateful to Lisandro Milocco for advice on covariance matrix comparisons and
510 to funding from the Knut and Alice Wallenberg Foundation (Wallenberg Academy fellowship
511 2018.0138 to CKC) and the Swedish Research Council (VR grant number 2017-03880 to CKC;
512 VR postdoc grant number 2019-06407 to CHW).

513 **Author contributions**

514 Conceptualization - CKC, EO, PD, ASG. Methodology: CKC, CHW, EO, PD. Investigation:
515 CKC, CHW, EO. Visualization and analysis: CKC, EO. Funding acquisition: CKC, CHW.
516 Project administration: CKC. Supervision: CKC. Writing – original draft: CKC. Writing – review
517 & editing: CKC, CHW, EO, PD, ASG.

518 **Corresponding authors**

519 Correspondence to charlie.cornwallis@biol.lu.se

520 **Ethics declarations**

521 **Competing interests**

522 The authors have no competing interests.

523 **Supplementary Information**

524 [Supplementary Tables](#) are provided in xlsx and html format in the file

525 “SupplementaryTables.xlsx”. Full citations of references in [Supplementary Tables](#) are given in

526 the method references⁹⁵⁻⁵²⁶.

527

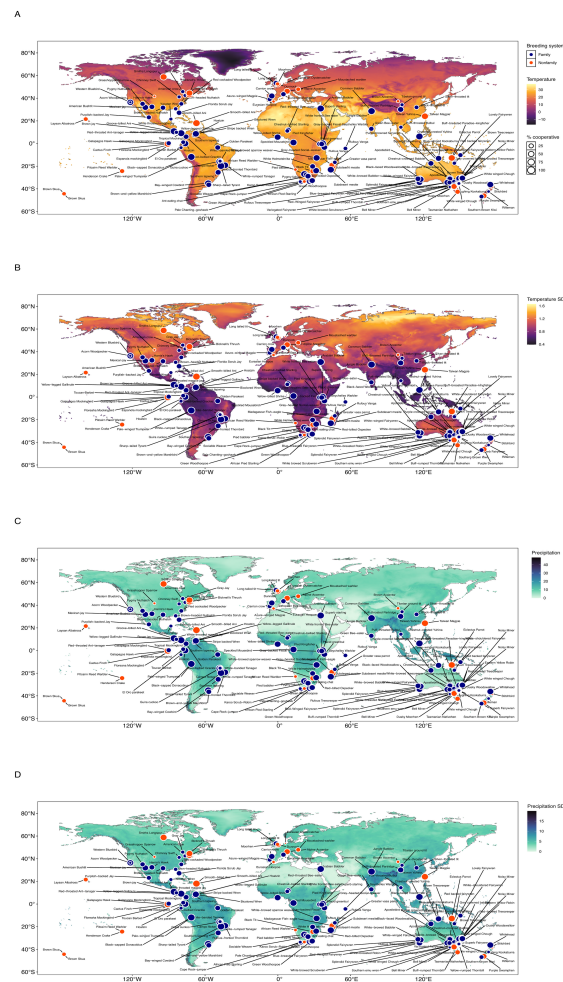


fig. S1: Geographic distribution of family and nonfamily cooperative breeders in relation to median temperature (C) (A), median precipitation (sqrt mm/month) (B), temperature variation across years (C), and precipitation variation across years (D). Variation in temperature and precipitation is calculated as the square-root-transformed standard deviation of yearly values from 1979 to 2018. Points represent study sites labelled by species common names. Circle color indicates breeding system, and circle size represents the percentage of cooperative nests in the population. Median temperature is measured in centigrade and precipitation variation is shown as the square-root-transformed standard deviation of monthly precipitation (mm/month) across years.

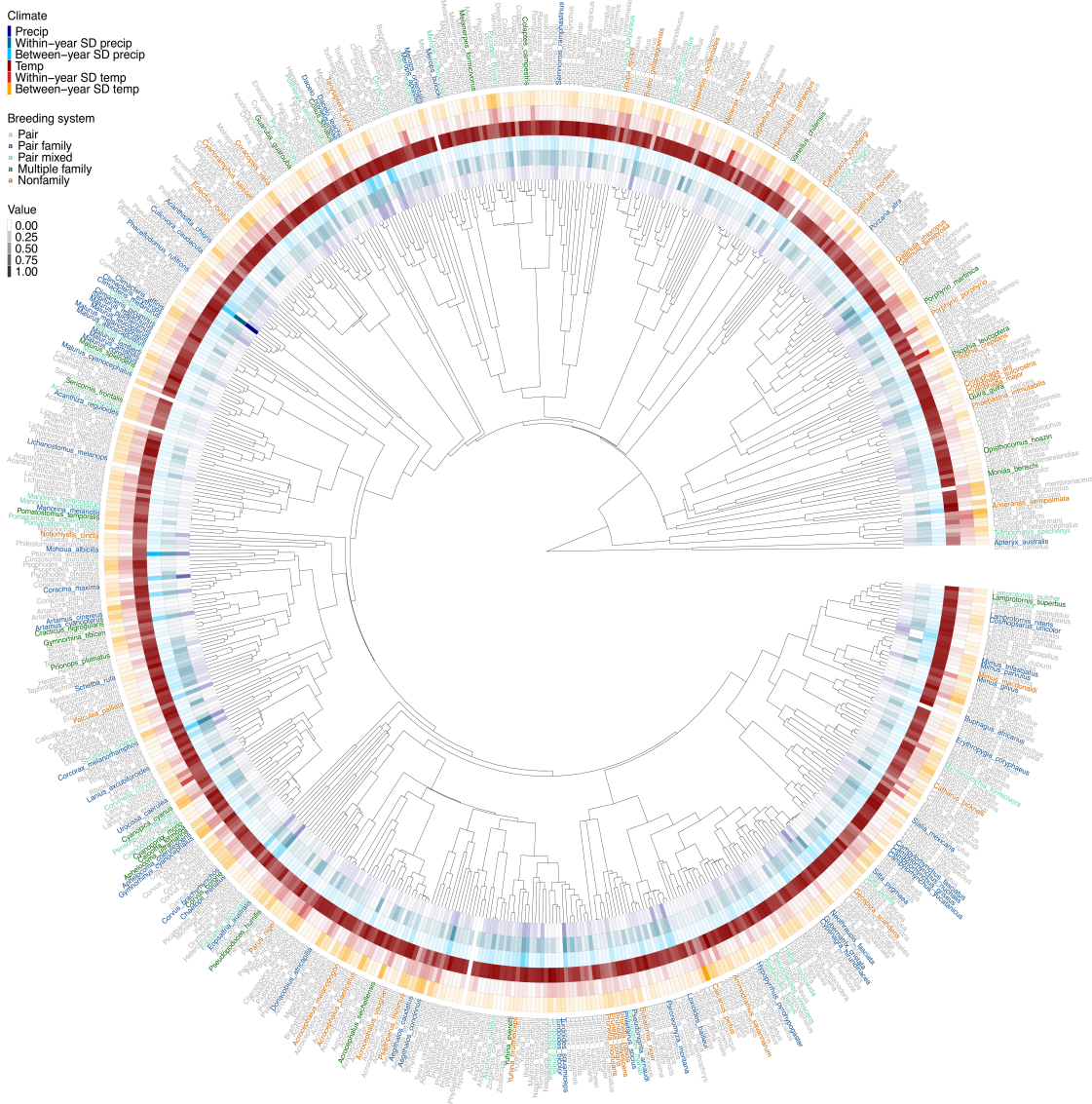


fig. S2: Phylogenetic distribution of cooperative breeding systems in relation to climatic variation. Tip label colors indicate different breeding systems. Color rings from inner to outer circle represent: median precipitation (dark blue), precipitation variation within breeding seasons (aqua), precipitation variation across breeding seasons (turquoise), median temperature (dark red), temperature variation within breeding seasons (pink), and temperature variation across breeding seasons (orange). Climate data were restricted to months during which each species breeds.

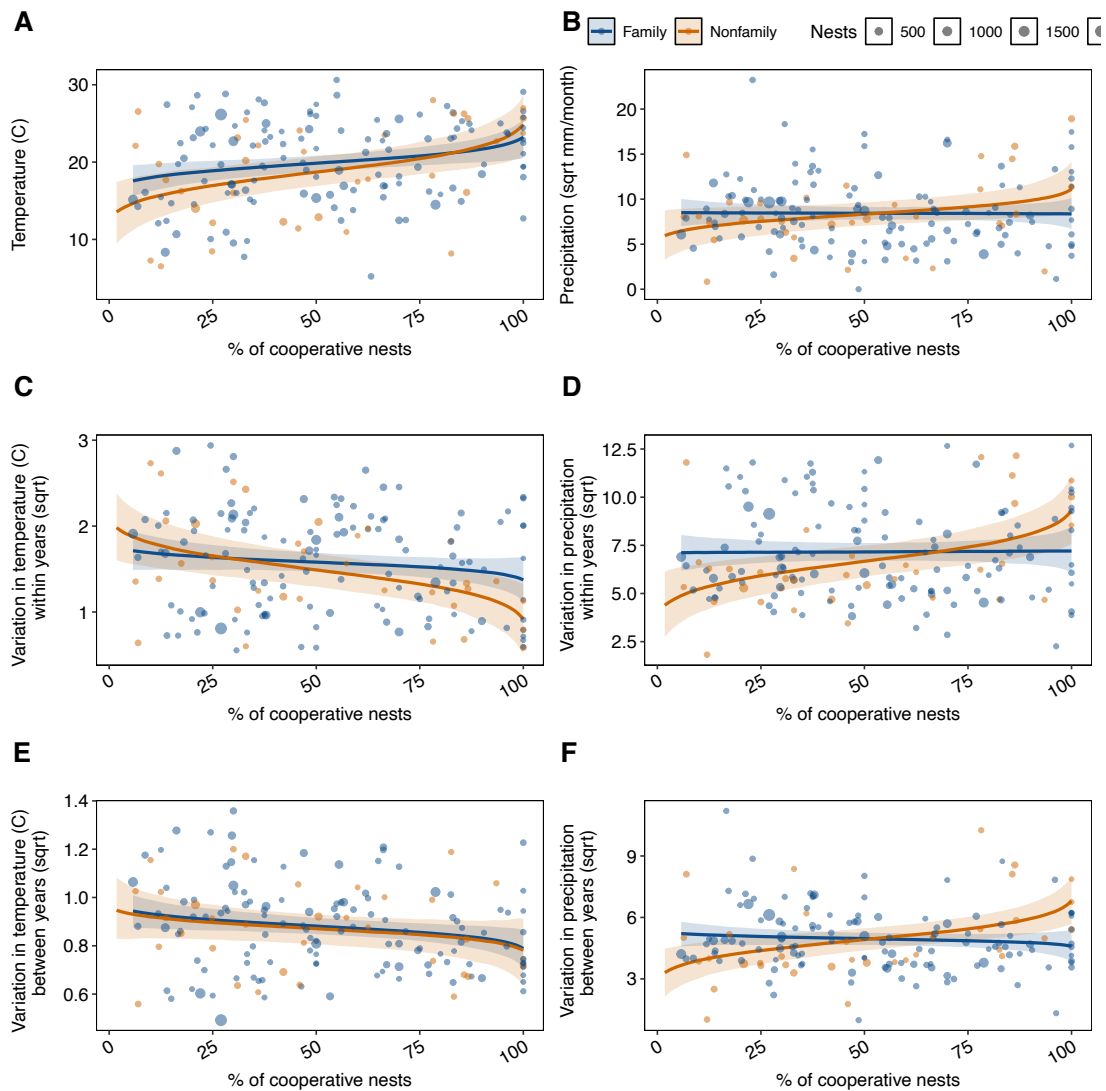


fig. S3: Variation in the frequency of cooperation between nonfamily and family groups in relation to (A) median temperature, (B) median precipitation, (C) temperature variation within breeding seasons, (D) precipitation variation within breeding seasons, (E) temperature variation across breeding seasons, and (F) precipitation variation across breeding seasons. Climate data were restricted to months during which each species breeds. Lines show posterior median fixed-effect predictions with shaded areas indicating 95% credible intervals from Bayesian phylogenetic mixed models. Point size is proportional to the number of nests studied for each species.

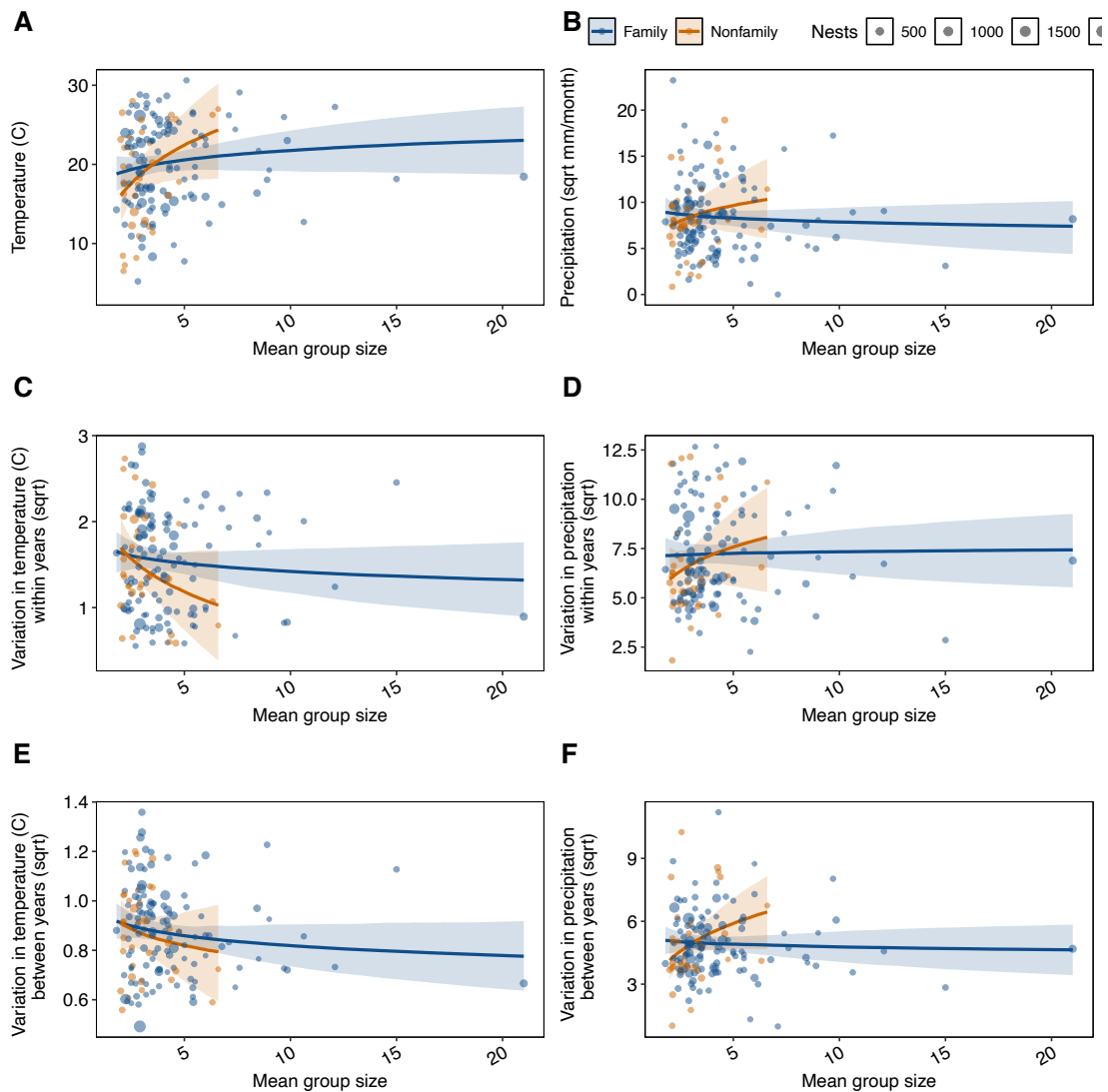


fig. S4: Variation in group size in nonfamily and family groups in relation to (A) median temperature, (B) median precipitation, (C) temperature variation within breeding seasons, (D) precipitation variation within breeding seasons, (E) temperature variation across breeding seasons, and (F) precipitation variation across breeding seasons. Climate data were restricted to months during which each species breeds. Lines show posterior median fixed-effect predictions with shaded areas indicating 95% credible intervals from Bayesian phylogenetic mixed models. Point size is proportional to the number of nests studied for each species.

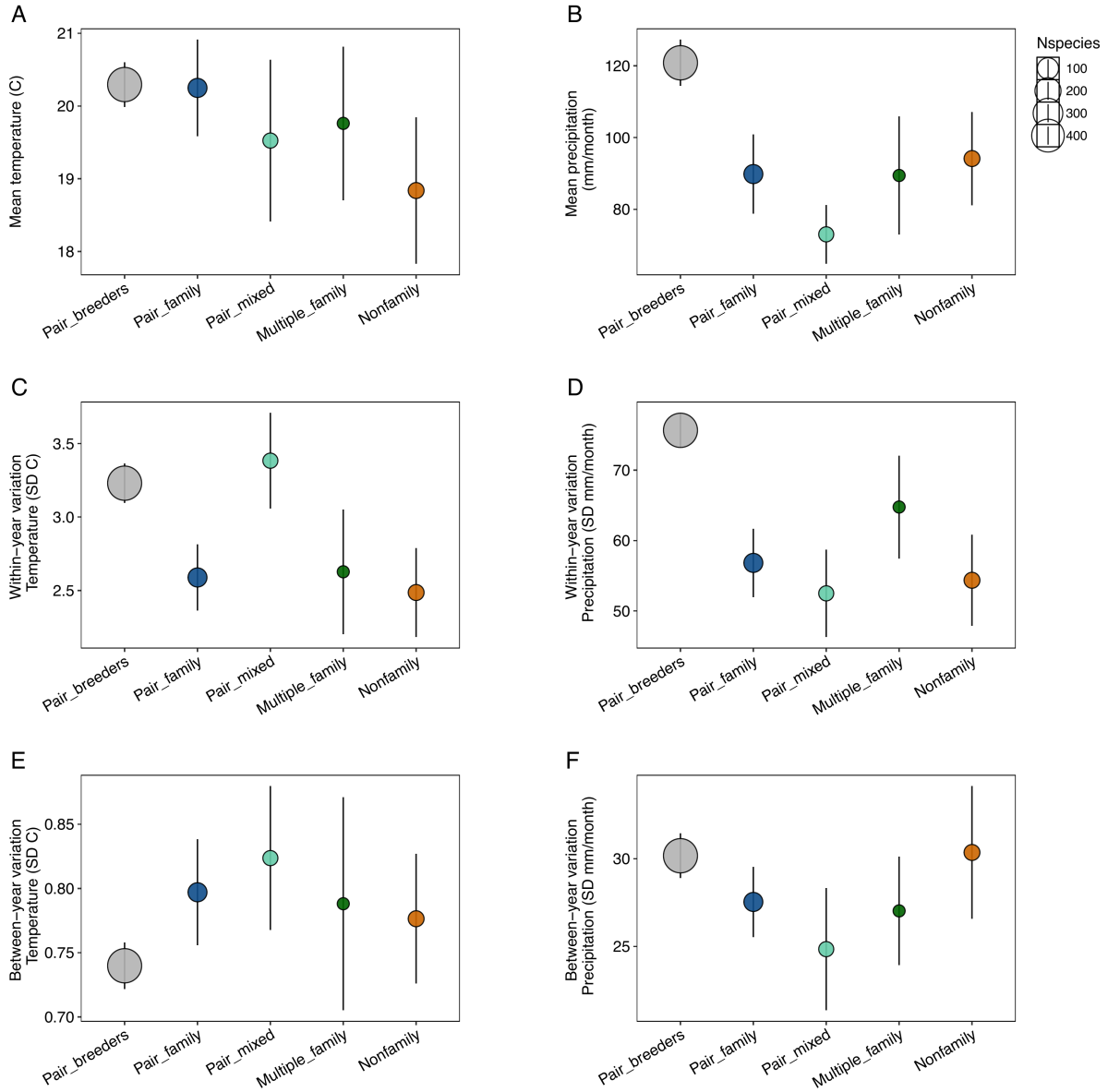


fig. S5: Comparison of environmental conditions among cooperative breeding species with different breeding structures and helper relatedness versus pair-breeding species. Mean values and standard errors are shown for different breeding systems, with circle size proportional to the number of species in each category.

533 **Supplementary Tables**

534 **Data used for analyses**

535 Tables S1 and S2 can be found in the SItables.xlsx.

536 **Results of analyses**

537 Variation in response variables attributable to each random effect was quantified as the
 538 percentage of total random-effect variance on the latent data scale (I^2).

table S3: Variation in the frequency of cooperative breeding (percentage of nests with group breeding, logit transformed) in nonfamily and family groups in relation to climate.

Fixed Effects	Posterior Mode (CI)	pMCMC
Family temp	0.05 (-0.17, 0.18)	-
Family precip	-0.03 (-0.19, 0.17)	-
Family temp within-year	0.08 (-0.1, 0.26)	-
Family precip within-year	-0.01 (-0.16, 0.21)	-
Family temp between-year	0.05 (-0.11, 0.25)	-
Family precip between-year	0.01 (-0.19, 0.17)	-
Nonfamily temp	-0.22 (-0.53, 0.12)	-
Nonfamily precip	-0.06 (-0.34, 0.32)	-
Nonfamily temp within-year	-0.11 (-0.39, 0.25)	-
Nonfamily precip within-year	-0.15 (-0.5, 0.16)	-
Nonfamily temp between-year	-0.01 (-0.36, 0.32)	-
Nonfamily precip between-year	-0.03 (-0.38, 0.28)	-
Family temp: coop frequency	0.19 (0.03, 0.26)	0.012
Family precip: coop frequency	-0.01 (-0.13, 0.11)	0.924
Family temp within-year: coop frequency	-0.06 (-0.2, 0.02)	0.14
Family precip within-year: coop frequency	-0.01 (-0.11, 0.13)	0.914

Family temp between-year: coop frequency	-0.13 (-0.26, -0.02)	0.02
Family precip between-year: coop frequency	-0.09 (-0.18, 0.07)	0.324
Nonfamily temp: coop frequency	0.28 (0.1, 0.45)	0.001
Nonfamily precip: coop frequency	0.17 (0.01, 0.39)	0.042
Nonfamily temp within-year: coop frequency	-0.31 (-0.44, -0.09)	0.002
Nonfamily precip within-year: coop frequency	0.32 (0.11, 0.47)	0.001
Nonfamily temp between-year: coop frequency	-0.12 (-0.33, 0.04)	0.124
Nonfamily precip between-year: coop frequency	0.34 (0.13, 0.5)	0.001
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.55 (0.27, 0.8)	52.74 (29.61, 73.49)
Phylogeny temp within-year	0.52 (0.26, 0.86)	51.22 (26.8, 77.44)
Phylogeny temp between-year	0.49 (0.26, 0.85)	50.48 (27.3, 75.88)
Phylogeny precip	0.56 (0.26, 0.91)	51.61 (26.8, 78.24)
Phylogeny precip within-year	0.45 (0.26, 0.9)	49.02 (25.76, 71.24)
Phylogeny precip between-year	0.53 (0.26, 0.89)	52.01 (25.2, 77.74)
Residual temp	0.51 (0.26, 0.77)	47.26 (26.51, 70.39)
Residual temp within-year	0.5 (0.26, 0.83)	48.78 (22.56, 73.2)
Residual temp between-year	0.55 (0.29, 0.84)	49.52 (24.12, 72.7)
Residual precip	0.64 (0.26, 0.88)	48.39 (21.76, 73.2)
Residual precip within-year	0.56 (0.22, 0.83)	50.98 (28.76, 74.24)
Residual precip between-year	0.46 (0.23, 0.83)	47.99 (22.26, 74.8)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	0.08 (-0.37, 0.41)	0.874
Phylogeny temp between-year : Phylogeny temp	-0.6 (-0.75, -0.2)	0.008
Phylogeny precip : Phylogeny temp	0.39 (-0.02, 0.64)	0.11

Phylogeny precip within-year : Phylogeny temp	-0.43 (-0.67, -0.06)	0.034
Phylogeny precip between-year : Phylogeny temp	0.24 (-0.12, 0.58)	0.188
Phylogeny temp between-year : Phylogeny temp within-year	-0.52 (-0.73, -0.06)	0.052
Phylogeny precip : Phylogeny temp within-year	0.64 (0.26, 0.8)	0.002
Phylogeny precip within-year : Phylogeny temp within-year	-0.37 (-0.67, 0)	0.076
Phylogeny precip between-year : Phylogeny temp within-year	0.65 (0.34, 0.82)	0.001
Phylogeny precip : Phylogeny temp between-year	-0.46 (-0.72, -0.05)	0.04
Phylogeny precip within-year : Phylogeny temp between-year	0.72 (0.39, 0.84)	0.001
Phylogeny precip between-year : Phylogeny temp between-year	-0.68 (-0.77, -0.19)	0.004
Phylogeny precip within-year : Phylogeny precip	-0.6 (-0.75, -0.15)	0.016
Phylogeny precip between-year : Phylogeny precip	0.73 (0.35, 0.82)	0.002
Phylogeny precip between-year : Phylogeny precip within-year	-0.41 (-0.63, 0.1)	0.166
Residual temp within-year : Residual temp	0.05 (-0.4, 0.43)	0.968
Residual temp between-year : Residual temp	-0.41 (-0.68, -0.04)	0.03
Residual precip : Residual temp	0.3 (-0.08, 0.62)	0.162
Residual precip within-year : Residual temp	-0.4 (-0.64, 0)	0.09
Residual precip between-year : Residual temp	0.26 (-0.18, 0.58)	0.266
Residual temp between-year : Residual temp within-year	-0.41 (-0.71, -0.03)	0.054
Residual precip : Residual temp within- year	0.61 (0.24, 0.79)	0.004
Residual precip within-year : Residual temp within-year	-0.37 (-0.69, 0.02)	0.1

Residual precip between-year : Residual temp within-year	0.62 (0.28, 0.82)	0.001
Residual precip : Residual temp between-year	-0.45 (-0.67, 0.05)	0.118
Residual precip within-year : Residual temp between-year	0.7 (0.43, 0.84)	0.001
Residual precip between-year : Residual temp between-year	-0.54 (-0.73, -0.03)	0.05
Residual precip within-year : Residual precip	-0.54 (-0.68, -0.05)	0.05
Residual precip between-year : Residual precip	0.69 (0.3, 0.82)	0.001
Residual precip between-year : Residual precip within-year	-0.37 (-0.6, 0.19)	0.314

539

table S4: Variation in mean group size (log transformed) in nonfamily and family groups in relation to climate.

Fixed Effects	Posterior Mode (CI)	pMCMC
Family temp	-0.22 (-0.95, 0.26)	-
Family precip	0.34 (-0.39, 0.87)	-
Family temp within-year	0.42 (-0.31, 0.94)	-
Family precip within-year	-0.06 (-0.6, 0.62)	-
Family temp between-year	0.51 (-0.16, 1.11)	-
Family precip between-year	0.14 (-0.4, 0.81)	-
Nonfamily temp	-1.41 (-2.73, -0.05)	-
Nonfamily precip	-0.88 (-2.1, 0.56)	-
Nonfamily temp within-year	0.8 (-0.33, 2.28)	-
Nonfamily precip within-year	-0.86 (-2.34, 0.32)	-
Nonfamily temp between-year	0.53 (-0.66, 1.9)	-
Nonfamily precip between-year	-1.32 (-2.52, 0.06)	-
Family temp: group size	0.25 (-0.09, 0.76)	0.194

Family precip: group size	-0.12 (-0.6, 0.25)	0.502
Family temp within-year: group size	-0.35 (-0.68, 0.17)	0.314
Family precip within-year: group size	0.04 (-0.36, 0.52)	0.78
Family temp between-year: group size	-0.38 (-0.78, 0.11)	0.14
Family precip between-year: group size	-0.11 (-0.57, 0.28)	0.59
Nonfamily temp: group size	1.44 (0.04, 2.39)	0.046
Nonfamily precip: group size	0.71 (-0.59, 1.9)	0.304
Nonfamily temp within-year: group size	-0.79 (-2.11, 0.23)	0.134
Nonfamily precip within-year: group size	0.76 (-0.41, 2.03)	0.25
Nonfamily temp between-year: group size	-0.29 (-1.67, 0.7)	0.376
Nonfamily precip between-year: group size	0.97 (0, 2.36)	0.058
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.64 (0.34, 0.92)	53.85 (31.98, 77.09)
Phylogeny temp within-year	0.53 (0.27, 0.89)	50.87 (26.64, 76.45)
Phylogeny temp between-year	0.48 (0.26, 0.87)	51.22 (26.36, 76.2)
Phylogeny precip	0.53 (0.27, 0.92)	52.18 (22.81, 75.76)
Phylogeny precip within-year	0.65 (0.26, 0.95)	50.26 (27.64, 73.32)
Phylogeny precip between-year	0.45 (0.25, 0.88)	51.33 (25.74, 76.28)
Residual temp	0.49 (0.23, 0.76)	46.15 (22.91, 68.02)
Residual temp within-year	0.5 (0.24, 0.85)	49.13 (23.55, 73.36)
Residual temp between-year	0.39 (0.29, 0.85)	48.78 (23.8, 73.64)
Residual precip	0.5 (0.26, 0.92)	47.82 (24.24, 77.19)
Residual precip within-year	0.44 (0.25, 0.92)	49.74 (26.68, 72.36)
Residual precip between-year	0.47 (0.24, 0.87)	48.67 (23.72, 74.26)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	0.02 (-0.44, 0.38)	0.836
Phylogeny temp between-year : Phylogeny temp	-0.59 (-0.72, -0.15)	0.008

Phylogeny precip : Phylogeny temp	0.4 (-0.07, 0.66)	0.124
Phylogeny precip within-year : Phylogeny temp	-0.51 (-0.71, -0.11)	0.028
Phylogeny precip between-year : Phylogeny temp	0.37 (-0.16, 0.62)	0.26
Phylogeny temp between-year : Phylogeny temp within-year	-0.51 (-0.7, -0.02)	0.054
Phylogeny precip : Phylogeny temp within-year	0.72 (0.3, 0.81)	0.002
Phylogeny precip within-year : Phylogeny temp within-year	-0.52 (-0.68, 0.03)	0.12
Phylogeny precip between-year : Phylogeny temp within-year	0.65 (0.33, 0.81)	0.002
Phylogeny precip : Phylogeny temp between-year	-0.55 (-0.77, -0.07)	0.048
Phylogeny precip within-year : Phylogeny temp between-year	0.66 (0.37, 0.83)	0.002
Phylogeny precip between-year : Phylogeny temp between-year	-0.57 (-0.78, -0.14)	0.014
Phylogeny precip within-year : Phylogeny precip	-0.56 (-0.76, -0.11)	0.028
Phylogeny precip between-year : Phylogeny precip	0.68 (0.32, 0.83)	0.001
Phylogeny precip between-year : Phylogeny precip within-year	-0.31 (-0.66, 0.15)	0.23
Residual temp within-year : Residual temp	0.04 (-0.43, 0.41)	0.932
Residual temp between-year : Residual temp	-0.38 (-0.71, -0.02)	0.074
Residual precip : Residual temp	0.39 (-0.1, 0.67)	0.21
Residual precip within-year : Residual temp	-0.33 (-0.61, 0.11)	0.146
Residual precip between-year : Residual temp	0.38 (-0.23, 0.58)	0.338
Residual temp between-year : Residual temp within-year	-0.44 (-0.73, -0.06)	0.056
Residual precip : Residual temp within- year	0.64 (0.25, 0.8)	0.006

Residual precip within-year : Residual temp within-year	-0.46 (-0.68, 0.01)	0.086
Residual precip between-year : Residual temp within-year	0.68 (0.33, 0.84)	0.001
Residual precip : Residual temp between-year	-0.54 (-0.72, 0)	0.084
Residual precip within-year : Residual temp between-year	0.69 (0.41, 0.83)	0.001
Residual precip between-year : Residual temp between-year	-0.49 (-0.74, -0.09)	0.034
Residual precip within-year : Residual precip	-0.6 (-0.7, -0.05)	0.046
Residual precip between-year : Residual precip	0.7 (0.3, 0.83)	0.001
Residual precip between-year : Residual precip within-year	-0.33 (-0.64, 0.15)	0.29

540

table S5: Environmental differences among pair-breeding, family cooperative breeding, and nonfamily cooperative breeding species.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.11 (-0.14, 0.31)	0.358
Pair temp vs Nonfamily temp	0.23 (-0.12, 0.47)	0.222
Pair precip vs Family precip	0.28 (0.01, 0.58)	0.048
Pair precip vs Nonfamily precip	0.42 (0.05, 0.81)	0.034
Pair temp within-year vs Family temp within-year	0.01 (-0.34, 0.19)	0.836
Pair temp within-year vs Nonfamily temp within-year	0.09 (-0.23, 0.47)	0.42
Pair precip within-year vs Family precip within-year	0.36 (0.12, 0.69)	0.004
Pair precip within-year vs Nonfamily precip within-year	0.7 (0.3, 1.11)	0.001
Pair temp between-year vs Family temp between-year	-0.27 (-0.58, -0.04)	0.018

Pair temp between-year vs Nonfamily temp between-year	-0.22 (-0.53, 0.17)	0.326
Pair precip between-year vs Family precip between-year	-0.03 (-0.27, 0.31)	0.776
Pair precip between-year vs Nonfamily precip between-year	0.24 (-0.08, 0.7)	0.126
Family temp vs Nonfamily temp	0.04 (-0.28, 0.42)	0.654
Family precip vs Nonfamily precip	0.17 (-0.26, 0.61)	0.528
Family temp within-year vs Nonfamily temp within-year	0.17 (-0.23, 0.61)	0.412
Family precip within-year vs Nonfamily precip within-year	0.3 (-0.18, 0.77)	0.248
Family temp between-year vs Nonfamily temp between-year	0.07 (-0.35, 0.54)	0.558
Family precip between-year vs Nonfamily precip between-year	0.15 (-0.17, 0.72)	0.282
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.33 (0.2, 0.41)	49.59 (32.59, 66.63)
Phylogeny temp within-year	0.41 (0.24, 0.65)	49.79 (22.64, 76.87)
Phylogeny temp between-year	0.41 (0.23, 0.67)	49.63 (26.04, 71.24)
Phylogeny precip	0.56 (0.21, 0.78)	49.56 (24.81, 75.6)
Phylogeny precip within-year	0.46 (0.24, 0.77)	50.16 (27.64, 76.22)
Phylogeny precip between-year	0.47 (0.23, 0.78)	49.61 (23.14, 75.42)
Residual temp	0.31 (0.18, 0.41)	50.41 (33.37, 67.41)
Residual temp within-year	0.48 (0.23, 0.65)	50.21 (23.13, 77.36)
Residual temp between-year	0.42 (0.21, 0.66)	50.37 (28.76, 73.96)
Residual precip	0.43 (0.21, 0.78)	50.44 (24.4, 75.19)
Residual precip within-year	0.53 (0.25, 0.8)	49.84 (23.78, 72.36)
Residual precip between-year	0.56 (0.22, 0.78)	50.39 (24.58, 76.86)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	0.1 (-0.34, 0.36)	0.78
Phylogeny temp between-year : Phylogeny temp	-0.38 (-0.58, -0.07)	0.014

Phylogeny precip : Phylogeny temp	0.24 (-0.03, 0.55)	0.112
Phylogeny precip within-year : Phylogeny temp	-0.42 (-0.63, -0.14)	0.018
Phylogeny precip between-year : Phylogeny temp	0.16 (-0.15, 0.48)	0.376
Phylogeny temp between-year : Phylogeny temp within-year	-0.63 (-0.74, -0.17)	0.016
Phylogeny precip : Phylogeny temp within-year	0.62 (0.24, 0.77)	0.001
Phylogeny precip within-year : Phylogeny temp within-year	-0.52 (-0.68, -0.05)	0.036
Phylogeny precip between-year : Phylogeny temp within-year	0.81 (0.57, 0.87)	0.001
Phylogeny precip : Phylogeny temp between-year	-0.4 (-0.57, 0.17)	0.272
Phylogeny precip within-year : Phylogeny temp between-year	0.62 (0.33, 0.79)	0.001
Phylogeny precip between-year : Phylogeny temp between-year	-0.59 (-0.75, -0.2)	0.006
Phylogeny precip within-year : Phylogeny precip	-0.62 (-0.74, -0.21)	0.004
Phylogeny precip between-year : Phylogeny precip	0.61 (0.3, 0.81)	0.002
Phylogeny precip between-year : Phylogeny precip within-year	-0.5 (-0.64, 0.07)	0.146
Residual temp within-year : Residual temp	0.07 (-0.3, 0.4)	0.768
Residual temp between-year : Residual temp	-0.42 (-0.61, -0.11)	0.014
Residual precip : Residual temp	0.37 (-0.05, 0.52)	0.104
Residual precip within-year : Residual temp	-0.45 (-0.63, -0.13)	0.02
Residual precip between-year : Residual temp	0.2 (-0.17, 0.46)	0.344
Residual temp between-year : Residual temp within-year	-0.55 (-0.72, -0.12)	0.014
Residual precip : Residual temp within- year	0.64 (0.27, 0.8)	0.006

Residual precip within-year : Residual temp within-year	-0.47 (-0.72, -0.05)	0.06
Residual precip between-year : Residual temp within-year	0.83 (0.57, 0.88)	0.001
Residual precip : Residual temp between-year	-0.4 (-0.59, 0.15)	0.28
Residual precip within-year : Residual temp between-year	0.62 (0.33, 0.78)	0.001
Residual precip between-year : Residual temp between-year	-0.61 (-0.76, -0.18)	0.012
Residual precip within-year : Residual precip	-0.63 (-0.75, -0.22)	0.001
Residual precip between-year : Residual precip	0.67 (0.3, 0.81)	0.004
Residual precip between-year : Residual precip within-year	-0.4 (-0.65, 0.11)	0.178

541

table S6: Correlations between climate variables across different breeding systems.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.1 (-0.11, 0.34)	0.324
Pair temp vs Nonfamily temp	0.26 (-0.15, 0.56)	0.274
Pair precip vs Family precip	0.23 (0.04, 0.58)	0.034
Pair precip vs Nonfamily precip	0.5 (0.09, 0.88)	0.03
Pair temp within-year vs Family temp within-year	-0.04 (-0.28, 0.21)	0.814
Pair temp within-year vs Nonfamily temp within-year	0.14 (-0.24, 0.51)	0.414
Pair precip within-year vs Family precip within-year	0.37 (0.15, 0.68)	0.002
Pair precip within-year vs Nonfamily precip within-year	0.69 (0.33, 1.05)	0.001
Pair temp between-year vs Family temp between-year	-0.27 (-0.6, -0.07)	0.026
Pair temp between-year vs Nonfamily temp between-year	-0.17 (-0.6, 0.2)	0.34

Pair precip between-year vs Family precip between-year	0.01 (-0.23, 0.31)	0.75
Pair precip between-year vs Nonfamily precip between-year	0.34 (-0.08, 0.74)	0.152
Family temp vs Nonfamily temp	0.04 (-0.3, 0.48)	0.676
Family precip vs Nonfamily precip	0.05 (-0.31, 0.61)	0.488
Family temp within-year vs Nonfamily temp within-year	0.17 (-0.29, 0.59)	0.384
Family precip within-year vs Nonfamily precip within-year	0.22 (-0.13, 0.76)	0.236
Family temp between-year vs Nonfamily temp between-year	0.05 (-0.32, 0.6)	0.616
Family precip between-year vs Nonfamily precip between-year	0.35 (-0.21, 0.72)	0.294
Random Effects	Posterior Mode (CI)	I² % (CI)
Pair Phylogeny temp	0.37 (0.23, 0.45)	21.27 (12.92, 28.78)
Pair Phylogeny precip	0.72 (0.43, 0.94)	31.86 (19.08, 44.04)
Pair Phylogeny temp within-year	0.61 (0.4, 0.78)	31.45 (21.38, 42.38)
Pair Phylogeny precip within-year	0.63 (0.39, 0.88)	30.02 (18.84, 41.6)
Pair Phylogeny temp between-year	0.56 (0.32, 0.74)	24.92 (15.12, 34.8)
Pair Phylogeny precip between-year	0.65 (0.42, 0.93)	29.18 (18.13, 40.28)
Family Phylogeny temp	0.41 (0.23, 0.63)	25.05 (14.82, 37.1)
Family Phylogeny precip	0.39 (0.24, 0.74)	20.84 (11.01, 31.16)
Family Phylogeny temp within-year	0.35 (0.19, 0.63)	20.89 (11.11, 31.58)
Family Phylogeny precip within-year	0.48 (0.24, 0.85)	23.27 (13.32, 37.3)
Family Phylogeny temp between-year	0.49 (0.25, 0.81)	23.77 (12.42, 34.39)
Family Phylogeny precip between-year	0.37 (0.22, 0.82)	21.86 (11.15, 32.92)
Nonfamily Phylogeny temp	0.56 (0.25, 1)	36.62 (21.2, 51.45)
Nonfamily Phylogeny precip	0.55 (0.25, 1.06)	28.5 (15.26, 43.18)
Nonfamily Phylogeny temp within-year	0.52 (0.24, 0.97)	29.99 (16.48, 43.7)
Nonfamily Phylogeny precip within-year	0.56 (0.27, 1.08)	27.04 (13.9, 40.97)

Nonfamily Phylogeny temp between-year	0.54 (0.3, 1.24)	32.68 (17.84, 49.18)
Nonfamily Phylogeny precip between-year	0.6 (0.3, 1.26)	30.83 (17.67, 46.56)
Residual Phylogeny temp	0.28 (0.18, 0.37)	17.06 (9.84, 26.38)
Residual Phylogeny precip	0.4 (0.2, 0.61)	18.79 (8.67, 30.72)
Residual Phylogeny temp within-year	0.3 (0.19, 0.5)	17.67 (8.26, 28.62)
Residual Phylogeny precip within-year	0.36 (0.2, 0.64)	19.66 (8.92, 33.41)
Residual Phylogeny temp between-year	0.35 (0.21, 0.57)	18.63 (8.22, 29.11)
Residual Phylogeny precip between-year	0.39 (0.2, 0.62)	18.14 (7.58, 30.1)
Correlations	Posterior Mode (CI)	pMCMC
Pair Phylogeny precip : Pair Phylogeny temp	0.12 (-0.21, 0.32)	0.54
Pair Phylogeny temp within-year : Pair Phylogeny temp	-0.4 (-0.55, -0.13)	0.004
Pair Phylogeny precip within-year : Pair Phylogeny temp	0.29 (0, 0.47)	0.048
Pair Phylogeny temp between-year : Pair Phylogeny temp	-0.44 (-0.62, -0.19)	0.006
Pair Phylogeny precip between-year : Pair Phylogeny temp	0.13 (-0.1, 0.41)	0.232
Pair Phylogeny temp within-year : Pair Phylogeny precip	-0.59 (-0.69, -0.33)	0.001
Pair Phylogeny precip within-year : Pair Phylogeny precip	0.63 (0.38, 0.74)	0.001
Pair Phylogeny temp between-year : Pair Phylogeny precip	-0.51 (-0.67, -0.25)	0.002
Pair Phylogeny precip between-year : Pair Phylogeny precip	0.83 (0.73, 0.9)	0.001
Pair Phylogeny precip within-year : Pair Phylogeny temp within-year	-0.24 (-0.44, 0.08)	0.152
Pair Phylogeny temp between-year : Pair Phylogeny temp within-year	0.6 (0.43, 0.74)	0.001
Pair Phylogeny precip between-year : Pair Phylogeny temp within-year	-0.6 (-0.72, -0.36)	0.001

Pair Phylogeny temp between-year : Pair Phylogeny precip within-year	-0.58 (-0.71, -0.34)	0.001
Pair Phylogeny precip between-year : Pair Phylogeny precip within-year	0.64 (0.4, 0.75)	0.001
Pair Phylogeny precip between-year : Pair Phylogeny temp between-year	-0.36 (-0.62, -0.13)	0.018
Family Phylogeny precip : Family Phylogeny temp	-0.2 (-0.43, 0.27)	0.572
Family Phylogeny temp within-year : Family Phylogeny temp	-0.31 (-0.55, 0.12)	0.21
Family Phylogeny precip within-year : Family Phylogeny temp	0.17 (-0.19, 0.54)	0.428
Family Phylogeny temp between-year : Family Phylogeny temp	-0.17 (-0.45, 0.23)	0.492
Family Phylogeny precip between-year : Family Phylogeny temp	0.08 (-0.23, 0.46)	0.606
Family Phylogeny temp within-year : Family Phylogeny precip	-0.27 (-0.58, 0.11)	0.236
Family Phylogeny precip within-year : Family Phylogeny precip	0.37 (-0.04, 0.66)	0.086
Family Phylogeny temp between-year : Family Phylogeny precip	-0.24 (-0.57, 0.15)	0.306
Family Phylogeny precip between-year : Family Phylogeny precip	0.45 (0.06, 0.69)	0.038
Family Phylogeny precip within-year : Family Phylogeny temp within-year	-0.37 (-0.65, 0.04)	0.096
Family Phylogeny temp between-year : Family Phylogeny temp within-year	0.42 (0.08, 0.69)	0.018
Family Phylogeny precip between-year : Family Phylogeny temp within-year	-0.4 (-0.67, -0.04)	0.03
Family Phylogeny temp between-year : Family Phylogeny precip within-year	-0.45 (-0.68, -0.03)	0.052
Family Phylogeny precip between-year : Family Phylogeny precip within-year	0.4 (0.09, 0.75)	0.028
Family Phylogeny precip between-year : Family Phylogeny temp between-year	-0.05 (-0.56, 0.23)	0.43
Nonfamily Phylogeny precip : Nonfamily Phylogeny temp	0 (-0.55, 0.36)	0.72

Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny temp	-0.3 (-0.68, 0.1)	0.162
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp	0.19 (-0.31, 0.59)	0.53
Nonfamily Phylogeny temp between- year : Nonfamily Phylogeny temp	-0.31 (-0.65, 0.2)	0.302
Nonfamily Phylogeny precip between- year : Nonfamily Phylogeny temp	0.16 (-0.25, 0.63)	0.462
Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny precip	-0.14 (-0.48, 0.4)	0.846
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny precip	0.41 (-0.15, 0.7)	0.21
Nonfamily Phylogeny temp between- year : Nonfamily Phylogeny precip	-0.03 (-0.5, 0.41)	0.844
Nonfamily Phylogeny precip between- year : Nonfamily Phylogeny precip	0.15 (-0.29, 0.6)	0.432
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp within-year	-0.03 (-0.5, 0.39)	0.834
Nonfamily Phylogeny temp between- year : Nonfamily Phylogeny temp within- year	0.45 (-0.04, 0.74)	0.134
Nonfamily Phylogeny precip between- year : Nonfamily Phylogeny temp within- year	-0.29 (-0.64, 0.25)	0.39
Nonfamily Phylogeny temp between- year : Nonfamily Phylogeny precip within-year	-0.21 (-0.57, 0.35)	0.622
Nonfamily Phylogeny precip between- year : Nonfamily Phylogeny precip within-year	0.37 (-0.22, 0.65)	0.232
Nonfamily Phylogeny precip between- year : Nonfamily Phylogeny temp between-year	0.04 (-0.46, 0.46)	0.926

542

table S7: Reanalysis of climate correlations with downsampling to verify that the greater number of pair-breeding species does not affect results.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	-0.04 (-0.28, 0.36)	0.95

Pair temp vs Nonfamily temp	0.14 (-0.34, 0.48)	0.63
Pair precip vs Family precip	0.18 (-0.11, 0.57)	0.148
Pair precip vs Nonfamily precip	0.46 (-0.05, 0.82)	0.06
Pair temp within-year vs Family temp within-year	-0.04 (-0.3, 0.33)	0.996
Pair temp within-year vs Nonfamily temp within-year	0.21 (-0.29, 0.61)	0.418
Pair precip within-year vs Family precip within-year	0.56 (0.13, 0.86)	0.01
Pair precip within-year vs Nonfamily precip within-year	0.67 (0.37, 1.28)	0.002
Pair temp between-year vs Family temp between-year	-0.41 (-0.74, 0.01)	0.052
Pair temp between-year vs Nonfamily temp between-year	-0.2 (-0.73, 0.2)	0.314
Pair precip between-year vs Family precip between-year	0.09 (-0.31, 0.41)	0.834
Pair precip between-year vs Nonfamily precip between-year	0.3 (-0.15, 0.8)	0.228
Family temp vs Nonfamily temp	0.18 (-0.34, 0.53)	0.704
Family precip vs Nonfamily precip	0.21 (-0.24, 0.61)	0.474
Family temp within-year vs Nonfamily temp within-year	0.26 (-0.28, 0.55)	0.426
Family precip within-year vs Nonfamily precip within-year	0.22 (-0.2, 0.73)	0.276
Family temp between-year vs Nonfamily temp between-year	0.13 (-0.35, 0.61)	0.558
Family precip between-year vs Nonfamily precip between-year	0.16 (-0.19, 0.73)	0.276
Random Effects	Posterior Mode (CI)	I2 % (CI)
Pair Phylogeny temp	0.4 (0.28, 0.73)	27.22 (15.46, 38.64)
Pair Phylogeny precip	0.59 (0.29, 0.91)	27.53 (14.84, 40.79)
Pair Phylogeny temp within-year	0.49 (0.27, 0.88)	29.72 (16.43, 42.56)
Pair Phylogeny precip within-year	0.69 (0.29, 1.09)	29.93 (15.55, 43.98)
Pair Phylogeny temp between-year	0.62 (0.3, 1.02)	27.41 (13.82, 40.98)

Pair Phylogeny precip between-year	0.46 (0.31, 1.02)	28.04 (14.6, 41.3)
Family Phylogeny temp	0.4 (0.2, 0.63)	22.65 (12.37, 33.25)
Family Phylogeny precip	0.39 (0.23, 0.77)	22.89 (11.57, 34.6)
Family Phylogeny temp within-year	0.34 (0.19, 0.62)	21.16 (12.44, 32.69)
Family Phylogeny precip within-year	0.45 (0.21, 0.84)	22.64 (11.82, 35.77)
Family Phylogeny temp between-year	0.46 (0.25, 0.8)	22.37 (11.42, 33.7)
Family Phylogeny precip between-year	0.43 (0.23, 0.82)	22.02 (11.44, 35.05)
Nonfamily Phylogeny temp	0.44 (0.25, 1.03)	32.76 (17.75, 49.28)
Nonfamily Phylogeny precip	0.54 (0.22, 1.14)	30.61 (16.84, 48)
Nonfamily Phylogeny temp within-year	0.47 (0.23, 0.98)	30.33 (16.91, 46.59)
Nonfamily Phylogeny precip within-year	0.48 (0.26, 1.07)	27.26 (14.22, 42.13)
Nonfamily Phylogeny temp between-year	0.67 (0.29, 1.3)	31.2 (17.06, 48.06)
Nonfamily Phylogeny precip between-year	0.53 (0.28, 1.27)	30.5 (15.5, 47.69)
Residual Phylogeny temp	0.3 (0.18, 0.44)	17.37 (8.96, 26.52)
Residual Phylogeny precip	0.35 (0.21, 0.58)	18.97 (8.73, 30.69)
Residual Phylogeny temp within-year	0.34 (0.19, 0.51)	18.79 (8.91, 29.79)
Residual Phylogeny precip within-year	0.37 (0.23, 0.69)	20.17 (9.09, 33.05)
Residual Phylogeny temp between-year	0.4 (0.24, 0.64)	19.02 (10.02, 31.62)
Residual Phylogeny precip between-year	0.37 (0.23, 0.65)	19.44 (9.17, 31.85)
Correlations	Posterior Mode (CI)	pMCMC
Pair Phylogeny precip : Pair Phylogeny temp	0.22 (-0.26, 0.48)	0.518
Pair Phylogeny temp within-year : Pair Phylogeny temp	-0.35 (-0.62, 0.03)	0.088
Pair Phylogeny precip within-year : Pair Phylogeny temp	0.31 (-0.13, 0.57)	0.182
Pair Phylogeny temp between-year : Pair Phylogeny temp	-0.46 (-0.67, -0.03)	0.058
Pair Phylogeny precip between-year : Pair Phylogeny temp	0.26 (-0.14, 0.56)	0.278

Pair Phylogeny temp within-year : Pair Phylogeny precip	-0.45 (-0.7, -0.08)	0.01
Pair Phylogeny precip within-year : Pair Phylogeny precip	0.52 (0.15, 0.75)	0.01
Pair Phylogeny temp between-year : Pair Phylogeny precip	-0.46 (-0.71, -0.06)	0.042
Pair Phylogeny precip between-year : Pair Phylogeny precip	0.7 (0.41, 0.84)	0.001
Pair Phylogeny precip within-year : Pair Phylogeny temp within-year	-0.34 (-0.62, 0.09)	0.16
Pair Phylogeny temp between-year : Pair Phylogeny temp within-year	0.55 (0.26, 0.78)	0.004
Pair Phylogeny precip between-year : Pair Phylogeny temp within-year	-0.51 (-0.72, -0.1)	0.028
Pair Phylogeny temp between-year : Pair Phylogeny precip within-year	-0.6 (-0.76, -0.18)	0.016
Pair Phylogeny precip between-year : Pair Phylogeny precip within-year	0.59 (0.19, 0.79)	0.012
Pair Phylogeny precip between-year : Pair Phylogeny temp between-year	-0.43 (-0.7, -0.01)	0.074
Family Phylogeny precip : Family Phylogeny temp	-0.07 (-0.44, 0.3)	0.612
Family Phylogeny temp within-year : Family Phylogeny temp	-0.24 (-0.56, 0.14)	0.246
Family Phylogeny precip within-year : Family Phylogeny temp	0.21 (-0.22, 0.5)	0.446
Family Phylogeny temp between-year : Family Phylogeny temp	-0.23 (-0.45, 0.25)	0.496
Family Phylogeny precip between-year : Family Phylogeny temp	0 (-0.3, 0.44)	0.688
Family Phylogeny temp within-year : Family Phylogeny precip	-0.29 (-0.57, 0.18)	0.27
Family Phylogeny precip within-year : Family Phylogeny precip	0.45 (-0.04, 0.65)	0.088
Family Phylogeny temp between-year : Family Phylogeny precip	-0.19 (-0.59, 0.18)	0.326
Family Phylogeny precip between-year : Family Phylogeny precip	0.46 (0.07, 0.72)	0.054

Family Phylogeny precip within-year : Family Phylogeny temp within-year	-0.38 (-0.65, 0.08)	0.118
Family Phylogeny temp between-year : Family Phylogeny temp within-year	0.54 (0.05, 0.68)	0.04
Family Phylogeny precip between-year : Family Phylogeny temp within-year	-0.48 (-0.67, -0.01)	0.056
Family Phylogeny temp between-year : Family Phylogeny precip within-year	-0.46 (-0.67, 0.03)	0.08
Family Phylogeny precip between-year : Family Phylogeny precip within-year	0.41 (0.09, 0.74)	0.038
Family Phylogeny precip between-year : Family Phylogeny temp between-year	-0.33 (-0.51, 0.26)	0.442
Nonfamily Phylogeny precip : Nonfamily Phylogeny temp	-0.07 (-0.52, 0.38)	0.7
Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny temp	-0.28 (-0.68, 0.11)	0.194
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp	0.24 (-0.37, 0.55)	0.584
Nonfamily Phylogeny temp between- year : Nonfamily Phylogeny temp	-0.24 (-0.64, 0.16)	0.314
Nonfamily Phylogeny precip between- year : Nonfamily Phylogeny temp	0.22 (-0.3, 0.61)	0.558
Nonfamily Phylogeny temp within-year : Nonfamily Phylogeny precip	-0.13 (-0.5, 0.38)	0.798
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny precip	0.45 (-0.14, 0.68)	0.18
Nonfamily Phylogeny temp between- year : Nonfamily Phylogeny precip	-0.11 (-0.52, 0.37)	0.754
Nonfamily Phylogeny precip between- year : Nonfamily Phylogeny precip	0.17 (-0.22, 0.68)	0.394
Nonfamily Phylogeny precip within-year : Nonfamily Phylogeny temp within-year	-0.15 (-0.5, 0.42)	0.834
Nonfamily Phylogeny temp between- year : Nonfamily Phylogeny temp within- year	0.47 (-0.06, 0.71)	0.122
Nonfamily Phylogeny precip between- year : Nonfamily Phylogeny temp within- year	-0.28 (-0.61, 0.28)	0.484

Nonfamily Phylogeny temp between-year : Nonfamily Phylogeny precip within-year	-0.14 (-0.58, 0.34)	0.654
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny precip within-year	0.34 (-0.18, 0.66)	0.262
Nonfamily Phylogeny precip between-year : Nonfamily Phylogeny temp between-year	-0.01 (-0.45, 0.47)	0.938

table S8: Environmental differences among pair-breeding, nonfamily cooperative breeding, and family cooperative breeding species with classifications assigned without a threshold (>0%).

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.02 (-0.12, 0.17)	0.63
Pair temp vs Nonfamily temp	0.14 (-0.06, 0.42)	0.15
Pair precip vs Family precip	0.3 (0.08, 0.46)	0.01
Pair precip vs Nonfamily precip	0.17 (-0.15, 0.48)	0.286
Pair temp within-year vs Family temp within-year	0.08 (-0.1, 0.25)	0.37
Pair temp within-year vs Nonfamily temp within-year	0.21 (-0.09, 0.51)	0.186
Pair precip within-year vs Family precip within-year	0.34 (0.13, 0.51)	0.002
Pair precip within-year vs Nonfamily precip within-year	0.5 (0.11, 0.75)	0.01
Pair temp between-year vs Family temp between-year	-0.16 (-0.35, -0.01)	0.036
Pair temp between-year vs Nonfamily temp between-year	-0.06 (-0.46, 0.15)	0.41
Pair precip between-year vs Family precip between-year	0.1 (-0.13, 0.27)	0.394
Pair precip between-year vs Nonfamily precip between-year	-0.12 (-0.35, 0.29)	0.976
Family temp vs Nonfamily temp	0.12 (-0.12, 0.43)	0.3

Family precip vs Nonfamily precip	-0.1 (-0.45, 0.23)	0.632
Family temp within-year vs Nonfamily temp within-year	0.18 (-0.23, 0.44)	0.432
Family precip within-year vs Nonfamily precip within-year	0.01 (-0.26, 0.44)	0.632
Family temp between-year vs Nonfamily temp between-year	0.03 (-0.28, 0.38)	0.722
Family precip between-year vs Nonfamily precip between-year	-0.11 (-0.44, 0.24)	0.596
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.28 (0.19, 0.41)	51.36 (33.04, 68.73)
Phylogeny temp within-year	0.45 (0.25, 0.62)	51.23 (22.71, 78.02)
Phylogeny temp between-year	0.5 (0.22, 0.63)	49.84 (29.02, 72.43)
Phylogeny precip	0.41 (0.2, 0.76)	51.46 (26.24, 77.33)
Phylogeny precip within-year	0.41 (0.24, 0.75)	49.64 (25.02, 70.94)
Phylogeny precip between-year	0.44 (0.23, 0.78)	51.31 (23.16, 78.32)
Residual temp	0.27 (0.18, 0.39)	48.64 (31.27, 66.96)
Residual temp within-year	0.49 (0.24, 0.63)	48.77 (21.98, 77.29)
Residual temp between-year	0.4 (0.25, 0.66)	50.16 (27.57, 70.98)
Residual precip	0.49 (0.18, 0.73)	48.54 (22.67, 73.76)
Residual precip within-year	0.42 (0.21, 0.74)	50.36 (29.06, 74.98)
Residual precip between-year	0.53 (0.21, 0.77)	48.69 (21.68, 76.84)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	0.07 (-0.31, 0.36)	0.678
Phylogeny temp between-year : Phylogeny temp	-0.43 (-0.62, -0.11)	0.014
Phylogeny precip : Phylogeny temp	0.31 (-0.04, 0.54)	0.098
Phylogeny precip within-year : Phylogeny temp	-0.44 (-0.63, -0.15)	0.01
Phylogeny precip between-year : Phylogeny temp	0.25 (-0.15, 0.46)	0.28
Phylogeny temp between-year : Phylogeny temp within-year	-0.58 (-0.74, -0.2)	0.012

Phylogeny precip : Phylogeny temp within-year	0.73 (0.29, 0.8)	0.002
Phylogeny precip within-year : Phylogeny temp within-year	-0.54 (-0.7, -0.04)	0.052
Phylogeny precip between-year : Phylogeny temp within-year	0.84 (0.57, 0.88)	0.001
Phylogeny precip : Phylogeny temp between-year	-0.44 (-0.59, 0.14)	0.196
Phylogeny precip within-year : Phylogeny temp between-year	0.66 (0.36, 0.78)	0.001
Phylogeny precip between-year : Phylogeny temp between-year	-0.63 (-0.78, -0.24)	0.012
Phylogeny precip within-year : Phylogeny precip	-0.58 (-0.77, -0.24)	0.004
Phylogeny precip between-year : Phylogeny precip	0.69 (0.28, 0.79)	0.001
Phylogeny precip between-year : Phylogeny precip within-year	-0.41 (-0.66, 0.07)	0.14
Residual temp within-year : Residual temp	0.12 (-0.33, 0.35)	0.78
Residual temp between-year : Residual temp	-0.37 (-0.59, -0.08)	0.02
Residual precip : Residual temp	0.32 (-0.05, 0.53)	0.098
Residual precip within-year : Residual temp	-0.36 (-0.63, -0.14)	0.024
Residual precip between-year : Residual temp	0.22 (-0.17, 0.47)	0.362
Residual temp between-year : Residual temp within-year	-0.58 (-0.75, -0.17)	0.008
Residual precip : Residual temp within-year	0.69 (0.24, 0.79)	0.004
Residual precip within-year : Residual temp within-year	-0.54 (-0.71, -0.07)	0.042
Residual precip between-year : Residual temp within-year	0.8 (0.56, 0.89)	0.001
Residual precip : Residual temp between-year	-0.25 (-0.57, 0.17)	0.274
Residual precip within-year : Residual temp between-year	0.67 (0.39, 0.77)	0.001

Residual precip between-year : Residual temp between-year	-0.6 (-0.72, -0.16)	0.01
Residual precip within-year : Residual precip	-0.59 (-0.74, -0.19)	0.004
Residual precip between-year : Residual precip	0.69 (0.27, 0.79)	0.002
Residual precip between-year : Residual precip within-year	-0.43 (-0.65, 0.09)	0.184

544

table S9: Environmental differences among pair-breeding, nonfamily cooperative breeding, and family cooperative breeding species with classifications assigned using a 30% nests threshold.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Family temp	0.1 (-0.23, 0.3)	0.804
Pair temp vs Nonfamily temp	0 (-0.37, 0.32)	0.974
Pair precip vs Family precip	0.4 (0.06, 0.75)	0.028
Pair precip vs Nonfamily precip	0.36 (-0.06, 0.79)	0.126
Pair temp within-year vs Family temp within-year	-0.17 (-0.36, 0.23)	0.61
Pair temp within-year vs Nonfamily temp within-year	0.32 (-0.14, 0.68)	0.204
Pair precip within-year vs Family precip within-year	0.43 (0.08, 0.78)	0.016
Pair precip within-year vs Nonfamily precip within-year	0.47 (0.05, 0.93)	0.026
Pair temp between-year vs Family temp between-year	-0.29 (-0.66, -0.03)	0.032
Pair temp between-year vs Nonfamily temp between-year	-0.15 (-0.56, 0.25)	0.628
Pair precip between-year vs Family precip between-year	0.07 (-0.23, 0.49)	0.41
Pair precip between-year vs Nonfamily precip between-year	-0.02 (-0.38, 0.47)	0.87
Family temp vs Nonfamily temp	-0.06 (-0.45, 0.39)	0.908

Family precip vs Nonfamily precip	-0.09 (-0.57, 0.51)	0.856
Family temp within-year vs Nonfamily temp within-year	0.42 (-0.15, 0.85)	0.158
Family precip within-year vs Nonfamily precip within-year	-0.01 (-0.6, 0.5)	0.898
Family temp between-year vs Nonfamily temp between-year	0.29 (-0.3, 0.72)	0.35
Family precip between-year vs Nonfamily precip between-year	-0.04 (-0.62, 0.44)	0.692
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.32 (0.19, 0.41)	50.1 (33.5, 68.27)
Phylogeny temp within-year	0.49 (0.25, 0.67)	50.19 (23.32, 77.76)
Phylogeny temp between-year	0.4 (0.22, 0.66)	50.75 (28.38, 73.74)
Phylogeny precip	0.47 (0.22, 0.8)	50.21 (26.44, 74.64)
Phylogeny precip within-year	0.55 (0.27, 0.78)	50.24 (28.97, 74.58)
Phylogeny precip between-year	0.55 (0.24, 0.82)	50.43 (22.49, 76.72)
Residual temp	0.32 (0.2, 0.41)	49.9 (31.73, 66.5)
Residual temp within-year	0.39 (0.22, 0.64)	49.81 (22.24, 76.68)
Residual temp between-year	0.47 (0.23, 0.65)	49.25 (26.26, 71.62)
Residual precip	0.43 (0.22, 0.8)	49.79 (25.36, 73.56)
Residual precip within-year	0.41 (0.25, 0.78)	49.76 (25.42, 71.03)
Residual precip between-year	0.43 (0.24, 0.81)	49.57 (23.28, 77.51)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	0.15 (-0.29, 0.38)	0.66
Phylogeny temp between-year : Phylogeny temp	-0.39 (-0.59, -0.08)	0.016
Phylogeny precip : Phylogeny temp	0.4 (-0.03, 0.54)	0.086
Phylogeny precip within-year : Phylogeny temp	-0.42 (-0.62, -0.13)	0.012
Phylogeny precip between-year : Phylogeny temp	0.25 (-0.15, 0.52)	0.264
Phylogeny temp between-year : Phylogeny temp within-year	-0.6 (-0.73, -0.16)	0.016

Phylogeny precip : Phylogeny temp within-year	0.66 (0.26, 0.79)	0.008
Phylogeny precip within-year : Phylogeny temp within-year	-0.55 (-0.7, -0.05)	0.044
Phylogeny precip between-year : Phylogeny temp within-year	0.83 (0.58, 0.89)	0.001
Phylogeny precip : Phylogeny temp between-year	-0.35 (-0.57, 0.19)	0.254
Phylogeny precip within-year : Phylogeny temp between-year	0.64 (0.36, 0.8)	0.001
Phylogeny precip between-year : Phylogeny temp between-year	-0.64 (-0.73, -0.2)	0.006
Phylogeny precip within-year : Phylogeny precip	-0.63 (-0.75, -0.24)	0.006
Phylogeny precip between-year : Phylogeny precip	0.67 (0.29, 0.79)	0.006
Phylogeny precip between-year : Phylogeny precip within-year	-0.47 (-0.64, 0.07)	0.156
Residual temp within-year : Residual temp	0.04 (-0.31, 0.36)	0.736
Residual temp between-year : Residual temp	-0.37 (-0.6, -0.07)	0.04
Residual precip : Residual temp	0.36 (-0.03, 0.54)	0.098
Residual precip within-year : Residual temp	-0.4 (-0.6, -0.12)	0.022
Residual precip between-year : Residual temp	0.29 (-0.2, 0.45)	0.354
Residual temp between-year : Residual temp within-year	-0.57 (-0.73, -0.16)	0.016
Residual precip : Residual temp within-year	0.67 (0.26, 0.78)	0.002
Residual precip within-year : Residual temp within-year	-0.48 (-0.69, -0.05)	0.042
Residual precip between-year : Residual temp within-year	0.82 (0.56, 0.88)	0.001
Residual precip : Residual temp between-year	-0.36 (-0.55, 0.19)	0.29
Residual precip within-year : Residual temp between-year	0.63 (0.32, 0.77)	0.004

Residual precip between-year : Residual temp between-year	-0.53 (-0.74, -0.2)	0.012
Residual precip within-year : Residual precip	-0.57 (-0.75, -0.22)	0.004
Residual precip between-year : Residual precip	0.65 (0.28, 0.77)	0.001
Residual precip between-year : Residual precip within-year	-0.47 (-0.64, 0.07)	0.142

545

table S10: Variation in the frequency of cooperative breeding (% nests with group breeding, logit transformed) in groups with a breeding pair versus multiple breeders (2+) and with only family helpers versus a mix of family and nonfamily helpers in relation to climate.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair Family temp	0.08 (-0.17, 0.34)	-
Pair Family precip	-0.06 (-0.23, 0.31)	-
Pair Family temp within-year	-0.05 (-0.3, 0.22)	-
Pair Family precip within-year	-0.01 (-0.27, 0.24)	-
Pair Family temp between-year	0.02 (-0.23, 0.31)	-
Pair Family precip between-year	0.01 (-0.21, 0.27)	-
Pair Mixed temp	-0.07 (-0.46, 0.3)	-
Pair Mixed precip	-0.12 (-0.43, 0.33)	-
Pair Mixed temp within-year	0.31 (-0.05, 0.68)	-
Pair Mixed precip within-year	0.01 (-0.39, 0.36)	-
Pair Mixed temp between-year	0.2 (-0.24, 0.53)	-
Pair Mixed precip between-year	0.01 (-0.44, 0.28)	-
Multiple Family temp	-0.14 (-0.56, 0.3)	-
Multiple Family precip	-0.18 (-0.47, 0.42)	-
Multiple Family temp within-year	0.09 (-0.21, 0.65)	-
Multiple Family precip within-year	0.12 (-0.26, 0.65)	-
Multiple Family temp between-year	0.25 (-0.29, 0.62)	-

Multiple Family precip between-year	0.07 (-0.39, 0.46)	-
Pair Family temp: coop frequency	0.15 (0.04, 0.35)	0.022
Pair Family precip: coop frequency	0 (-0.13, 0.2)	0.584
Pair Family temp within-year: coop frequency	-0.09 (-0.27, 0.04)	0.186
Pair Family precip within-year: coop frequency	0.02 (-0.16, 0.17)	0.858
Pair Family temp between-year: coop frequency	-0.12 (-0.3, 0.03)	0.146
Pair Family precip between-year: coop frequency	-0.02 (-0.16, 0.16)	0.888
Pair Mixed temp: coop frequency	0 (-0.23, 0.29)	0.844
Pair Mixed precip: coop frequency	-0.13 (-0.42, 0.09)	0.196
Pair Mixed temp within-year: coop frequency	0.13 (-0.14, 0.36)	0.366
Pair Mixed precip within-year: coop frequency	-0.14 (-0.4, 0.11)	0.264
Pair Mixed temp between-year: coop frequency	-0.02 (-0.31, 0.2)	0.626
Pair Mixed precip between-year: coop frequency	-0.18 (-0.46, 0.02)	0.062
Multiple Family temp: coop frequency	0.19 (0.02, 0.56)	0.032
Multiple Family precip: coop frequency	0.03 (-0.23, 0.33)	0.662
Multiple Family temp within-year: coop frequency	-0.41 (-0.65, -0.09)	0.012
Multiple Family precip within-year: coop frequency	0.13 (-0.15, 0.4)	0.382
Multiple Family temp between-year: coop frequency	-0.25 (-0.62, -0.03)	0.044
Multiple Family precip between-year: coop frequency	-0.06 (-0.25, 0.3)	1
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.52 (0.28, 0.81)	52.39 (31.33, 73.29)
Phylogeny temp within-year	0.53 (0.26, 0.9)	51.7 (26.26, 75.85)
Phylogeny temp between-year	0.62 (0.27, 0.93)	52.04 (25.98, 77.38)

Phylogeny precip	0.7 (0.28, 0.95)	52.2 (25.57, 77.87)
Phylogeny precip within-year	0.43 (0.26, 0.95)	50.57 (26.1, 73.65)
Phylogeny precip between-year	0.48 (0.27, 0.85)	52.09 (26.47, 77.44)
Residual temp	0.46 (0.24, 0.76)	47.61 (26.71, 68.67)
Residual temp within-year	0.51 (0.22, 0.84)	48.3 (24.15, 73.74)
Residual temp between-year	0.48 (0.26, 0.91)	47.96 (22.62, 74.02)
Residual precip	0.42 (0.26, 0.94)	47.8 (22.13, 74.43)
Residual precip within-year	0.44 (0.24, 0.91)	49.43 (26.35, 73.9)
Residual precip between-year	0.39 (0.23, 0.84)	47.91 (22.56, 73.53)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	0.07 (-0.36, 0.44)	0.854
Phylogeny temp between-year : Phylogeny temp	-0.43 (-0.71, -0.08)	0.036
Phylogeny precip : Phylogeny temp	0.44 (-0.07, 0.63)	0.112
Phylogeny precip within-year : Phylogeny temp	-0.46 (-0.66, -0.01)	0.068
Phylogeny precip between-year : Phylogeny temp	0.16 (-0.21, 0.54)	0.324
Phylogeny temp between-year : Phylogeny temp within-year	-0.48 (-0.74, -0.08)	0.032
Phylogeny precip : Phylogeny temp within-year	0.71 (0.24, 0.79)	0.004
Phylogeny precip within-year : Phylogeny temp within-year	-0.46 (-0.66, 0.07)	0.104
Phylogeny precip between-year : Phylogeny temp within-year	0.66 (0.35, 0.81)	0.001
Phylogeny precip : Phylogeny temp between-year	-0.56 (-0.74, -0.06)	0.038
Phylogeny precip within-year : Phylogeny temp between-year	0.71 (0.37, 0.83)	0.002
Phylogeny precip between-year : Phylogeny temp between-year	-0.61 (-0.77, -0.16)	0.014
Phylogeny precip within-year : Phylogeny precip	-0.59 (-0.78, -0.14)	0.016

Phylogeny precip between-year : Phylogeny precip	0.71 (0.31, 0.81)	0.001
Phylogeny precip between-year : Phylogeny precip within-year	-0.34 (-0.67, 0.09)	0.16
Residual temp within-year : Residual temp	0.07 (-0.43, 0.4)	0.936
Residual temp between-year : Residual temp	-0.39 (-0.66, 0.04)	0.114
Residual precip : Residual temp	0.29 (-0.12, 0.61)	0.236
Residual precip within-year : Residual temp	-0.31 (-0.63, 0.11)	0.214
Residual precip between-year : Residual temp	0.09 (-0.23, 0.57)	0.416
Residual temp between-year : Residual temp within-year	-0.58 (-0.73, -0.03)	0.056
Residual precip : Residual temp within- year	0.67 (0.17, 0.79)	0.012
Residual precip within-year : Residual temp within-year	-0.46 (-0.67, 0.07)	0.132
Residual precip between-year : Residual temp within-year	0.63 (0.28, 0.81)	0.006
Residual precip : Residual temp between-year	-0.44 (-0.74, 0.02)	0.108
Residual precip within-year : Residual temp between-year	0.67 (0.36, 0.84)	0.001
Residual precip between-year : Residual temp between-year	-0.53 (-0.76, -0.09)	0.036
Residual precip within-year : Residual precip	-0.47 (-0.71, 0.01)	0.088
Residual precip between-year : Residual precip	0.65 (0.29, 0.82)	0.001
Residual precip between-year : Residual precip within-year	-0.34 (-0.63, 0.17)	0.312

546

table S11: Variation in the size of groups (log transformed) with a breeding pair versus multiple breeders (2+) and with only family helpers versus a mix of family and nonfamily helpers in relation to climate.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair Family temp	-0.32 (-1.37, 0.68)	-
Pair Family precip	0.45 (-0.66, 1.53)	-
Pair Family temp within-year	0.2 (-0.86, 1.19)	-
Pair Family precip within-year	0.2 (-0.88, 1.16)	-
Pair Family temp between-year	-0.14 (-1.09, 0.98)	-
Pair Family precip between-year	0.26 (-0.92, 1.08)	-
Pair Mixed temp	-0.76 (-2.14, 0.47)	-
Pair Mixed precip	0.32 (-0.86, 1.76)	-
Pair Mixed temp within-year	0.64 (-0.62, 1.85)	-
Pair Mixed precip within-year	-0.28 (-1.26, 1.33)	-
Pair Mixed temp between-year	0.87 (-0.51, 2.26)	-
Pair Mixed precip between-year	0.4 (-0.78, 1.61)	-
Multiple Family temp	-0.09 (-1.45, 0.99)	-
Multiple Family precip	-0.59 (-1.58, 1.12)	-
Multiple Family temp within-year	0.49 (-0.49, 2.09)	-
Multiple Family precip within-year	-0.3 (-1.22, 1.4)	-
Multiple Family temp between-year	1 (-0.29, 2.41)	-
Multiple Family precip between-year	0.14 (-1.48, 1.07)	-
Pair Family temp: group size	0.37 (-0.48, 1.07)	0.464
Pair Family precip: group size	-0.41 (-1.09, 0.58)	0.5
Pair Family temp within-year: group size	-0.3 (-1.04, 0.55)	0.52
Pair Family precip within-year: group size	-0.04 (-0.95, 0.7)	0.818
Pair Family temp between-year: group size	0.31 (-0.72, 0.86)	0.854
Pair Family precip between-year: group size	-0.19 (-0.73, 0.8)	0.952
Pair Mixed temp: group size	0.45 (-0.34, 1.35)	0.204
Pair Mixed precip: group size	-0.38 (-1.34, 0.41)	0.382

Pair Mixed temp within-year: group size	-0.18 (-0.93, 0.7)	0.72
Pair Mixed precip within-year: group size	0.13 (-0.98, 0.72)	0.85
Pair Mixed temp between-year: group size	-0.57 (-1.45, 0.35)	0.294
Pair Mixed precip between-year: group size	-0.39 (-1.18, 0.37)	0.322
Multiple Family temp: group size	0.26 (-0.47, 1.01)	0.472
Multiple Family precip: group size	0.16 (-0.66, 0.94)	0.756
Multiple Family temp within-year: group size	-0.58 (-1.23, 0.31)	0.196
Multiple Family precip within-year: group size	0.27 (-0.63, 0.9)	0.706
Multiple Family temp between-year: group size	-0.61 (-1.35, 0.2)	0.112
Multiple Family precip between-year: group size	0.08 (-0.61, 0.89)	0.788
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.59 (0.3, 0.93)	53.49 (30.18, 74.58)
Phylogeny temp within-year	0.58 (0.26, 0.95)	51.42 (27.18, 79.37)
Phylogeny temp between-year	0.62 (0.28, 0.98)	52.31 (25, 76.93)
Phylogeny precip	0.62 (0.29, 1.05)	52.08 (24.55, 79.28)
Phylogeny precip within-year	0.67 (0.2, 0.97)	51.17 (26, 74.88)
Phylogeny precip between-year	0.44 (0.24, 0.89)	51.7 (25.59, 78.83)
Residual temp	0.43 (0.26, 0.82)	46.51 (25.42, 69.82)
Residual temp within-year	0.44 (0.24, 0.9)	48.58 (20.63, 72.82)
Residual temp between-year	0.53 (0.27, 0.9)	47.69 (23.07, 75)
Residual precip	0.51 (0.24, 0.95)	47.92 (20.72, 75.45)
Residual precip within-year	0.48 (0.22, 0.96)	48.83 (25.12, 74)
Residual precip between-year	0.4 (0.19, 0.82)	48.3 (21.17, 74.41)
Correlations	Posterior Mode (CI)	pMCMC
Phylogeny temp within-year : Phylogeny temp	0.03 (-0.39, 0.45)	0.824

Phylogeny temp between-year : Phylogeny temp	-0.34 (-0.68, -0.07)	0.02
Phylogeny precip : Phylogeny temp	0.39 (-0.04, 0.66)	0.102
Phylogeny precip within-year : Phylogeny temp	-0.38 (-0.67, 0.02)	0.08
Phylogeny precip between-year : Phylogeny temp	0.31 (-0.19, 0.58)	0.332
Phylogeny temp between-year : Phylogeny temp within-year	-0.5 (-0.75, -0.07)	0.044
Phylogeny precip : Phylogeny temp within-year	0.65 (0.19, 0.8)	0.022
Phylogeny precip within-year : Phylogeny temp within-year	-0.47 (-0.68, 0.07)	0.112
Phylogeny precip between-year : Phylogeny temp within-year	0.67 (0.32, 0.83)	0.004
Phylogeny precip : Phylogeny temp between-year	-0.59 (-0.75, -0.06)	0.04
Phylogeny precip within-year : Phylogeny temp between-year	0.73 (0.35, 0.85)	0.001
Phylogeny precip between-year : Phylogeny temp between-year	-0.57 (-0.77, -0.1)	0.02
Phylogeny precip within-year : Phylogeny precip	-0.58 (-0.77, -0.08)	0.048
Phylogeny precip between-year : Phylogeny precip	0.68 (0.28, 0.84)	0.002
Phylogeny precip between-year : Phylogeny precip within-year	-0.44 (-0.66, 0.15)	0.204
Residual temp within-year : Residual temp	0.1 (-0.46, 0.37)	0.99
Residual temp between-year : Residual temp	-0.43 (-0.65, 0.09)	0.158
Residual precip : Residual temp	0.31 (-0.13, 0.63)	0.236
Residual precip within-year : Residual temp	-0.29 (-0.56, 0.19)	0.24
Residual precip between-year : Residual temp	0.21 (-0.24, 0.57)	0.472
Residual temp between-year : Residual temp within-year	-0.5 (-0.72, -0.02)	0.048

Residual precip : Residual temp within-year	0.59 (0.16, 0.79)	0.01
Residual precip within-year : Residual temp within-year	-0.35 (-0.67, 0.06)	0.134
Residual precip between-year : Residual temp within-year	0.69 (0.3, 0.83)	0.002
Residual precip : Residual temp between-year	-0.49 (-0.74, 0.02)	0.11
Residual precip within-year : Residual temp between-year	0.66 (0.31, 0.82)	0.002
Residual precip between-year : Residual temp between-year	-0.59 (-0.72, -0.05)	0.046
Residual precip within-year : Residual precip	-0.52 (-0.75, -0.05)	0.064
Residual precip between-year : Residual precip	0.65 (0.28, 0.83)	0.001
Residual precip between-year : Residual precip within-year	-0.33 (-0.64, 0.21)	0.332

547

table S12: Differences in the environments of pair breeding species and cooperative breeding species with cobreeders (pair versus multiple breeders) and nonfamily, family and a mix of both nonfamily and family group members.

Fixed Effects	Posterior Mode (CI)	pMCMC
Pair temp vs Pair_family temp	0.16 (-0.17, 0.46)	0.454
Pair temp vs Pair_mixed temp	0.18 (-0.26, 0.49)	0.522
Pair temp vs Multiple_family temp	-0.02 (-0.35, 0.48)	0.81
Pair temp vs Nonfamily temp	0.24 (-0.1, 0.52)	0.228
Pair precip vs Pair_family precip	0.19 (-0.24, 0.63)	0.356
Pair precip vs Pair_mixed precip	0.4 (-0.13, 0.88)	0.172
Pair precip vs Multiple_family precip	0.49 (-0.14, 0.87)	0.162
Pair precip vs Nonfamily precip	0.41 (0.05, 0.8)	0.024
Pair temp within-year vs Pair_family temp within-year	-0.02 (-0.42, 0.36)	0.682

Pair temp within-year vs Pair_mixed temp within-year	-0.07 (-0.51, 0.38)	0.786
Pair temp within-year vs Multiple_family temp within-year	0.12 (-0.46, 0.55)	0.832
Pair temp within-year vs Nonfamily temp within-year	0.15 (-0.21, 0.49)	0.436
Pair precip within-year vs Pair_family precip within-year	0.71 (0.19, 1.06)	0.004
Pair precip within-year vs Pair_mixed precip within-year	0.22 (-0.26, 0.78)	0.31
Pair precip within-year vs Multiple_family precip within-year	0.14 (-0.35, 0.65)	0.548
Pair precip within-year vs Nonfamily precip within-year	0.67 (0.31, 1.11)	0.001
Pair temp between-year vs Pair_family temp between-year	-0.46 (-0.85, -0.04)	0.02
Pair temp between-year vs Pair_mixed temp between-year	-0.16 (-0.62, 0.27)	0.46
Pair temp between-year vs Multiple_family temp between-year	-0.29 (-0.79, 0.19)	0.296
Pair temp between-year vs Nonfamily temp between-year	-0.21 (-0.52, 0.2)	0.332
Pair precip between-year vs Pair_family precip between-year	0.17 (-0.26, 0.58)	0.502
Pair precip between-year vs Pair_mixed precip between-year	-0.07 (-0.54, 0.45)	0.87
Pair precip between-year vs Multiple_family precip between-year	0.05 (-0.55, 0.5)	0.96
Pair precip between-year vs Nonfamily precip between-year	0.27 (-0.08, 0.68)	0.126
Pair_family temp vs Pair_mixed temp	0.02 (-0.46, 0.55)	0.968
Pair_family temp vs Multiple_family temp	0.04 (-0.6, 0.45)	0.79
Pair_family temp vs Nonfamily temp	0.02 (-0.38, 0.49)	0.76
Pair_family precip vs Pair_mixed precip	0.01 (-0.46, 0.82)	0.612
Pair_family precip vs Multiple_family precip	0.33 (-0.53, 0.77)	0.582
Pair_family precip vs Nonfamily precip	0.3 (-0.33, 0.76)	0.434

Pair_family temp within-year vs Pair_mixed temp within-year	-0.05 (-0.6, 0.57)	0.998
Pair_family temp within-year vs Multiple_family temp within-year	0.03 (-0.5, 0.73)	0.664
Pair_family temp within-year vs Nonfamily temp within-year	0.15 (-0.35, 0.68)	0.412
Pair_family precip within-year vs Pair_mixed precip within-year	-0.24 (-1.06, 0.27)	0.258
Pair_family precip within-year vs Multiple_family precip within-year	-0.46 (-1.14, 0.11)	0.162
Pair_family precip within-year vs Nonfamily precip within-year	0.05 (-0.52, 0.62)	0.87
Pair_family temp between-year vs Pair_mixed temp between-year	0.17 (-0.23, 0.95)	0.32
Pair_family temp between-year vs Multiple_family temp between-year	0.22 (-0.36, 0.85)	0.532
Pair_family temp between-year vs Nonfamily temp between-year	0.36 (-0.26, 0.76)	0.308
Pair_family precip between-year vs Pair_mixed precip between-year	-0.07 (-0.79, 0.49)	0.582
Pair_family precip between-year vs Multiple_family precip between-year	-0.34 (-0.87, 0.42)	0.638
Pair_family precip between-year vs Nonfamily precip between-year	0.15 (-0.38, 0.67)	0.532
Pair_mixed temp vs Multiple_family temp	0.14 (-0.66, 0.46)	0.828
Pair_mixed temp vs Nonfamily temp	0.1 (-0.39, 0.57)	0.778
Pair_mixed precip vs Multiple_family precip	0.04 (-0.66, 0.79)	0.918
Pair_mixed precip vs Nonfamily precip	-0.08 (-0.53, 0.73)	0.812
Pair_mixed temp within-year vs Multiple_family temp within-year	0.17 (-0.52, 0.81)	0.738
Pair_mixed temp within-year vs Nonfamily temp within-year	0.23 (-0.35, 0.75)	0.454
Pair_mixed precip within-year vs Multiple_family precip within-year	-0.04 (-0.81, 0.62)	0.778
Pair_mixed precip within-year vs Nonfamily precip within-year	0.51 (-0.31, 1.03)	0.23

Pair_mixed temp between-year vs Multiple_family temp between-year	-0.19 (-0.77, 0.55)	0.772
Pair_mixed temp between-year vs Nonfamily temp between-year	-0.07 (-0.58, 0.59)	0.948
Pair_mixed precip between-year vs Multiple_family precip between-year	-0.09 (-0.7, 0.73)	0.95
Pair_mixed precip between-year vs Nonfamily precip between-year	0.3 (-0.27, 0.96)	0.262
Multiple_family temp vs Nonfamily temp	0.16 (-0.35, 0.65)	0.584
Multiple_family precip vs Nonfamily precip	0.05 (-0.56, 0.68)	0.876
Multiple_family temp within-year vs Nonfamily temp within-year	-0.12 (-0.53, 0.64)	0.786
Multiple_family precip within-year vs Nonfamily precip within-year	0.38 (-0.08, 1.22)	0.102
Multiple_family temp between-year vs Nonfamily temp between-year	0.14 (-0.51, 0.66)	0.82
Multiple_family precip between-year vs Nonfamily precip between-year	0.35 (-0.37, 0.89)	0.34
Random Effects	Posterior Mode (CI)	I2 % (CI)
Phylogeny temp	0.27 (0.2, 0.42)	50 (32.75, 66.63)
Phylogeny temp within-year	0.5 (0.24, 0.65)	50.1 (22.92, 74.78)
Phylogeny temp between-year	0.42 (0.23, 0.67)	49.73 (28.29, 72.86)
Phylogeny precip	0.61 (0.22, 0.77)	49.97 (23.96, 72.73)
Phylogeny precip within-year	0.63 (0.24, 0.76)	50.3 (26.75, 73.98)
Phylogeny precip between-year	0.57 (0.23, 0.76)	50.06 (24, 75.49)
Residual temp	0.31 (0.2, 0.42)	50 (33.37, 67.25)
Residual temp within-year	0.37 (0.25, 0.65)	49.9 (25.22, 77.08)
Residual temp between-year	0.45 (0.23, 0.67)	50.27 (27.14, 71.71)
Residual precip	0.46 (0.24, 0.79)	50.03 (27.27, 76.04)
Residual precip within-year	0.53 (0.27, 0.79)	49.7 (26.02, 73.25)
Residual precip between-year	0.44 (0.22, 0.77)	49.94 (24.51, 76)
Correlations	Posterior Mode (CI)	pMCMC

Phylogeny temp within-year : Phylogeny temp	0.17 (-0.34, 0.36)	0.786
Phylogeny temp between-year : Phylogeny temp	-0.45 (-0.58, -0.07)	0.016
Phylogeny precip : Phylogeny temp	0.29 (-0.03, 0.6)	0.12
Phylogeny precip within-year : Phylogeny temp	-0.45 (-0.62, -0.14)	0.008
Phylogeny precip between-year : Phylogeny temp	0.18 (-0.19, 0.47)	0.36
Phylogeny temp between-year : Phylogeny temp within-year	-0.61 (-0.75, -0.17)	0.016
Phylogeny precip : Phylogeny temp within-year	0.67 (0.25, 0.79)	0.002
Phylogeny precip within-year : Phylogeny temp within-year	-0.55 (-0.68, -0.04)	0.046
Phylogeny precip between-year : Phylogeny temp within-year	0.83 (0.57, 0.88)	0.001
Phylogeny precip : Phylogeny temp between-year	-0.37 (-0.61, 0.14)	0.264
Phylogeny precip within-year : Phylogeny temp between-year	0.66 (0.35, 0.78)	0.001
Phylogeny precip between-year : Phylogeny temp between-year	-0.64 (-0.76, -0.2)	0.006
Phylogeny precip within-year : Phylogeny precip	-0.6 (-0.75, -0.21)	0.002
Phylogeny precip between-year : Phylogeny precip	0.7 (0.3, 0.8)	0.001
Phylogeny precip between-year : Phylogeny precip within-year	-0.4 (-0.62, 0.11)	0.198
Residual temp within-year : Residual temp	0.1 (-0.31, 0.37)	0.762
Residual temp between-year : Residual temp	-0.38 (-0.62, -0.09)	0.032
Residual precip : Residual temp	0.31 (-0.06, 0.55)	0.124
Residual precip within-year : Residual temp	-0.41 (-0.61, -0.09)	0.012
Residual precip between-year : Residual temp	0.17 (-0.19, 0.46)	0.318

Residual temp between-year : Residual temp within-year	-0.54 (-0.73, -0.19)	0.008
Residual precip : Residual temp within-year	0.62 (0.28, 0.79)	0.006
Residual precip within-year : Residual temp within-year	-0.44 (-0.7, -0.08)	0.032
Residual precip between-year : Residual temp within-year	0.82 (0.57, 0.88)	0.001
Residual precip : Residual temp between-year	-0.37 (-0.56, 0.19)	0.246
Residual precip within-year : Residual temp between-year	0.67 (0.33, 0.79)	0.001
Residual precip between-year : Residual temp between-year	-0.59 (-0.74, -0.2)	0.004
Residual precip within-year : Residual precip	-0.62 (-0.75, -0.25)	0.001
Residual precip between-year : Residual precip	0.67 (0.3, 0.81)	0.01
Residual precip between-year : Residual precip within-year	-0.45 (-0.63, 0.07)	0.142

548 **References**

- 549 1. M. C. Urban, [Climate change extinctions](#). *Science* **386**, 1123–1128 (2024).
- 550 2. B. S. Walsh, S. R. Parratt, A. A. Hoffmann, D. Atkinson, R. R. Snook, A. Bretman, T. A.
551 R. Price, [The Impact of Climate Change on Fertility](#). *Trends in Ecology & Evolution* **34**, 249–259
552 (2019).
- 553 3. E. A. Riddell, K. J. Iknayan, B. O. Wolf, B. Sinervo, S. R. Beissinger, [Cooling](#)
554 [requirements fueled the collapse of a desert bird community from climate change](#). *Proceedings of*
555 *the National Academy of Sciences* **116**, 21609–21615 (2019).
- 556 4. V. Radchuk, T. Reed, C. Teplitsky, M. van de Pol, A. Charmantier, C. Hassall, P.
557 Adamík, F. Adriaensen, M. P. Ahola, P. Arcese, J. Miguel Avilés, J. Balbontin, K. S. Berg, A.
558 Borrás, S. Burthe, J. Clobert, N. Dehnhard, F. de Lope, A. A. Dhondt, N. J. Dingemanse, H. Doi,
559 T. Eeva, J. Fickel, I. Filella, F. Fossøy, A. E. Goodenough, S. J. G. Hall, B. Hansson, M. Harris,
560 D. Hasselquist, T. Hickler, J. Joshi, H. Kharouba, J. G. Martínez, J.-B. Mihoub, J. A. Mills, M.
561 Molina-Morales, A. Moksnes, A. Ozgul, D. Parejo, P. Pilard, M. Poisbleau, F. Rousset, M.-O.

- 562 Rödel, D. Scott, J. C. Senar, C. Stefanescu, B. G. Stokke, T. Kusano, M. Tarka, C. E. Tarwater,
563 K. Thonicke, J. Thorley, A. Wilting, P. Tryjanowski, J. Merilä, B. C. Sheldon, A. Pape Møller, E.
564 Matthysen, F. Janzen, F. S. Dobson, M. E. Visser, S. R. Beissinger, A. Courtiol, S. Kramer-
565 Schadt, [Adaptive responses of animals to climate change are most likely insufficient](#). *Nature*
566 *Communications* **10**, 3109 (2019).
- 567 5. D. T. Blumstein, L. D. Hayes, N. Pinter-Wollman, [Social consequences of rapid](#)
568 [environmental change](#). *Trends in Ecology & Evolution* **38**, 337–345 (2023).
- 569 6. J. Komdeur, L. Ma, [Keeping up with environmental change: The importance of sociality](#).
570 *Ethology* **127**, 790–807 (2021).
- 571 7. F. Groenewoud, T. Clutton-Brock, [Meerkat helpers buffer the detrimental effects of](#)
572 [adverse environmental conditions on fecundity, growth and survival](#). *Journal of Animal Ecology*
573 **90**, 641–652 (2021).
- 574 8. J. S. Martin, E. J. Ringen, P. Duda, A. V. Jaeggi, [Harsh environments promote](#)
575 [alloparental care across human societies](#). *Proceedings of the Royal Society B: Biological Sciences*
576 **287**, 20200758 (2020).
- 577 9. S. Chen, Z. Li, X. Lu, [Cooperative breeding in birds increases the within-year fecundity](#)
578 [mean without increasing the variance: A potential mechanism to buffer environmental](#)
579 [uncertainty](#). *Behavioral Ecology* **36**, araf031 (2025).
- 580 10. G. Bernasconi, J. E. Strassmann, [Cooperation among unrelated individuals: The ant](#)
581 [foundress case](#). *Trends in Ecology & Evolution* **14**, 477–482 (1999).
- 582 11. W. D. Koenig, J. L. Dickinson, [Cooperative Breeding in Vertebrates: Studies of Ecology,](#)
583 [Evolution, and Behavior](#) (Cambridge University Press, Cambridge, 2016).
- 584 12. T. Clutton-Brock, [Breeding Together: Kin Selection and Mutualism in Cooperative](#)
585 [Vertebrates](#). *Science* **296**, 69–72 (2002).
- 586 13. D. R. Rubenstein, [Comparative Social Evolution](#) (Cambridge University Press,
587 Cambridge, 2017).
- 588 14. D. Lukas, T. Clutton-Brock, [Social complexity and kinship in animal societies](#). *Ecology*
589 *Letters* **21**, 1129–1134 (2018).

- 590 15. P. A. Downing, A. S. Griffin, C. K. Cornwallis, [Group formation and the evolutionary](#)
591 [pathway to complex sociality in birds](#). *Nature Ecology & Evolution*, 1–8 (2020).
- 592 16. M. dos Santos, P. A. Downing, A. S. Griffin, C. K. Cornwallis, S. A. West, [Altruism and](#)
593 [natural selection in a variable environment](#). *Proceedings of the National Academy of Sciences*
594 **121**, e2402974121 (2024).
- 595 17. S. T. C. Chak, J. E. Duffy, K. M. Hultgren, D. R. Rubenstein, [Evolutionary transitions](#)
596 [towards eusociality in snapping shrimps](#). *Nature Ecology & Evolution* **1**, 1–7 (2017).
- 597 18. B. S. Bowen, R. R. Koford, S. L. Vehrencamp, [Dispersal in the Communally Breeding](#)
598 [Groove-Billed Ani \(*Crotophaga sulcirostris*\)](#). *The Condor* **91**, 52–64 (1989).
- 599 19. A. Cockburn, [EVOLUTION OF HELPING BEHAVIOR IN COOPERATIVELY](#)
600 [BREEDING BIRDS](#). *Annual Review of Ecology and Systematics* **29**, 141–177 (1998).
- 601 20. C. Riehl, [Living with strangers: Direct benefits favour non-kin cooperation in a](#)
602 [communally nesting bird](#). *Proceedings of the Royal Society B: Biological Sciences* **278**, 1728–
603 1735 (2011).
- 604 21. S. L. Vehrencamp, [A model for the evolution of despotic versus egalitarian societies](#).
605 *Animal Behaviour* **31**, 667–682 (1983).
- 606 22. S. A. Kingma, [Direct benefits explain interspecific variation in helping behaviour among](#)
607 [cooperatively breeding birds](#). *Nature Communications* **8**, 1094 (2017).
- 608 23. I. García-Ruiz, A. Quiñones, M. Taborsky, [The evolution of cooperative breeding by](#)
609 [direct and indirect fitness effects](#). *Science Advances* **8**, eabl7853 (2022).
- 610 24. S. S. Shah, D. R. Rubenstein, [Group augmentation underlies the evolution of complex](#)
611 [sociality in the face of environmental instability](#). *Proceedings of the National Academy of*
612 *Sciences* **120**, e2212211120 (2023).
- 613 25. A. D. Earl, G. G. Carter, A. G. Berlinger, E. Korir, S. S. Shah, W. N. Watetu, D. R.
614 Rubenstein, [A cryptic role for reciprocal helping in a cooperatively breeding bird](#). *Nature* **642**,
615 381–388 (2025).
- 616 26. W. D. Koenig, F. A. Pitelka, W. J. Carmen, R. L. Mumme, M. T. Stanback, [The](#)
617 [Evolution of Delayed Dispersal in Cooperative Breeders](#). *The Quarterly Review of Biology* **67**,
618 111–150 (1992).

- 619 27. B. J. Hatchwell, [The evolution of cooperative breeding in birds: Kinship, dispersal and](#)
620 [life history](#). *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 3217–
621 3227 (2009).
- 622 28. P. A. Downing, C. K. Cornwallis, A. S. Griffin, [Sex, long life and the evolutionary](#)
623 [transition to cooperative breeding in birds](#). *Proceedings of the Royal Society B: Biological*
624 *Sciences* **282**, 20151663 (2015).
- 625 29. P. Dierkes, D. Heg, M. Taborsky, E. Skubic, R. Achmann, [Genetic relatedness in groups](#)
626 [is sex-specific and declines with age of helpers in a cooperatively breeding cichlid](#). *Ecology*
627 *Letters* **8**, 968–975 (2005).
- 628 30. S. T. Emlen, [The Evolution of Helping. I. An Ecological Constraints Model](#). *The*
629 *American Naturalist* **119**, 29–39 (1982).
- 630 31. D. R. Rubenstein, I. J. Lovette, [Temporal Environmental Variability Drives the Evolution](#)
631 [of Cooperative Breeding in Birds](#). *Current Biology* **17**, 1414–1419 (2007).
- 632 32. S. G. Pruett-Jones, M. J. Lewis, [Sex ratio and habitat limitation promote delayed dispersal](#)
633 [in superb fairy-wrens](#). *Nature* **348**, 541–542 (1990).
- 634 33. A. R. Bourne, S. J. Cunningham, C. N. Spottiswoode, A. R. Ridley, [High temperatures](#)
635 [drive offspring mortality in a cooperatively breeding bird](#). *Proceedings of the Royal Society B:*
636 *Biological Sciences* **287**, 20201140 (2020).
- 637 34. S.-F. Shen, S. L. Vehrencamp, R. A. Johnstone, H.-C. Chen, S.-F. Chan, W.-Y. Liao, K.-
638 Y. Lin, H.-W. Yuan, [Unfavourable environment limits social conflict in Yuhina brunneiceps](#).
639 *Nature Communications* **3**, 885 (2012).
- 640 35. S.-F. Shen, S. T. Emlen, W. D. Koenig, D. R. Rubenstein, [The ecology of cooperative](#)
641 [breeding behaviour](#). *Ecology Letters* **20**, 708–720 (2017).
- 642 36. W. D. Hamilton, [The genetical evolution of social behaviour. I & II](#). *Journal of*
643 *Theoretical Biology* **7**, 1–16 (1964).
- 644 37. J. J. Boomsma, [Lifetime monogamy and the evolution of eusociality](#). *Philosophical*
645 *Transactions of the Royal Society B: Biological Sciences* **364**, 3191–3207 (2009).
- 646 38. G. A. Cooper, S. A. West, [Division of labour and the evolution of extreme specialization](#).
647 *Nature Ecology & Evolution* **2**, 1161–1167 (2018).

- 648 39. M. Taborsky, [The evolution of division of labour: Preconditions and evolutionary](#)
649 [feedback](#). *Philosophical Transactions of the Royal Society B: Biological Sciences* **380**, 20230262
650 (2025).
- 651 40. C. Riehl, Z. F. Smart, [Climate fluctuations influence variation in group size in a](#)
652 [cooperative bird](#). *Current Biology* **32**, 4264–4269.e3 (2022).
- 653 41. H. Kokko, J. Ekman, [Delayed Dispersal as a Route to Breeding: Territorial Inheritance,](#)
654 [Safe Havens, and Ecological Constraints](#). *The American Naturalist* **160**, 468–484 (2002).
- 655 42. P. L. Hooper, K. Demps, M. Gurven, D. Gerkey, H. S. Kaplan, [Skills, division of labour](#)
656 [and economies of scale among Amazonian hunters and South Indian honey collectors](#).
657 *Philosophical Transactions of the Royal Society B: Biological Sciences* **370**, 20150008 (2015).
- 658 43. C. Netz, T. W. Fawcett, A. D. Higginson, M. Taborsky, B. Taborsky, [Group size and](#)
659 [labour demands determine division of labour as a consequence of demographic stochasticity](#).
660 *Philosophical Transactions of the Royal Society B: Biological Sciences* **380**, 20240206 (2025).
- 661 44. T. Pöldmaa, R. Montgomerie, P. Boag, [Mating System of the Cooperatively Breeding](#)
662 [Noisy Miner *Manorina melanocephala*, as Revealed by DNA Profiling](#). *Behavioral Ecology and*
663 *Sociobiology* **37**, 137–143 (1995).
- 664 45. G. Schmaltz, J. S. Quinn, C. Lentz, [Competition and waste in the communally breeding](#)
665 [smooth-billed ani: Effects of group size on egg-laying behaviour](#). *Animal Behaviour* **76**, 153–162
666 (2008).
- 667 46. M. J. Sheehan, C. A. Botero, T. A. Hendry, B. E. Sedio, J. M. Jandt, S. Weiner, A. L.
668 Toth, E. A. Tibbetts, [Different axes of environmental variation explain the presence vs. Extent of](#)
669 [cooperative nest founding associations in *Polistes* paper wasps](#). *Ecology Letters* **18**, 1057–1067
670 (2015).
- 671 47. D. Bolopo, A. M. Lowney, R. L. Thomson, [Helpers improve fledgling body condition in](#)
672 [bigger broods of cooperatively breeding African pygmy falcon](#). *Behavioral Ecology and*
673 *Sociobiology* **73**, 16 (2019).
- 674 48. A. E. Johnson, J. F. Welklin, I. R. Hoppe, D. Shizuka, [Ecogeography of group size](#)
675 [suggests differences in drivers of sociality among cooperatively breeding fairywrens](#).
676 *Proceedings of the Royal Society B: Biological Sciences* **290**, 20222397 (2023).

- 677 49. J. D. Hadfield, S. Nakagawa, [General quantitative genetic methods for comparative](#)
678 [biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical](#)
679 [characters](#). *Journal of Evolutionary Biology* **23**, 494–508 (2010).
- 680 50. M. Westoby, L. Yates, B. Holland, B. Halliwell, [Phylogenetically conservative trait](#)
681 [correlation: Quantification and interpretation](#). *Journal of Ecology* **111**, 2105–2117 (2023).
- 682 51. C. K. Cornwallis, A. S. Griffin, [A Guided Tour of Phylogenetic Comparative Methods for](#)
683 [Studying Trait Evolution](#). *Annual Review of Ecology, Evolution, and Systematics* **55**, 181–204
684 (2024).
- 685 52. B. Halliwell, B. R. Holland, L. A. Yates, [Multi-response phylogenetic mixed models:](#)
686 [Concepts and application](#). *Biological Reviews* **100**, 1294–1316 (2025).
- 687 53. F. Andreasson, J.-Å. Nilsson, A. Nord, [Avian Reproduction in a Warming World](#).
688 *Frontiers in Ecology and Evolution* **8** (2020).
- 689 54. S. Guindre-Parker, D. R. Rubenstein, [Multiple benefits of alloparental care in a](#)
690 [fluctuating environment](#). *Royal Society Open Science* **5**, 172406 (2018).
- 691 55. S. T. Emlen, [An evolutionary theory of the family](#). *Proceedings of the National Academy*
692 *of Sciences* **92**, 8092–8099 (1995).
- 693 56. V. Federico, D. Allainé, J.-M. Gaillard, A. Cohas, [Evolutionary Pathways to Communal](#)
694 [and Cooperative Breeding in Carnivores](#). *The American Naturalist* **195**, 1037–1055 (2020).
- 695 57. M. A. Du Plessis, W. R. Siegfried, A. J. Armstrong, [Ecological and life-history correlates](#)
696 [of cooperative breeding in South African birds](#). *Oecologia* **102**, 180–188 (1995).
- 697 58. K. E. Arnold, [Cooperative breeding in birds: The role of ecology](#). *Behavioral Ecology* **10**,
698 465–471 (1999).
- 699 59. W. Jetz, D. R. Rubenstein, [Environmental Uncertainty and the Global Biogeography of](#)
700 [Cooperative Breeding in Birds](#). *Current Biology* **21**, 72–78 (2011).
- 701 60. C. K. Cornwallis, C. A. Botero, D. R. Rubenstein, P. A. Downing, S. A. West, A. S.
702 Griffin, [Cooperation facilitates the colonization of harsh environments](#). *Nature Ecology &*
703 *Evolution* **1**, 1–10 (2017).

- 704 61. D. Lukas, T. Clutton-Brock, [Climate and the distribution of cooperative breeding in](#)
705 [mammals](#). *Royal Society Open Science* **4**, 160897 (2017).
- 706 62. R. C. Firman, D. R. Rubenstein, J. M. Moran, K. C. Rowe, B. A. Buzatto, [Extreme and](#)
707 [Variable Climatic Conditions Drive the Evolution of Sociality in Australian Rodents](#). *Current*
708 *Biology* **0** (2020).
- 709 63. C. Riehl, [Evolutionary routes to non-kin cooperative breeding in birds](#). *Proceedings of the*
710 *Royal Society B: Biological Sciences* **280**, 20132245 (2013).
- 711 64. P. B. D'Amelio, A. C. Ferreira, R. Fortuna, M. Paquet, L. R. Silva, F. Theron, C.
712 Doutrelant, R. Covas, [Disentangling climatic and nest predator impact on reproductive output](#)
713 [reveals adverse high-temperature effects regardless of helper number in an arid-region](#)
714 [cooperative bird](#). *Ecology Letters* **25**, 151–162 (2021).
- 715 65. M. J. Nelson-Flower, E. M. Wiley, T. P. Flower, A. R. Ridley, [Individual dispersal delays](#)
716 [in a cooperative breeder: Ecological constraints, the benefits of philopatry and the social queue](#)
717 [for dominance](#). *Journal of Animal Ecology* **87**, 1227–1238 (2018).
- 718 66. C. Leon, S. Banks, N. Beck, R. Heinsohn, [Population genetic structure and dispersal](#)
719 [patterns of a cooperative breeding bird in variable environmental conditions](#). *Animal Behaviour*
720 **183**, 127–137 (2022).
- 721 67. D. Rabaiotti, T. Coulson, R. Woodroffe, [Climate change is predicted to cause population](#)
722 [collapse in a cooperative breeder](#). *Global Change Biology* **29**, 6002–6017 (2023).
- 723 68. M. S. Crossley, D. Lagos-Kutz, T. S. Davis, S. D. Eigenbrode, G. L. Hartman, D. J.
724 Voegtlin, W. E. Snyder, [Precipitation change accentuates or reverses temperature effects on](#)
725 [aphid dispersal](#). *Ecological Applications* **32**, e2593 (2022).
- 726 69. J. A. Harvey, K. Tougeron, R. Gols, R. Heinen, M. Abarca, P. K. Abram, Y. Basset, M.
727 Berg, C. Boggs, J. Brodeur, P. Cardoso, J. G. de Boer, G. R. De Snoo, C. Deacon, J. E. Dell, N.
728 Desneux, M. E. Dillon, G. A. Duffy, L. A. Dyer, J. Ellers, A. Espíndola, J. Fordyce, M. L.
729 Forister, C. Fukushima, M. J. G. Gage, C. García-Robledo, C. Gely, M. Gobbi, C. Hallmann, T.
730 Hance, J. Harte, A. Hochkirch, C. Hof, A. A. Hoffmann, J. G. Kingsolver, G. P. A. Lamarre, W.
731 F. Laurance, B. Lavandero, S. R. Leather, P. Lehmann, C. Le Lann, M. M. López-Uribe, C.-S.
732 Ma, G. Ma, J. Moiroux, L. Monticelli, C. Nice, P. J. Ode, S. Pincebourde, W. J. Ripple, M.
733 Rowe, M. J. Samways, A. Sentis, A. A. Shah, N. Stork, J. S. Terblanche, M. P. Thakur, M. B.
734 Thomas, J. M. Tylianakis, J. Van Baaren, M. Van de Pol, W. H. Van der Putten, H. Van Dyck,

- 735 W. C. E. P. Verberk, D. L. Wagner, W. W. Weisser, W. C. Wetzel, H. A. Woods, K. A. G.
736 Wyckhuys, S. L. Chown, [Scientists' warning on climate change and insects](#). *Ecological*
737 *Monographs* **93**, e1553 (2023).
- 738 70. S. Guindre-Parker, D. R. Rubenstein, [Survival Benefits of Group Living in a Fluctuating](#)
739 [Environment](#). *The American Naturalist* **195**, 1027–1036 (2020).
- 740 71. P. A. Downing, [Michener's group-size paradox in cooperatively breeding birds](#). *Journal*
741 *of Evolutionary Biology* **37**, 353–359 (2024).
- 742 72. P. Santema, T. Clutton-Brock, [Meerkat helpers increase sentinel behaviour and bipedal](#)
743 [vigilance in the presence of pups](#). *Animal Behaviour* **85**, 655–661 (2013).
- 744 73. F. Groenewoud, J. G. Frommen, D. Josi, H. Tanaka, A. Jungwirth, M. Taborsky,
745 [Predation risk drives social complexity in cooperative breeders](#). *Proceedings of the National*
746 *Academy of Sciences of the United States of America* **113**, 4104–4109 (2016).
- 747 74. A. Freudiger, D. Josi, F. Henning, M. Taborsky, [Behavioural flexibility and](#)
748 [morphological differentiation in response to environmental variation in cooperatively breeding](#)
749 [cichlids](#). *Functional Ecology* **35**, 2266–2281 (2021).
- 750 75. P. Ibbotson, C. Jimenez-Romero, K. M. Page, [Dying to cooperate: The role of](#)
751 [environmental harshness in human collaboration](#). *Behavioral Ecology* **33**, 190–201 (2022).
- 752 76. E. M. Brumfiel, T. K. Earle, Eds., *Specialization, Exchange and Complex Societies*
753 (Cambridge University Press, Cambridge, 2008).
- 754 77. S. T. Emlen, [The Evolution of Helping. II. The Role of Behavioral Conflict](#). *The*
755 *American Naturalist* **119**, 40–53 (1982).
- 756 78. I. Pen, F. J. Weissing, [Towards a unified theory of cooperative breeding: The role of](#)
757 [ecology and life history re-examined](#). *Proceedings of the Royal Society of London. Series B:*
758 *Biological Sciences* **267**, 2411–2418 (2000).
- 759 79. B. J. Hatchwell, J. Komdeur, [Ecological constraints, life history traits and the evolution of](#)
760 [cooperative breeding](#). *Animal Behaviour* **59**, 1079–1086 (2000).
- 761 80. P. E. Smaldino, J. C. Schank, R. McElreath, [Increased Costs of Cooperation Help](#)
762 [Cooperators in the Long Run](#). *The American Naturalist* **181**, 451–463 (2013).

- 763 81. P. Kennedy, A. D. Higginson, A. N. Radford, S. Sumner, [Altruism in a volatile world](#).
764 *Nature* **555**, 359–362 (2018).
- 765 82. W. Jetz, G. H. Thomas, J. B. Joy, K. Hartmann, A. O. Mooers, [The global diversity of](#)
766 [birds in space and time](#). *Nature* **491**, 444–448 (2012).
- 767 83. A. Cockburn, [Prevalence of different modes of parental care in birds](#). *Proceedings of the*
768 *Royal Society B: Biological Sciences* **273**, 1375–1383 (2006).
- 769 84. J. del Hoyo, A. Elliott, J. Sargatal, José. Cabot, *Handbook of the Birds of the World* (Lynx
770 Edicions, Barcelona, 1992).
- 771 85. H. Wouters, Global bioclimatic indicators from 1979 to 2018 derived from reanalysis.
772 Copernicus Climate Change Service (C3S) Climate Data Store (CDS) (2021).
- 773 86. J. D. Hadfield, [MCMC Methods for Multi-Response Generalized Linear Mixed Models:](#)
774 [The MCMCglmm R Package](#). *Journal of Statistical Software* **33**, 1–22 (2010).
- 775 87. H. Hersbach, B. Bell, P. Berrisford, S. Hirahara, A. Horányi, J. Muñoz-Sabater, J.
776 Nicolas, C. Peubey, R. Radu, D. Schepers, A. Simmons, C. Soci, S. Abdalla, X. Abellan, G.
777 Balsamo, P. Bechtold, G. Biavati, J. Bidlot, M. Bonavita, G. De Chiara, P. Dahlgren, D. Dee, M.
778 Diamantakis, R. Dragani, J. Flemming, R. Forbes, M. Fuentes, A. Geer, L. Haimberger, S. Healy,
779 R. J. Hogan, E. Hólm, M. Janisková, S. Keeley, P. Laloyaux, P. Lopez, C. Lupu, G. Radnoti, P.
780 de Rosnay, I. Rozum, F. Vamborg, S. Villaume, J.-N. Thépaut, [The ERA5 global reanalysis](#).
781 *Quarterly Journal of the Royal Meteorological Society* **146**, 1999–2049 (2020).
- 782 88. O. Vincze, A. Kosztoányi, Z. Barta, C. Küpper, M. Alrashidi, J. A. Amat, A. Argüelles
783 Ticó, F. Burns, J. Cavitt, W. C. Conway, M. Cruz-López, A. E. Desucre-Medrano, N. dos
784 Remedios, J. Figuerola, D. Galindo-Espinosa, G. E. García-Peña, S. Gómez Del Angel, C.
785 Gratto-Trevor, P. Jönsson, P. Lloyd, T. Montalvo, J. E. Parra, R. Pruner, P. Que, Y. Liu, S. T.
786 Saalfeld, R. Schulz, L. Serra, J. J. H. St Clair, L. E. Stenzel, M. A. Weston, M. Yasué, S. Zefania,
787 T. Székely, [Parental cooperation in a changing climate: Fluctuating environments predict shifts in](#)
788 [care division](#). *Global Ecology and Biogeography* **26**, 347–358 (2017).
- 789 89. B. Hassler, A. Lauer, [Comparison of Reanalysis and Observational Precipitation Datasets](#)
790 [Including ERA5 and WFDE5](#). *Atmosphere* **12**, 1462 (2021).

- 791 90. D. A. Lavers, A. Simmons, F. Vamborg, M. J. Rodwell, [An evaluation of ERA5](#)
792 [precipitation for climate monitoring](#). *Quarterly Journal of the Royal Meteorological Society* **148**,
793 3152–3165 (2022).
- 794 91. B. International, Bird species distribution maps of the world (2021).
- 795 92. R. J. Hijmans, J. van Etten, M. Sumner, J. Cheng, D. Baston, A. Bevan, R. Bivand, L.
796 Busetto, M. Canty, B. Fasoli, D. Forrest, A. Ghosh, D. Golicher, J. Gray, J. A. Greenberg, P.
797 Hiemstra, K. Hingee, A. Ilich, I. for M. A. Geosciences, C. Karney, M. Mattiuzzi, S. Mosher, B.
798 Naimi, J. Nowosad, E. Pebesma, O. P. Lamigueiro, E. B. Racine, B. Rowlingson, A. Shortridge,
799 B. Venables, R. Wueest, Raster: Geographic Data Analysis and Modeling (2023).
- 800 93. M. Plummer, N. Best, K. Cowles, K. Vines, CODA: Convergence diagnosis and output
801 analysis for MCMC. *R News* **6**, 7–11 (2006).
- 802 94. S. Nakagawa, H. Schielzeth, [Repeatability for Gaussian and non-Gaussian data: A](#)
803 [practical guide for biologists](#). *Biological Reviews*, 935–956 (2010).
- 804 95. P. de Villemereuil, H. Schielzeth, S. Nakagawa, M. Morrissey, [General Methods for](#)
805 [Evolutionary Quantitative Genetic Inference from Generalized Mixed Models](#). *Genetics* **204**,
806 1281–1294 (2016).
- 807 96. D. Allan, White Helmetshrike (*Prionops plumatus*) (2020).
- 808 97. M. A. S. Alves, [Social System and Helping Behavior in the White-Banded Tanager](#)
809 [\(*Neothraupis fasciata*\)](#). *The Condor* **92**, 470 (1990).
- 810 98. J. Armingier, “Breeding biology of a tropical cooperative passerine: The Yucatan Wren
811 (*Campylorhynchus yucatanicus*),” thesis, Villanova University, United States (2014).
- 812 99. S. Asai, C. Shimoda, I. Nishiumi, K. EGUCHIà, S. Yamagishi, Isolation of microsatellite
813 loci for paternity testing in the rufous vanga. *Molecular Ecology*, 13 (1999).
- 814 100. J. Awkerman, D. Anderson, G. Whittow, Laysan Albatross (*Phoebastria immutabilis*)
815 (2020).
- 816 101. V. Baglione, J. M. Marcos, D. Canestrari, Cooperatively breeding groups of carrion crow
817 (*Corvus corone corone*) in northern Spain. *The Auk* **119**, 790–799 (2002).

- 818 102. V. Baglione, J. M. Marcos, D. Canestrari, J. Ekman, [Direct fitness benefits of group](#)
819 [living in a complex cooperative society of carrion crows, *Corvus corone corone*](#). *Animal*
820 *Behaviour* **64**, 887–893 (2002).
- 821 103. V. Baglione, D. Canestrari, J. M. Marcos, J. Ekman, [Kin Selection in Cooperative](#)
822 [Alliances of Carrion Crows](#). *Science* **300**, 1947–1949 (2003).
- 823 104. G. C. Bain, M. L. Hall, R. A. Mulder, [Territory configuration moderates the frequency of](#)
824 [extra-group mating in superb fairy-wrens](#). *Molecular Ecology* **23**, 5619–5627 (2014).
- 825 105. P. Baker, H. Baker, Maui Alauahio (*Paroreomyza montana*) (2020).
- 826 106. P. Banko, L. Johnson, G. Lindsey, S. Fancy, T. Pratt, J. Jacobi, W. Banko, Palila
827 (*Loxioides bailleui*) (2020).
- 828 107. A. Barati, “Cooperative breeding in the Noisy Miner (*Manorina melanocephala*): The role
829 of genetic relatedness, sex, extra-pair paternity and acoustic signals,” thesis, Department of
830 Zoology, School of Environment; Rural Sciences, University of New England (2016).
- 831 108. A. Barati, R. L. Andrew, J. C. Gorrell, P. G. McDonald, [Extra-pair paternity is not driven](#)
832 [by inbreeding avoidance and does not affect provisioning rates in a cooperatively breeding bird,](#)
833 [the noisy miner \(*Manorina melanocephala*\)](#). *Behavioral Ecology* **29**, 244–252 (2018).
- 834 109. F. Barker, “The evolution of cooperative breeding in *Campylorhynchus* wrens: A
835 comparative approach,” thesis, University of Chicago (1999).
- 836 110. J. Barnaby, “Cooperative Breeding in the Southern Anteater-Chat: Sexual Disparity,
837 Survival and Dispersal,” thesis, Uppsala Univeristy, Uppsala, Sweden (2012).
- 838 111. J. C. Bednarz, [Pair and Group Reproductive Success, Polyandry, and Cooperative](#)
839 [Breeding in Harris’ Hawks](#). *The Auk* **104**, 393–404 (1987).
- 840 112. J. C. Bednarz, J. D. Ligon, [A Study of the Ecological Bases of Cooperative Breeding in](#)
841 [the Harris’ Hawk](#). *Ecology* **69**, 1176–1187 (1988).
- 842 113. C. Beier, M. Repenning, M. S. da Pereira, A. Pereira, C. S. Fontana, [Cooperative breeding](#)
843 [and demography of Yellow Cardinal *Gubernatrix cristata* in Brazil](#). *Revista Brasileira de*
844 *Ornitologia* **25**, 12–19 (2017).

- 845 114. H. L. Bell, H. A. Ford, [A comparison of the social organization of three syntopic species](#)
846 [of Australian thornbill, *Acanthiza*](#). *Behavioral Ecology and Sociobiology* **19**, 381–392 (1986).
- 847 115. L. Bennun, The contribution of helpers to feeding nestlings in gray-capped social
848 weavers, *Pseudonigrita arnaudi*. *Animal Behaviour* **47**, 1047–1056 (1994).
- 849 116. F. M. Benson, [Field-notes from Nyasaland](#). *The Ostrich* **17**, 297–319 (1946).
- 850 117. E. C. Berg, [Parentage and reproductive success in the white-throated magpie-jay,](#)
851 [*Calocitta formosa*, a cooperative breeder with female helpers](#). *Animal Behaviour* **70**, 375–385
852 (2005).
- 853 118. E. C. Berg, J. M. Eadie, T. A. Langen, A. F. Russell, [Reverse sex-biased philopatry in a](#)
854 [cooperative bird: Genetic consequences and a social cause](#). *Molecular Ecology* **18**, 3486–3499
855 (2009).
- 856 119. K. Berthier, F. Leippert, L. Fumagalli, R. Arlettaz, [Massive Nest-Box Supplementation](#)
857 [Boosts Fecundity, Survival and Even Immigration without Altering Mating and Reproductive](#)
858 [Behaviour in a Rapidly Recovered Bird Population](#). *PLoS ONE* **7**, e36028 (2012).
- 859 120. J. Bertran, A. Margalida, Social organization of a trio of bearded vultures (*Gypaetus*
860 *barbatus*): Sexual and parental roles. *Journal of Raptor Research* **36**, 66–70 (2002).
- 861 121. B. Best, M. Checker, R. Thewlis, A. Best, W. Duckworth, New breeding data from
862 Sothwestern Ecuador. *Ornithologica Neotropical* **7**, 69–73 (1996).
- 863 122. R. Bierregaard, G. Kirwan, D. Christie, Galapagos Hawk (*Buteo galapagoensis*) (2020).
- 864 123. C. J. Blackmore, R. Heinsohn, [Variable mating strategies and incest avoidance in](#)
865 [cooperatively breeding grey-crowned babblers](#). *Animal Behaviour* **75**, 63–70 (2008).
- 866 124. L. Blanchard, “An Investigation of the Communal Breeding System of the Smooth-billed
867 Ani (*Crotophaga ani*).” thesis, McMaster University (2000).
- 868 125. D. Blomqvist, B. Fessl, H. Herbert, S. Kleindorfer, [High frequency of extra-pair](#)
869 [fertilisations in the moustached warbler, a songbird with a variable breeding system](#). *Behaviour*
870 **142**, 1133–1148 (2005).
- 871 126. E. Boehm, Extension of range of the Ground Cuckoo-shrike. *South Australian*
872 *Ornithologist* **29**, 74 (1983).

- 873 127. W. Boles, Eastern Yellow Robin (*Eopsaltria australis*) (2020).
- 874 128. J. J. Boomsma, [Kin Selection versus Sexual Selection: Why the Ends Do Not Meet.](#)
875 *Current Biology* **17**, R673–R683 (2007).
- 876 129. P. Brekke, P. Cassey, C. Ariani, J. G. Ewen, [Evolution of extreme-mating behaviour:](#)
877 [Patterns of extrapair paternity in a species with forced extrapair copulation.](#) *Behavioral Ecology*
878 *and Sociobiology* **67**, 963–972 (2013).
- 879 130. J. V. Briskie, R. Montgomerie, T. Poldmaa, P. T. Boag, [Paternity and paternal care in the](#)
880 [polygynandrous Smith’s longspur.](#) *Behavioral Ecology and Sociobiology* **43**, 181–190 (1998).
- 881 131. J. Briskie, Smith’s Longspur (*Calcarius pictus*) (2020).
- 882 132. M. de L. Brooke, I. R. Hartley, [Nesting Henderson Reed-Warblers \(*Acrocephalus*](#)
883 [vaughani taiti\) Studied by DNA Fingerprinting: Unrelated Coalitions in a Stable Habitat?](#) *The*
884 *Auk* **112**, 77–86 (1995).
- 885 133. M. G. Brooker, I. Rowley, M. Adams, P. R. Baverstock, [Promiscuity: An inbreeding](#)
886 [avoidance mechanism in a socially monogamous species?](#) *Behavioral Ecology and Sociobiology*
887 **26** (1990).
- 888 134. L. Brouwer, M. V. D. Pol, E. Atema, A. Cockburn, [Strategic promiscuity helps avoid](#)
889 [inbreeding at multiple levels in a cooperative breeder where both sexes are philopatric.](#) *Molecular*
890 *Ecology* **20**, 4796–4807 (2011).
- 891 135. J. L. Brown, [Communal feeding of nestlings in the Mexican jay \(*Aphelocoma*](#)
892 [ultramarina\): Interflock comparisons.](#) *Animal Behaviour* **20**, 395–403 (1972).
- 893 136. J. L. Brown, [Cooperative breeding and altruistic behaviour in the mexican jay,](#)
894 [Aphelocoma ultramarina.](#) *Animal Behaviour* **18**, 366–378 (1970).
- 895 137. J. L. Brown, E. R. Brown, [Extended Family System in a Communal Bird.](#) *Science* **211**,
896 959–960 (1981).
- 897 138. J. Brown, E. Brown, “Mexican Jays: Uncooperative breeding” in *Cooperative Breeding in*
898 *Birds: Long-term Studies of Ecology and Behavior* (Cambridge: Cambridge University Press,
899 1990).

- 900 139. L. E. Browning, C. M. Young, J. L. Savage, D. J. F. Russell, H. Barclay, S. C. Griffith, A.
901 F. Russell, [Carer provisioning rules in an obligate cooperative breeder: Prey type, size and](#)
902 [delivery rate](#). *Behavioral Ecology and Sociobiology* **66**, 1639–1649 (2012).
- 903 140. J. P. Bruce, J. S. Quinn, S. A. Sloane, B. N. White, [DNA Fingerprinting Reveals](#)
904 [Monogamy in the Bushtit, a Cooperatively Breeding Species](#). *The Auk* **113**, 511–516 (1996).
- 905 141. T. Burke, N. B. Davies, M. W. Bruford, B. J. Hatchwell, [Parental care and mating](#)
906 [behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA](#)
907 [fingerprinting](#). *Nature* **338**, 249–251 (1989).
- 908 142. D. B. Burt, [SOCIAL AND BREEDING BIOLOGY OF BEE-EATERS IN THAILAND](#).
909 *The Wilson Bulletin* **114**, 275–279 (2002).
- 910 143. C. D. Cadena, A. S. M. Cuervo, S. M. Lanyon, Phylogenetic relationships of the red-
911 bellied grackle (Icteridae: *Hypopyrrhus pyrohypogaster*) inferred from mitochondrial DNA
912 sequence data. *The Condor* **106**, 664–670 (2004).
- 913 144. C. Caffrey, Female-Biased Delayed Dispersal and Helping in American Crows. *The Auk*
914 **109**, 609–619 (1992).
- 915 145. P. Cale, “The spatial dynamics of the White-browed Babbler in a fragmented agricultural
916 landscape,” thesis, Univ. of New England, Armidale (1999).
- 917 146. T. Callens, “Genetic and demographic signatures of population fragmentation in a
918 cooperatively-breeding bird from south-east Kenya.” thesis, Ghent University, Belgium (2012).
- 919 147. F. Canário, S. Matos, M. Soler, [Environmental Constraints and Cooperative Breeding in](#)
920 [the Azure-Winged Magpie](#). *The Condor* **106**, 608–617 (2004).
- 921 148. C. Carboneras, G. Kirwan, Magpie Goose (*Anseranas semipalmata*) (2020).
- 922 149. I. Castro, K. M. Mason, D. P. Armstrong, D. M. Lambert, [Effect of Extra-Pair Paternity](#)
923 [on Effective Population Size in a Reintroduced Population of the Endangered Hihi, and Potential](#)
924 [for Behavioural Management](#). *Conservation Genetics* **5**, 381–393 (2004).
- 925 150. I. Castro, E. O. Minot, R. A. Fordham, T. R. Birkhead, [Polygynandry, face-to-face](#)
926 [copulation and sperm competition in the Hihi *Notiomystis cincta* \(Aves: Meliphagidae\)](#). *Ibis* **138**,
927 765–771 (1996).

- 928 151. R. A. S. Cerboncini, T. V. Braga, J. J. Roper, F. C. Passos, [Southern Lapwing *Vanellus*](#)
929 [chilensis cooperative helpers at nests are older siblings](#). *Ibis* **162**, 227–231 (2020).
- 930 152. P. Chantler, “Family Apodidae (Swifts)” in *Handbook of the Birds of the World. Vol 5.*
931 *Barn-Owls to Hummingbirds* (Lynx Editions: Barcelona, 1999), pp. 388–457.
- 932 153. I. Chiver, B. J. M. Stutchbury, E. S. Morton, [The function of seasonal song in a tropical](#)
933 [resident species, the Red-throated Ant-tanager \(*Habia fuscicauda*\)](#). *Journal of Ornithology* **156**,
934 55–63 (2015).
- 935 154. I. Chiver, S. Morton, Red-throated Ant-Tanager (*Habia fuscicauda*) (2020).
- 936 155. R. Clarke, R. Boulton, M. Clarke, [Translocation of the socially complex Black-eared](#)
937 [Miner *Manorina melanotis*: A trial using hard and soft release techniques](#). *Pacific Conservation*
938 *Biology* **8**, 223–234 (2002).
- 939 156. T. H. Clutton-Brock, D. Gaynor, R. Kansky, A. D. C. MacColl, G. McIlrath, P.
940 Chadwick, P. N. M. Brotherton, J. M. O’Riain, M. Manser, J. D. Skinner, [Costs of cooperative](#)
941 [behaviour in suricates \(*Suricata suricatta*\)](#). *Proceedings of the Royal Society of London. Series B:*
942 *Biological Sciences* **265**, 185–190 (1998).
- 943 157. T. h. Clutton-Brock, P. n. m. Brotherton, M. j. O’Riain, A. s. Griffin, D. Gaynor, L.
944 Sharpe, R. Kansky, M. b. Manser, G. m. McIlrath, [Individual contributions to babysitting in a](#)
945 [cooperative mongoose, *Suricata suricatta*](#). *Proceedings of the Royal Society of London. Series B:*
946 *Biological Sciences* **267**, 301–305 (2000).
- 947 158. M. Cody, Española Mockingbird (*Mimus macdonaldi*) (2020).
- 948 159. M. Cody, C. Sharpe, Floreana Mockingbird (*Mimus trifasciatus*) (2020).
- 949 160. M. Cody, Tropical Mockingbird (*Mimus gilvus*) (2020).
- 950 161. R. Colbourne, Incubation behaviour and egg physiology of kiwi (*Apteryx* spp.) in natural
951 habitats. *New Zealand Journal of Ecology* **26**, 129–138 (2022).
- 952 162. N. Collar, J. del Hoyo, C. Robson, D. Christie, Jungle Babbler (*Argya striata*) (2020).
- 953 163. N. Collar, C. Robson, A. Bonan, Taiwan Yuhina (*Yuhina brunneiceps*) (2020).
- 954 164. N. E. Collias, E. C. Collias, Behavior of the Grey-Capped Social Weaver (*Pseudonigrita*
955 *arnaudi*) in Kenya. *The Auk* **97**, 213–226 (1980).

- 956 165. K. F. Conrad, M. F. Clarke, R. J. Robertson, P. T. Boag, Paternity and the Relatedness of
957 Helpers in the Cooperatively Breeding Bell Miner. *The Condor* **100**, 343–349 (1998).
- 958 166. L. Cousseau, D. Van de Loock, M. Githiru, C. Vangestel, L. Lens, [Female need for](#)
959 [paternal care shapes variation in extra-pair paternity in a cooperative breeder](#). *Behavioral Ecology*
960 **31**, 548–558 (2020).
- 961 167. L. Cousseau, M. Hammers, D. Van de Loock, B. Apfelbeck, M. Githiru, E. Matthysen, L.
962 Lens, [Habitat fragmentation shapes natal dispersal and sociality in an Afrotropical cooperative](#)
963 [breeder](#). *Proceedings of the Royal Society B: Biological Sciences* **287**, 20202428 (2020).
- 964 168. R. Covas, A. Dalecky, A. Caizergues, C. Doutrelant, [Kin associations and direct vs](#)
965 [indirect fitness benefits in colonial cooperatively breeding sociable weavers *Philetairus socius*](#).
966 *Behavioral Ecology and Sociobiology* **60**, 323–331 (2006).
- 967 169. A. J. F. Craig, C. Feare, African Pied Starling (*Lamprotornis bicolor*) (2020).
- 968 170. A. J. F. K. Craig, [Allofeeding and dominance interactions in the cooperatively breeding](#)
969 [pied starling](#). *Animal Behaviour* **36**, 1251–1253 (1988).
- 970 171. A. Craig, C. Feare, Cape Starling (*Lamprotornis nitens*) (2020).
- 971 172. A. Craig, [Co-operative breeding in two African starlings, *Sturnidae*](#). *Ibis* **125**, 114–115
972 (1983).
- 973 173. A. J. F. K. Craig, [Co-operative breeding in the pied starling](#). *The Ostrich* **58**, 176–180
974 (1987).
- 975 174. A. J. F. Craig, Gray-headed Social-Weaver (*Pseudonigrita arnaudi*) (2020).
- 976 175. A. J. F. Craig, Red-billed Buffalo-Weaver (*Bubalornis niger*) (2020).
- 977 176. A. Craig, D. Christie, Sociable Weaver (*Philetairus socius*) (2020).
- 978 177. A. Craig, J. Feare, Superb Starling (*Lamprotornis superbus*) (2020).
- 979 178. A. J. F. Craig, Yellow-billed Oxpecker (*Buphagus africanus*) (2020).
- 980 179. H. Q. P. Crick, C. H. Fry, [Effects of Helpers on Parental Condition in Red-Throated Bee-](#)
981 [Eaters \(*Merops bullocki*\)](#). *The Journal of Animal Ecology* **55**, 893 (1986).

- 982 180. R. L. Curry, P. R. Grant, [Demography of the Cooperatively Breeding Galapagos](#)
983 [Mockingbird, *Nesomimus parvulus*, in a Climatically Variable Environment](#). *The Journal of*
984 *Animal Ecology* **58**, 441 (1989).
- 985 181. R. Curry, P. Grant, “Galapagos mockingbirds: Territorial cooperative breeding in a
986 climatically variable environment” in *Cooperative Breeding in Birds: Long-term Studies of*
987 *Ecology and Behavior* (Cambridge: Cambridge University Press, 1990).
- 988 182. R. L. Curry, Geographic variation in social organization of Galapagos mockingbirds:
989 Ecological correlates of group territoriality and cooperative breeding. *Behavioral Ecology and*
990 *Sociobiology*, 144–160 (1989).
- 991 183. R. L. Curry, Group structure, within-group conflict and reproductive tactics in
992 cooperatively breeding Galapagos mockingbirds, *Nesomimus parvulus*. *Animal Behaviour* **36**,
993 1708–1728 (1988).
- 994 184. R. L. Curry, Influence of kinship on helping behavior in Galapagos mockingbirds.
995 *Behavioral Ecology and Sociobiology* **22**, 141–152 (1988).
- 996 185. J. E. Danner, D. M. Small, T. B. Ryder, B. Lohr, B. S. Masters, D. E. Gill, R. C.
997 Fleischer, [Temporal patterns of extra-pair paternity in a population of Grasshopper Sparrows \(*Ammodramus*](#)
998 [savannarum\) in Maryland](#). *The Wilson Journal of Ornithology* **130**, 40–51 (2018).
- 999 186. N. Davies, *Dunnock Behaviour and Social Evolution* (Oxford University Press, 1992).
- 1000 187. N. B. Davies, A. Lundberg, [Food Distribution and a Variable Mating System in the](#)
1001 [Dunnock, *Prunella modularis*](#). *The Journal of Animal Ecology* **53**, 895–912 (1984).
- 1002 188. N. B. Davies, I. R. Hartley, B. J. Hatchwell, A. Desrochers, J. Skeer, The polygynandrous
1003 mating system of the alpine accentor, *Prunella collaris*. I. Ecological causes and reproductive
1004 conflicts. *Animal Behaviour*, 20.
- 1005 189. D. E. Davis, Social Nesting Habits of the Smooth-Billed Ani. *The Auk* **57**, 179–218
1006 (1940).
- 1007 190. J. W. Dawson, R. W. Mannan, [Dominance Hierarchies and Helper Contributions in](#)
1008 [Harris’ Hawks](#). *The Auk* **108**, 649–660 (1991).
- 1009 191. E. de Juana, “Family Coliidae (Mousebirds)” in *Handbook of the Birds of the World Vol*
1010 *6: Mousebirds to Hornbills* (Lynx Edicions, Barcelona, Spain, 2001).

- 1011 192. S. J. S. Debus, [Breeding and population parameters of robins in a woodland remnant in](#)
1012 [northern New South Wales, Australia](#). *Emu - Austral Ornithology* **106**, 147–156 (2006).
- 1013 193. J. Decoux, “Coliidae, mousebirds or colies” in *The Birds of Africa. Vol III* (Academic
1014 Press: London, 1988), pp. 197–242.
- 1015 194. J. Decoux, Les particularites demographiques et socioecologiques du coliou strie dans le
1016 nord-est du gabon 1. - donnees d’observation. **36**, 37–78 (1982).
- 1017 195. J. del Hoyo, J. Remsen Jr, G. Kirwan, N. Collar, Rufous-fronted Thornbird
1018 (*Phacellodomus rufifrons*) (2020).
- 1019 196. L. S. DeLay, J. Faaborg, J. Naranjo, S. M. Paz, T. de Vries, P. G. Parker, [Paternal Care in](#)
1020 [the Cooperatively Polyandrous Galapagos Hawk](#). *The Condor* **98**, 300–311 (1996).
- 1021 197. R. W. Dexter, Extra-parental cooperation in the nesting of chimney swifts. *The Wilson*
1022 *Bulletin* **64**, 133–139 (1952).
- 1023 198. R. I. Dias, R. H. Macedo, D. Goedert, M. S. Webster, [Cooperative Breeding in the Campo](#)
1024 [Flicker II: Patterns of Reproduction and Kinship](#). *The Condor* **115**, 855–862 (2013).
- 1025 199. R. I. Dias, M. S. Webster, D. Goedert, R. H. Macedo, [Cooperative Breeding in the Campo](#)
1026 [Flicker I: Breeding Ecology and Social Behavior](#). *The Condor* **115**, 847–854 (2013).
- 1027 200. J. L. Dickinson, J. J. Akre, [Extrapair paternity, inclusive fitness, and within-group](#)
1028 [benefits of helping in western bluebirds](#). *Molecular Ecology* **7**, 95–105 (1998).
- 1029 201. J. Dickinson, J. Haydock, W. Koenig, M. Stanback, F. Pitelka, [Genetic monogamy in](#)
1030 [single-male groups of acorn woodpeckers, *Melanerpes formicivorus*](#). *Molecular Ecology* **4**, 765–
1031 770 (1995).
- 1032 202. J. Dickinson, Ç. Akçay, E. Ferree, C. Stern, “Western bluebirds: Lessons from a marginal
1033 cooperative breeder” in *Cooperative Breeding in Vertebrates* (Cambridge: Cambridge University
1034 Press, 2016), pp. 19–38.
- 1035 203. E. D. Doerr, V. A. J. Doerr, [Comparative demography of treecreepers: Evaluating](#)
1036 [hypotheses for the evolution and maintenance of cooperative breeding](#). *Animal Behaviour* **72**,
1037 147–159 (2006).

- 1038 204. L. L. Dornak, D. B. Burt, D. W. Coble, R. N. Conner, [Relationships Between Habitat and](#)
1039 [Snag Characteristics and the Reproductive Success of the Brown-headed Nuthatch \(*Sitta pusilla*\)](#)
1040 [in Eastern Texas](#). *Southeastern Naturalist* **3**, 683–694 (2004).
- 1041 205. L. R. Dos Santos, M. Â. Marini, [Breeding biology of White-rumped Tanagers in central](#)
1042 [Brazil](#). *Journal of Field Ornithology* **81**, 252–258 (2010).
- 1043 206. M. C. Double, R. Peakall, N. R. Beck, A. Cockburn, [Dispersal, philopatry, and infidelity:](#)
1044 [Dissecting local genetic structure in superb fairy-wrens \(*Malurus cyaneus*\)](#). *Evolution* **59**, 625–
1045 635 (2005).
- 1046 207. M. Double, A. Cockburn, [Pre-dawn infidelity: Females control extra-pair mating in](#)
1047 [superb fairy-wrens](#). *Proceedings of the Royal Society of London. Series B: Biological Sciences*
1048 **267**, 465–470 (2000).
- 1049 208. M. C. Double, A. Cockburn, [Subordinate superb fairy-wrens \(*Malurus cyaneus*\)](#)
1050 [parasitize the reproductive success of attractive dominant males](#). *Proceedings of the Royal*
1051 *Society of London. Series B: Biological Sciences* **270**, 379–384 (2003).
- 1052 209. D. Dow, M. Whitmore, “Noisy Miners: Variations on the theme of communality” in
1053 *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Cambridge:
1054 Cambridge University Press, 1990).
- 1055 210. A. C. Driskell, J. A. Norman, S. Pruett-Jones, E. Mangall, S. Sonsthagen, L. Christidis, [A](#)
1056 [multigene phylogeny examining evolutionary and ecological relationships in the Australo-papuan](#)
1057 [wrens of the subfamily Malurinae \(Aves\)](#). *Molecular Phylogenetics and Evolution* **60**, 480–485
1058 (2011).
- 1059 211. B. Du, X. Lu, [Bi-parental vs. Cooperative breeding in a passerine: Fitness-maximizing](#)
1060 [strategies of males in response to risk of extra-pair paternity?](#) *Molecular Ecology* **18**, 3929–3939
1061 (2009).
- 1062 212. M. du Pleiss, “Behavioural ecology of the Redbilled Woodhoopoe *Phoeniculus Purpureus*
1063 in South Africa,” thesis, University of Cape Town, South Africa (1989).
- 1064 213. P. O. Dunn, A. Cockburn, R. A. Mulder, [Fairy-wren helpers often care for young to](#)
1065 [which they are unrelated](#). *Proceedings of the Royal Society of London. Series B: Biological*
1066 *Sciences* **259**, 339–343 (1995).

- 1067 214. K. L. Durrant, J. M. Hughes, [Differing rates of extra-group paternity between two](#)
1068 [populations of the Australian magpie \(*Gymnorhina tibicen*\)](#). *Behavioral Ecology and*
1069 *Sociobiology* **57**, 536–545 (2005).
- 1070 215. A. Dyrce, C. Sharpe, Seychelles Warbler (*Acrocephalus sechellensis*), (2020).
- 1071 216. P. Eason, P. Sherman, Dominance status, mating strategies and copulation success in
1072 cooperatively polyandrous white-winged trumpeters, *Psophia leucopteva* (Aves: Psophiidae).
1073 *Animal Behaviour* **49**, 725–736 (1995).
- 1074 217. D. Ebert, “Social Behaviour and Breeding Biology of the Yellow-Rumped Thornbill,”
1075 thesis, The Australian National University (2004).
- 1076 218. K. Eguchi, S. Yamagishi, S. Asai, H. Nagata, T. Hino, [Helping does not enhance](#)
1077 [reproductive success of cooperatively breeding rufous vanga in Madagascar](#). *Journal of Animal*
1078 *Ecology* **71**, 123–130 (2002).
- 1079 219. K. Eguchi, H. E. Amano, S. Yamagishi, [Roosting, range use and foraging behaviour of](#)
1080 [the Sickle-billed Vanga, *Falcullea palliata*, in Madagascar](#). *The Ostrich* **72**, 127–133 (2001).
- 1081 220. K. Eguchi, N. Yamaguchi, K. Ueda, H. Nagata, M. Takagi, R. Noske, [Social structure and](#)
1082 [helping behaviour of the Grey-crowned Babbler *Pomatostomus temporalis*](#). *Journal of*
1083 *Ornithology* **148**, 203–210 (2007).
- 1084 221. C. M. Eising, J. Komdeur, J. Buys, M. Reemer, D. S. Richardson, [Islands in a desert:](#)
1085 [Breeding ecology of the African Reed Warbler *Acrocephalus baeticatus* in Namibia](#). *Ibis* **143**,
1086 482–493 (2001).
- 1087 222. J. M. M. Ekstrom, T. Burke, L. Randrianaina, T. R. Birkhead, [Unusual sex roles in a](#)
1088 [highly promiscuous parrot: The Greater Vasa Parrot *Caracopsis vasa*](#). *Ibis* **149**, 313–320 (2007).
- 1089 223. S. T. Emlen, “White-fronted Bee-eaters: Helping in a colonially nesting species” in
1090 *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Cambridge:
1091 Cambridge University Press, 1990).
- 1092 224. E. D. Enbody, J. Boersma, J. A. Jones, M. W. H. Chatfield, S. Ketalo, D. Nason, D. T.
1093 Baldassarre, J. Hazlehurst, O. Gowen, H. Schwabl, J. Karubian, [Social organisation and breeding](#)
1094 [biology of the White-shouldered Fairywren \(*Malurus alboscapulatus*\)](#). *Emu - Austral*
1095 *Ornithology* **119**, 274–285 (2019).

- 1096 225. B. J. Ens, J. P. Kruijt, L. Jenkins, T. Burke, D. Heg, [Why Does the Typically](#)
1097 [Monogamous Oystercatcher \(Haematopus Ostralegus\) Engage in Extra-Pair Copulations?](#)
1098 *Behaviour* **126**, 247–289 (1993).
- 1099 226. J. G. Ewen, D. P. Armstrong, D. M. Lambert, Floater males gain reproductive success
1100 through extrapair fertilizations in the stitchbird. *Animal Behaviour* **58**, 321–328 (1999).
- 1101 227. J. G. Ewen, “A genetic and behavioural investigation of extra-pair copulation in
1102 stitchbirds (*Notiomystis cincta*) breeding on Tiritiri Matangi Island,” thesis, Massey Univeristy
1103 (1998).
- 1104 228. J. G. Ewen, R. H. Clarke, E. Moysey, R. L. Boulton, R. H. Crozier, M. F. Clarke, [Primary](#)
1105 [sex ratio bias in an endangered cooperatively breeding bird, the black-eared miner, and its](#)
1106 [implications for conservation](#). *Biological Conservation* **101**, 137–145 (2001).
- 1107 229. J. Faaborg, P. G. Parker, L. DeLay, T. de Vries, Confirmation of cooperative polyandry in
1108 the Galapagos hawk (*Buteo galapagoensis*). *Behavioral Ecology and Sociobiology* **36**, 83–90
1109 (1995).
- 1110 230. J. Faaborg, J. Bednarz, “Galapagos and Harris’ Hawks: Divergent causes of sociality in
1111 two raptors” in *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior*
1112 (Cambridge: Cambridge University Press, 1990).
- 1113 231. C. Feare, A. Craig, *Starlings and Mynas* (Christopher Helm: London, 1998).
- 1114 232. E. D. Ferree, J. L. Dickinson, [Natural extrapair paternity matches receptivity patterns in](#)
1115 [unguarded females: Evidence for importance of female choice](#). *Animal Behaviour* **82**, 1167–1173
1116 (2011).
- 1117 233. B. Fessl, S. Kleindorfer, H. Hoi, Extra Male Parental Behaviour: Evidence for an
1118 Alternative Mating Strategy in the Moustached Warbler *Acrocephalus melanopogon*. *Journal of*
1119 *Avian Biology* **27**, 88–91 (1996).
- 1120 234. J. Field, [Role specialization and reproductive division of labour at the origin of](#)
1121 [eusociality](#). *Philosophical Transactions of the Royal Society B: Biological Sciences* **380**,
1122 20230265 (2025).
- 1123 235. P. G. Finn, J. M. Hughes, [Helping behaviour in Australian Magpies, *Gymnorhina tibicen*](#).
1124 *Emu - Austral Ornithology* **101**, 57–63 (2001).

- 1125 236. R. C. Fleischer, C. L. Tarr, T. K. Pratt, [Genetic structure and mating system in the palila,](#)
1126 [an endangered Hawaiian honeycreeper, as assessed by DNA fingerprinting.](#) *Molecular Ecology* **3**,
1127 383–392 (1994).
- 1128 237. K. Fletcher, “Parentage and relatedness patterns in the cooperatively breeding southern
1129 ant-eating chat (*Myrmecocichla formicivora*),” thesis, Uppsala Univeristy, Uppsala, Sweden
1130 (2011).
- 1131 238. A. Folch, F. Jutglar, E. Garcia, Southern Brown Kiwi (*Apteryx australis*) (2020).
- 1132 239. J. Ford, Breeding behaviour of the yellow-tailed thornbill in south-western Australia. *The*
1133 *Emu* **63**, 185–20 (1963).
- 1134 240. H. A. Ford, H. Bell, R. Nias, R. Noske, [The Relationship between Ecology and the](#)
1135 [Incidence of Cooperative Breeding in Australian Birds.](#) *Behavioral Ecology and Sociobiology* **22**,
1136 239–249 (1988).
- 1137 241. D. Franklin, I. Smales, M. Miller, P. Menkhorst, [The reproductive biology of the](#)
1138 [helmeted honeyeater, *Lichenostomus melanops cassidix*.](#) *Wildlife Research* **22**, 173 (1995).
- 1139 242. A. Fremgen, Puerto Rican Tody (*Todus mexicanus*) (2020).
- 1140 243. H. Friedmann, Colombian birds collected by brother Niceforo. *Caldasia* **4**, 471–494
1141 (1947).
- 1142 244. H. Frith, S. Davies, Ecology of the magpie goose, *Anseranas semipalmata* Latham
1143 (*Anatidae*). *CSIRO Wildlife Research* **6**, 91–105 (1961).
- 1144 245. C. Fry, S. Keith, E. Urban, *The Birds of Africa Vol VI* (Academic Press: London,
1145 2000)vol. VI.
- 1146 246. H. Fry, P. Boesman, European Bee-eater (*Merops apiaster*) (2020).
- 1147 247. C. H. Fry, [The Social Organisation of Bee-Eaters \(meropidae\) and Co-Operative Breeding](#)
1148 [in Hot-Climature Birds.](#) *Ibis* **114**, 1–14 (1972).
- 1149 248. H. Fry, P. Boesman, White-fronted Bee-eater (*Merops bullockoides*) (2020).
- 1150 249. R. Furness, P. Boesman, E. Garcia, Brown Skua (*Stercorarius antarcticus*) (2020).

- 1151 250. L.-F. Gao, L.-L. Xian, J.-J. Luo, B. Du, [High level of extrapair fertilization in individual](#)
1152 [Tibetan azure-winged magpies and their adaptive responses](#). *Journal of Avian Biology* **49**, e01739
1153 (2018).
- 1154 251. A. J. Gaston, [Demography of the Jungle Babbler, *Turdoides striatus*](#). *The Journal of*
1155 *Animal Ecology* **47**, 845 (1978).
- 1156 252. A. J. Gaston, [Ecology of the common babbler *Turdoides caudatus*](#). *Ibis* **120**, 415–432
1157 (1978).
- 1158 253. R. Geldard, S. Harrap, J. del Hoyo, D. Christie, N. Collar, G. Kirwan, A. Spencer, Black-
1159 throated Tit (*Aegithalos concinnus*) (2020).
- 1160 254. D. W. Gibbons, Brood parasitism and cooperative nesting in the moorhen, *Gallinula*
1161 *chloropus*. *Behavioral Ecology and Sociobiology* **19**, 221–232 (1986).
- 1162 255. H. L. Gibbs, A. W. Goldizen, C. Bullough, A. R. Goldizen, Parentage analysis of multi-
1163 male social groups of tasmanian native hens (*Tribonyx mortierii*): Genetic evidence for
1164 monogamy and polyandry. *Behavioral Ecology and Sociobiology* **35**, 363–371 (1994).
- 1165 256. B. J. Gill, I. G. McLean, [Population Dynamics of the New Zealand Whitehead](#)
1166 [\(*Pachycephalidae*\): A Communal Breeder](#). *The Condor* **94**, 628–635 (1992).
- 1167 257. B. Gill, Rifleman (*Acanthisitta chloris*) (2020).
- 1168 258. J. Goetz, K. McFarland, C. Rimmer, M. Murphy, Multiple paternity and multiple male
1169 feeders in Bicknell's Thrush (*Catharus bicknelli*). *The Auk* **120**, 1044–1053 (2003).
- 1170 259. A. W. Goldizen, J. C. Buchan, D. A. Putland, A. R. Goldizen, E. A. Krebs, [Patterns of](#)
1171 [mate-sharing in a population of Tasmanian Native Hens *Gallinula mortierii*](#). *Ibis* **142**, 40–47
1172 (2000).
- 1173 260. D. G. Gosper, Contributions to the reproductive effort in a group of plural-breeding Pied
1174 Butcherbirds *Cracticus nigrogularis*. *Australian Field Ornithology* **83**, 857–864 (2012).
- 1175 261. P. R. Grant, R. L. Curry, B. R. Grant, A remnant population of the Floreana mockingbird
1176 on Champion island, Galapagos. *Biological Conservation*, 6 (2000).
- 1177 262. P. Gregory, Buff-rumped Thornbill (*Acanthiza reguloides*) (2020).
- 1178 263. P. Gregory, White-browed Scrubwren (*Sericornis frontalis*) (2020).

- 1179 264. M. Griesser, S. M. Drobniak, S. Nakagawa, C. A. Botero, [Family living sets the stage for](#)
1180 [cooperative breeding and ecological resilience in birds](#). *PLOS Biology* **15**, e2000483 (2017).
- 1181 265. L. G. Grimes, [Observations of Group Behaviour and Breeding Biology of the Yellow-](#)
1182 [Billed Shrike Corvinella Corvina](#). *Ibis* **122**, 166–192 (1980).
- 1183 266. S. M. Haig, J. R. Waiters, J. H. Plissner, Genetic evidence for monogamy in the
1184 cooperatively breeding red-cockaded woodpecker. *Behavioral Ecology and Sociobiology* **34**,
1185 295–303 (1994).
- 1186 267. W. D. Hamilton, [Altruism and Related Phenomena, Mainly in Social Insects](#). *Annual*
1187 *Review of Ecology and Systematics* **3**, 193–232 (1972).
- 1188 268. K.-L. Han, J. A. Cox, R. T. Kimball, [Uncommon Levels of Relatedness and Parentage in](#)
1189 [a Cooperatively Breeding Bird, the Brown-Headed Nuthatch \(*Sitta pusilla* \)](#). *The Wilson Journal*
1190 *of Ornithology* **127**, 593–600 (2015).
- 1191 269. T. Harris, K. Franklin, *Shrikes and Bush-Shrikes Including Wood-Shrikes, Helmet-*
1192 *Shrikes, Flycatcher-Shrikes, Philentomas, Batises and Wattle-Eyes* (Christopher Helm: London,
1193 2000).
- 1194 270. I. R. Hartley, N. B. Davies, B. J. Hatchwell, A. Desrochers, D. Nebel, T. Burke, The
1195 polygynandrous mating system of the alpine accentor, *Prunella collaris*. II. Multiple paternity and
1196 parental effort. *Animal Behaviour* **49**, 789–803 (1995).
- 1197 271. B. Hatchwell, Brown Accentor (*Prunella fulvescens*) (2020).
- 1198 272. B. Hatchwell, Dunnock (*Prunella modularis*) (2020).
- 1199 273. B. J. Hatchwell, S. P. Sharp, A. P. Beckerman, J. Meade, [Ecological and demographic](#)
1200 [correlates of helping behaviour in a cooperatively breeding bird](#). *Journal of Animal Ecology* **82**,
1201 486–494 (2013).
- 1202 274. B. Hatchwell, Japanese Accentor (*Prunella rubida*) (2020).
- 1203 275. B. J. Hatchwell, D. J. Ross, N. Chaline, M. K. Fowlie, T. Burke, [Parentage in the](#)
1204 [cooperative breeding system of long-tailed tits, *Aegithalos caudatus*](#). *Animal Behaviour* **64**, 55–
1205 63 (2002).

- 1206 276. J. Haydock, P. G. Parker, K. N. Rabenold, [Extra-pair paternity uncommon in the](#)
1207 [cooperatively breeding bicolored wren](#). *Behavioral Ecology and Sociobiology* **38**, 1–16 (1996).
- 1208 277. J. Haydock, W. D. Koenig, M. T. Stanback, [Shared parentage and incest avoidance in the](#)
1209 [cooperatively breeding acorn woodpecker](#). *Molecular Ecology* **10**, 1515–1525 (2001).
- 1210 278. L. Heer, Cooperative breeding by alpine accentors *Prunella collaris*: Polygynandry,
1211 territoriality and multiple paternity. *Journal fur Ornithologie* **137**, 35–51 (1996).
- 1212 279. D. Heg, R. van Treuren, [Female–female cooperation in polygynous oystercatchers](#).
1213 *Nature* **391**, 687–691 (1998).
- 1214 280. R. Heinsohn, S. Legge, [Breeding biology of the reverse-dichromatic, co-operative parrot](#)
1215 [*Eclectus roratus*](#). *Journal of Zoology* **259**, 197–208 (2003).
- 1216 281. R. Heinsohn, P. Dunn, S. Legge, M. Double, [Coalitions of relatives and reproductive](#)
1217 [skew in cooperatively breeding white-winged choughs](#). *Proceedings of the Royal Society of*
1218 *London. Series B: Biological Sciences* **267**, 243–249 (2000).
- 1219 282. R. Heinsohn, D. Ebert, S. Legge, R. Peakall, [Genetic evidence for cooperative polyandry](#)
1220 [in reverse dichromatic *Eclectus* parrots](#). *Animal Behaviour* **74**, 1047–1054 (2007).
- 1221 283. R. Heredia, JoséA. Donázar, [High frequency of polyandrous trios in an endangered](#)
1222 [population of lammergeiers *Gypaetus barbatus* in Northern Spain](#). *Biological Conservation* **53**,
1223 163–171 (1990).
- 1224 284. N. Hidalgo Aranzamendi, M. L. Hall, S. A. Kingma, P. Sunnucks, A. Peters, [Incest](#)
1225 [avoidance, extrapair paternity, and territory quality drive divorce in a year-round territorial bird](#).
1226 *Behavioral Ecology* **27**, 1808–1819 (2016).
- 1227 285. P. Higgins, L. Christidis, H. Ford, Bell Miner (*Manorina melanophrys*) (2020).
- 1228 286. P. Higgins, L. Christidis, H. Ford, Black-eared Miner (*Manorina melanotis*) (2020).
- 1229 287. P. Higgins, J. Peter, *Handbook of Australian, New Zealand and Antarctic Birds. Volume*
1230 *6. Pardalotes to Figbird* (Oxford University Press: Melbourne, 2002).
- 1231 288. P. Higgins, J. Peter, W. Steele, *Handbook of Australian, New Zealand and Antarctic*
1232 *Birds. Volume 5: Tyrant-flycatchers to Chats* (Oxford University Press: Melbourne, 2001).

- 1233 289. P. Higgins, J. Peter, *Handbook of Australian, New Zealand and Antarctic Birds. Volume*
1234 *6. Pardalotes to Figbird* (Oxford University Press: Melbourne, 2002).
- 1235 290. P. Hockey, G. Kirwan, P. Boesman, Eurasian Oystercatcher (*Haematopus ostralegus*)
1236 (2020).
- 1237 291. R. T. Holmes, B. D. Frauenknecht, M. A. Du Pleiss, Breeding System of the Cape
1238 Rockjumper, a South African Fynbos Endemic. *The Condor* **104**, 188–192 (2002).
- 1239 292. P. L. Horn, J. A. Rafalski, P. J. Whitehead, [Molecular Genetic \(RAPD\) Analysis of](#)
1240 [Breeding Magpie Geese](#). *The Auk* **113**, 552–557 (1996).
- 1241 293. C. L. Horning, M. Hutchins, W. English, [Breeding and management of the common](#)
1242 [trumpeter \(*Psophia crepitans*\)](#). *Zoo Biology* **7**, 193–210 (1988).
- 1243 294. J. Huang, J. Liu, G. Li, H. Yan, S. Li, [Breeding biology and mating system of Brown](#)
1244 [Accentors *Prunella fulvescens* on the Tibet Plateau](#). *Bird study : the journal of the British Trust*
1245 *for Ornithology* **67**, 232–238 (2020).
- 1246 295. L. A. Hunter, [Cooperative breeding in purple gallinules: The role of helpers in feeding](#)
1247 [chicks](#). *Behavioral Ecology and Sociobiology* **20**, 171–177 (1987).
- 1248 296. L. A. Hunter, [The effects of helpers in cooperatively breeding purple gallinules](#).
1249 *Behavioral Ecology and Sociobiology* **18**, 147–153 (1985).
- 1250 297. A. C. Jacobs, J. M. Fair, M. Zuk, [Coloration, Paternity, and Assortative Mating in](#)
1251 [Western Bluebirds](#). *Ethology : formerly Zeitschrift für Tierpsychologie* **121**, 176–186 (2015).
- 1252 298. I. Jamieson, J. Quinn, P. Rose, B. White, Shared paternity among non-relatives is a result
1253 of an egalitarian mating system in a communally breeding bird, the pukeko. *Proceedings:*
1254 *Biological Sciences* **257**, 271–277 (1994).
- 1255 299. I. G. Jamieson, [Testing reproductive skew models in a communally breeding bird, the](#)
1256 [pukeko, *Porphyrio porphyrio*](#). *Proceedings of the Royal Society of London. Series B: Biological*
1257 *Sciences* **264**, 335–340 (1997).
- 1258 300. A. Jaramillo, D. Christie, Common Cactus-Finch (*Geospiza scandens*) (2020).

- 1259 301. A. E. Johnson, S. Pruett-Jones, [Reproductive promiscuity in the variegated fairy-wren: An](#)
1260 [alternative reproductive strategy in the absence of helpers?](#) *Animal Behaviour* **139**, 171–180
1261 (2018).
- 1262 302. P. et al Jones, Behaviour, natural history, and annual cycle of the Henderson Island rail
1263 Porzana atra (Aves: Rallidae). *Biological Journal of the Linnean Society* **56**, 167–183 (1995).
- 1264 303. M. Jones, Brown Jay (*Psilorhinus morio*) (2020).
- 1265 304. C. Jones, C. Lessells, J. Krebs, “Helpers-at-the-nest in European Bee-eaters (*Merops*
1266 *apiaster*): A Genetic Analysis” in *DNA Fingerprinting: Approaches and Applications* (Birkhäuser
1267 Basel, 1991)vol. 58.
- 1268 305. S. A. Kaiser, T. E. Martin, J. C. Oteyza, J. E. Danner, C. E. Armstad, R. C. Fleischer,
1269 [Within-group relatedness and patterns of reproductive sharing and cooperation in the tropical](#)
1270 [chestnut-crested yuhina.](#) *Animal Behaviour* **158**, 89–99 (2019).
- 1271 306. M. Kaspari, H. O’Leary, Nonparental Attendants in a North-temperate Migrant. *The Auk*
1272 **105**, 792–793 (1988).
- 1273 307. A. K. Kepler, *Comparative Study of Todies (Todidae), with Emphasis on the Puerto Rican*
1274 *Tody, Todus Mexicanus* (Nuttall Ornithological Club, Cambridge, MA, 1977).
- 1275 308. K. Kepler, G. Kirwan, “Puerto Rican Tody (*Todus mexicanus*)” in *Handbook of the Birds*
1276 *of the World Alive.* (Lynx Edicions, Barcelona, 2017).
- 1277 309. A. Keyser, M. Keyser, D. Promislow, Life-history variation and demography in western
1278 bluebirds (*Sialia mexicana*) in Oregon. *The Auk* **121**, 118–133 (2004).
- 1279 310. R. A. Kiltie, J. W. Fitzpatrick, [Reproduction and Social Organization of the Black-](#)
1280 [Capped Donacobius \(*Donacobius atricapillus*\) in Southeastern Peru.](#) *The Auk* **101**, 804–811
1281 (1984).
- 1282 311. H. Kingery, C. Ghalambor, Pygmy Nuthatch (*Sitta pygmaea*) (2020).
- 1283 312. S. A. Kingma, M. L. Hall, A. Peters, [Multiple Benefits Drive Helping Behavior in a](#)
1284 [Cooperatively Breeding Bird: An Integrated Analysis.](#) *The American Naturalist* **177**, 486–495
1285 (2011).

- 1286 313. S. A. Kingma, M. L. Hall, G. Segelbacher, A. Peters, Radical loss of an extreme extra-
1287 pair mating system. *BMC Ecology* **9**, 15 (2009).
- 1288 314. S. A. Kingma, M. L. Hall, A. Peters, [Sperm storage reflects within- and extra-pair mating](#)
1289 [opportunities in a cooperatively breeding bird](#). *Behavioral Ecology and Sociobiology* **66**, 1115–
1290 1123 (2012).
- 1291 315. S. A. Kingma, K. Bebbington, M. Hammers, D. S. Richardson, J. Komdeur, [Delayed](#)
1292 [dispersal and the costs and benefits of different routes to independent breeding in a cooperatively](#)
1293 [breeding bird](#). *Evolution* **70**, 2595–2610 (2016).
- 1294 316. N. Klauke, J. Jansen, J. Kramer, H. M. Schaefer, [Food allocation rules vary with age and](#)
1295 [experience in a cooperatively breeding parrot](#). *Behavioral Ecology and Sociobiology* **68**, 1037–
1296 1047 (2014).
- 1297 317. N. Klauke, G. Segelbacher, H. M. Schaefer, [Reproductive success depends on the quality](#)
1298 [of helpers in the endangered, cooperative El Oro parakeet \(*Pyrrhura orcesi* \)](#). *Molecular Ecology*
1299 **22**, 2011–2027 (2013).
- 1300 318. W. Koenig, E. Walters, P. Stacey, M. Stanback, R. Mumme, Acorn Woodpecker
1301 (*Melanerpes formicivorus*) (2020).
- 1302 319. W. D. Koenig, R. L. Mumme, M. T. Stanback, F. A. Pitelka, [Patterns and consequences](#)
1303 [of egg destruction among joint-nesting acorn woodpeckers](#). *Animal Behaviour* **50**, 607–621
1304 (1995).
- 1305 320. W. Koenig, R. Mumme, *Population Ecology of the Cooperatively Breeding Acorn*
1306 *Woodpecker* (Princeton University Press, 1987).
- 1307 321. D. R. Rubenstein, W. Koenig, J. Dickinson, “[Superb starlings: Cooperation and conflict](#)
1308 [in an unpredictable environment](#)” in *Cooperative Breeding in Vertebrates*, W. D. Koenig, J. L.
1309 Dickinson, Eds. (Cambridge University Press, ed. 1, 2016), pp. 181–196.
- 1310 322. S.-F. Shen, H.-W. Yuan, M. Liu, “[Taiwan yuhinas: Unrelated joint-nesters cooperate in](#)
1311 [unfavorable environments](#)” in *Cooperative Breeding in Vertebrates*, W. D. Koenig, J. L.
1312 Dickinson, Eds. (Cambridge University Press, Cambridge, 2016), pp. 237–256.
- 1313 323. J. Komdeur, Experimental evidence for helping and hindering by previous offspring in the
1314 cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*. *Behavioral Ecology and*
1315 *Sociobiology* **34**, 175–186 (1994).

- 1316 324. C. O. Kreckorian, Alloparental Care in the Purple Gallinule. *The Condor* **80**, 382–390
1317 (1978).
- 1318 325. A. Krištín, A. Kirwan, Eurasian Hoopoe (*Upupa epops*) (2020).
- 1319 326. D. Kroodsma, D. Brewer, “Family Troglodytidae (Wrens)” in *Handbook of the Birds of*
1320 *the World. Vol. 10. Cuckoo-shrikes to Thrushes* (Lynx edicions: Barcelona, 2005), pp. 356–447.
- 1321 327. D. Kroodsma, D. Brewer, Fasciated Wren (*Campylorhynchus fasciatus*) (2020).
- 1322 328. D. Kroodsma, D. Brewere, Stripe-backed Wren (*Campylorhynchus nuchalis*) (2020).
- 1323 329. T. Laranjeiras, Golden Parakeet (*Guaruba guarouba*) (2020).
- 1324 330. N. LeFranc, T. Worfolk, *Shrikes: A Guide to Shrikes of the World* (Pica Press: Sussex,
1325 1997).
- 1326 331. S. Legge, S. Legge, R. Heinsohn, R. Heinsohn, [Kingfishers in paradise: The breeding](#)
1327 [biology of *Tanysiptera sylvia* at the Iron Range National Park, Cape York](#). *Australian Journal of*
1328 *Zoology* **49**, 85 (2001).
- 1329 332. S. Legge, A. Cockburn, [Social and mating system of cooperatively breeding laughing](#)
1330 [kookaburras \(*Dacelo novaeguineae* \)](#). *Behavioral Ecology and Sociobiology* **47**, 220–229 (2000).
- 1331 333. A. V. Leitão, M. L. Hall, B. Venables, R. A. Mulder, [Ecology and breeding biology of a](#)
1332 [tropical bird, the Lovely Fairy-Wren \(*Malurus amabilis* \)](#). *Emu - Austral Ornithology* **119**, 1–13
1333 (2019).
- 1334 334. C. Lessells, “Helping at the nest in European bee-eaters: Who helps and why?” in
1335 *Population Biology of Passerine Birds: An Integrated Approach* (Berlin, Heidelberg: Springer
1336 Berlin Heidelberg, 1990), pp. 357–368.
- 1337 335. D. M. Lewis, [Cooperative Breeding in a Population of Whitebrowed Sparrow Weavers](#)
1338 [Plocepasser Mahali](#). *Ibis* **124**, 511–522 (1982).
- 1339 336. J. Li, L. Lv, Y. Wang, B. Xi, Z. Zhang, [Breeding biology of two sympatric *Aegithalos* tits](#)
1340 [with helpers at the nest](#). *Journal of Ornithology* **153**, 273–283 (2012).
- 1341 337. J. Li, Y. Wang, L. Lv, P. Wang, B. J. Hatchwell, Z. Zhang, [Context-dependent strategies](#)
1342 [of food allocation among offspring in a facultative cooperative breeder](#). *Behavioral Ecology* **30**,
1343 975–985 (2019).

- 1344 338. J. Li, Y. Liu, Y. Wang, Z. Zhang, [Extra-pair paternity in two sympatric Aegithalos tits: Patterns and implications](#). *Journal of Ornithology* **155**, 83–90 (2014).
- 1345
- 1346 339. S.-H. Li, J. L. Brown, [High frequency of extrapair fertilization in a plural breeding bird, the Mexican jay, revealed by DNA microsatellites](#). *Animal Behaviour* **60**, 867–877 (2000).
- 1347
- 1348 340. J. Li, Z. Zhang, L. Lv, C. Gao, Y. Wang, [Do Parents and Helpers Discriminate between Related and Unrelated Nestlings in the Cooperative Breeding Silver-Throated Tit? Ethology : formerly Zeitschrift für Tierpsychologie](#) **120**, 159–168 (2014).
- 1349
- 1350
- 1351 341. J. D. Ligon, S. H. Ligon, [Communal breeding in green woodhoopoes as a case for reciprocity](#). *Nature* **276**, 496–498 (1978).
- 1352
- 1353 342. J. Ligon, S. Ligon, “Green Woodhoopoes: Life history traits and sociality” in *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Cambridge: Cambridge University Press, 1990).
- 1354
- 1355
- 1356 343. J. Ligon, G. Kirwan, Green Woodhoopoe (*Phoeniculus purpureus*) (2020).
- 1357
- 1358 344. M. R. Lima, R. H. Macedo, L. Muniz, A. Pacheco, J. A. Graves, [Group Composition, Mating System, and Relatedness in the Communally Breeding Guira Cuckoo \(*Guira guira* \) in Central Brazil](#). *The Auk* **128**, 475–486 (2011).
- 1359
- 1360 345. I. Lippke von, “Ecology and evolution of cooperation in the Española mockingbird, *Nesomimus macdonaldi*, Galápagos - ProQuest,” thesis, University of California, Los Angeles (2008).
- 1361
- 1362
- 1363 346. Q. Liu, B. Wang, Y. Xu, X. Zhang, T. Zeng, J. Ran, [Characterization of Cooperative Breeding for the Buff-throated Partridge \(*Tetraophasis szechenyii*\) Based on Parentage Testing](#). *Pakistan Journal of Zoology* **53** (2021).
- 1364
- 1365
- 1366 347. P. Lloyd, W. Andrew Taylor, M. A. Du Plessis, T. E. Martin, [Females increase reproductive investment in response to helper-mediated improvements in allo-feeding, nest survival, nestling provisioning and post-fledging survival in the Karoo scrub-robin *Cercotrichas coryphaeus*](#). *Journal of Avian Biology* **40**, 400–411 (2009).
- 1367
- 1368
- 1369
- 1370 348. P. Lowther, R. Fraga, E. Garcia, Grayish Baywing (*Agelaioides badius*) (2020).
- 1371
- 1372 349. G. W. Luck, [The demography and cooperative breeding behaviour of the rufous treecreeper, *Climacteris rufa*](#). *Australian Journal of Zoology* **49**, 515 (2001).

- 1373 350. K. J. Lundy, P. G. Parker, A. Zahavi, [Reproduction by subordinates in cooperatively](#)
1374 [breeding Arabian babblers is uncommon but predictable](#). *Behavioral Ecology and Sociobiology*
1375 **43**, 173–180 (1998).
- 1376 351. R. Macedo, “Guira cuckoos: Cooperation, infanticide, and female reproductive
1377 investment in a joint-nesting species.” in *Cooperative Breeding in Vertebrates* (Cambridge:
1378 Cambridge University Press, 2016), pp. 257–27.
- 1379 352. S. Madge, Carrion Crow (*Corvus corone*) (2020).
- 1380 353. S. Madge, Taiwan Blue-Magpie (*Urocissa caerulea*) (2020).
- 1381 354. R. D. Magrath, L. A. Whittingham, [Subordinate males are more likely to help if unrelated](#)
1382 [to the breeding female in cooperatively breeding white-browed scrubwrens](#). *Behavioral Ecology*
1383 *and Sociobiology* **41**, 185–192 (1997).
- 1384 355. G. Maguire, “Behavioural Ecology of the Southern Emu-wren (*Stipiturus malachurus*),”
1385 thesis, University of Melbourne, Australia (2005).
- 1386 356. G. S. Maguire, R. A. Mulder, [Breeding biology and demography of the southern emu-](#)
1387 [wren \(*Stipiturus malachurus*\)](#). *Australian Journal of Zoology* **52**, 583 (2004).
- 1388 357. G. S. Maguire, R. A. Mulder, [Low levels of extra-pair paternity in southern emu-wrens](#)
1389 [\(*Aves : Maluridae*\)](#). *Australian Journal of Zoology* **56**, 79 (2008).
- 1390 358. G. Malan, T. M. Crowe, R. Biggs, J. J. Herholdt, [The social system of the Pale Chanting](#)
1391 [Goshawk *Melierax canorus*: monogamy v polyandry and delayed dispersal](#). *Ibis* **139**, 313–321
1392 (1997).
- 1393 359. G. Malan, A. R. Jenkins, [Territory and nest defence in polyandrous pale chanting](#)
1394 [goshawks: Do co-breeders Help?](#) *South African Journal of Zoology* **31**, 170–176 (1996).
- 1395 360. J. R. Malcolm, K. Marten, [Natural selection and the communal rearing of pups in African](#)
1396 [wild dogs \(*Lycaon pictus*\)](#). *Behavioral Ecology and Sociobiology* **10**, 1–13 (1982).
- 1397 361. L. T. Manica, M. Â. Marini, [Helpers at the nest of White-banded Tanager *Neothraupis*](#)
1398 [fasciata benefit male breeders but do not increase reproductive success](#). *Journal of Ornithology*
1399 **153**, 149–159 (2012).

- 1400 362. S. Marchant, P. Higgins, *Handbook of Australian, New Zealand and Antarctic Birds, Vol.*
1401 *I. Parts A and B* (Oxford University Press, Melbourne, 1990).
- 1402 363. M. Martín-Vivaldi, J. G. Martínez, J. J. Palomino, M. Soler, Extrapair paternity in the
1403 Hoopoe *Upupa epops*: An exploration of the influence of interactions between breeding pairs,
1404 non-pair males and strophe length. *Ibis* **144**, 236–247 (2002).
- 1405 364. J. Marzluff, R. Balda, “Pinyon Jays: Making the best of a bad situation by helping” in
1406 *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Cambridge:
1407 Cambridge University Press, 1990), pp. 189–237.
- 1408 365. J. Marzluff, R. Balda, *The Pinyon Jay: Behavioral Ecology of a Colonial and*
1409 *Cooperative Corvid* (London, T & AD Poyser Ltd, 1992).
- 1410 366. J. McCormack, J. Brown, Mexican Jay (*Aphelocoma wollweberi*) (2020).
- 1411 367. P. McGowan, G. Kirwan, E. de Juana, Buff-throated Monal-Partridge (*Tetraophasis*
1412 *szechenyii*) (2020).
- 1413 368. I. McLean, B. Gill, Breeding of an Island-endemic Bird: The New Zealand Whitehead
1414 *Mohoua albicilla*; Pachycephalinae. *Emu - Austral Ornithology* **88**, 177–182 (1988).
- 1415 369. S. B. McRAE, [Family values: Costs and benefits of communal nesting in the moorhen.](#)
1416 *Animal Behaviour* **52**, 225–245 (1996).
- 1417 370. S. B. McRae, T. Burke, [Intraspecific brood parasitism in the moorhen: Parentage and](#)
1418 [parasite-host relationships determined by DNA fingerprinting.](#) *Behavioral Ecology and*
1419 *Sociobiology* **38**, 115–129 (1996).
- 1420 371. M. E. Mermoz, C. Villarruel, A. de la Colina, B. Mahler, [Fledgling sex-ratio is biased](#)
1421 [towards the helping sex in a Neotropical cooperative breeder, the brown-and-yellow marshbird](#)
1422 [\(*Pseudoleistes virescens*\).](#) *Behaviour* **158**, 135–160 (2021).
- 1423 372. M. E. Mermoz, J. C. Reboreda, [Nesting Success in Brown-and-Yellow Marshbirds:](#)
1424 [Effects of Timing, Nest Site, and Brood Parasitism.](#) *The Auk* **115**, 871–878 (1998).
- 1425 373. M. Merola, Fruit in the Diet of Nestlings of the Puerto Rican Tody, a Tropical
1426 Insectivore. *The Wilson Bulletin* **107**, 181–182 (1995).

- 1427 374. C. D. Millar, I. Anthony, D. M. Lambert, P. M. Stapleton, C. C. Bergmann, A. R.
 1428 Bellamy, E. C. Young, [Patterns of reproductive success determined by DNA fingerprinting in a](#)
 1429 [communally breeding oceanic bird](#). *Biological Journal of the Linnean Society* **52**, 31–48 (1994).
- 1430 375. E. S. Morton, B. J. M. Stutchbury, W. H. Piper, COOPERATIVE BREEDING IN THE
 1431 TROPICAL MOCKINGBIRD (MIMUS GILVUS) IN THE PANAMA CANAL ZONE.
 1432 *Ornitología Neotropical* **15**, 417–421 (2004).
- 1433 376. R. A. Mulder, P. O. Dunn, A. Cockburn, K. A. Lazenby-Cohen, M. J. Howell, [Helpers](#)
 1434 [liberate female fairy-wrens from constraints on extra-pair mate choice](#). *Proceedings of the Royal*
 1435 *Society of London. Series B: Biological Sciences* **255**, 223–229 (1994).
- 1436 377. A. Müllner, “Breeding Ecology and Related Life-History Traits of the Hoatzin,
 1437 *Opisthocomus hoazin*, in a Primary Rainforest Habitat,” thesis, Bayerischen Julius-Maximilians-
 1438 Universität Würzburg, Würzburg, Germany (2004).
- 1439 378. P. J. Mundy, A. W. Cook, [Observations of the Yellow-Billed Oxpecker *Buphagus*](#)
 1440 [Africanus in Northern Nigeria](#). *Ibis* **117**, 504–506 (1975).
- 1441 379. M. J. Nelson-Flower, P. A. R. Hockey, C. O’Ryan, N. J. Raihani, M. A. du Plessis, A. R.
 1442 Ridley, [Monogamous dominant pairs monopolize reproduction in the cooperatively breeding pied](#)
 1443 [babblers](#). *Behavioral Ecology* **22**, 559–565 (2011).
- 1444 380. M. J. Nelson-Flower, A. R. Ridley, [Nepotism and subordinate tenure in a cooperative](#)
 1445 [breeder](#). *Biology Letters* **12**, 20160365 (2016).
- 1446 381. R. A. Noske, Black-tailed Treecreeper (*Climacteris melanurus*) (2020).
- 1447 382. R. A. Noske, [Cooperative Breeding by Treecreepers](#). *Emu - Austral Ornithology* **80**, 35–
 1448 36 (1980).
- 1449 383. R. A. Noske, A Demographic Comparison of Cooperatively Breeding and Non-
 1450 Cooperative Treecreepers (*Climacteridae*). *The Emu* **91**, 73–86 (1991).
- 1451 384. R. A. Noske, “Family Climacteridae (Australasian treecreepers)” in *Handbook of the*
 1452 *Birds of the World Vol 12: Picathartes to Tits and Chickadees* (Lynx Edicions, Barcelona, Spain,
 1453 2007), pp. 642–660.
- 1454 385. D. Ocampo, M. C. Estrada-F, J. M. Muñoz, L. V. Londoño, S. David, G. Valencia, P. A.
 1455 Morales, J. A. Garizábal, A. M. Cuervo, [Breeding Biology of the Red-Bellied Grackle](#)

- 1456 [\(Hypopyrrhus pyrohypogaster\): A Cooperative Breeder of the Colombian Andes](#). *The Wilson*
1457 *Journal of Ornithology* **124**, 538–546 (2012).
- 1458 386. S. Oppenheimer, “Endocrine correlates of social and reproductive behaviours in a group-
1459 living Australian passerine, the white-browed babbler,” thesis, University of Wollongong,
1460 Wollongong, New South Wales, Australia. (2005).
- 1461 387. D. C. Oren, F. C. Novaes, Observations on the Golden Parakeet *Arathga guarouba* in
1462 Northern Brazil. *Biological Conservation* **36**, 329–337 (1986).
- 1463 388. G. Orians, C. Orians, K. Orians, “Helpers at the nest in some Argentine blackbirds” in
1464 *Evolutionary Ecology* (University Park Press, Baltimore, MD, 1977), pp. 137–151.
- 1465 389. L. Patch-Highfill, “Estimating genetic diversity of Palila (*Loxioides bailleui*) and familial
1466 relationships of helper males,” thesis, University of Hawai’i at Hilo, Hawai’i (2008).
- 1467 390. K. Petren, B. R. Grant, P. R. Grant, Low Extrapair Paternity in the Cactus Finch
1468 (*Geospiza scandens*). *The Auk* **116**, 252–256 (1999).
- 1469 391. A. J. Pierce, K. Tokue, K. Pobprasert, W. Sankamethawee, Cooperative breeding in the
1470 puff-throated bulbul *Alophoixus pallidus* in Thailand. *Raff Bull Zool* **55**, 187–189 (2007).
- 1471 392. A. Potter, Gray-winged Trumpeter (*Psophia crepitans*) (2020).
- 1472 393. L. Power, C. Ghalambor, Purplish-backed Jay (*Cyanocorax beecheii*) (2020).
- 1473 394. S. A. J. Preston, J. V. Briskie, T. Burke, B. J. Hatchwell, [Genetic analysis reveals diverse](#)
1474 [kin-directed routes to helping in the rifleman *Acanthisitta chloris*](#). *Molecular Ecology* **22**, 5027–
1475 5039 (2013).
- 1476 395. T. Price, S. Millington, P. Grant, Helping at the Nest in Darwin’s Finches as Misdirected
1477 Parental Care. *The Auk* **100**, 192–194 (1983).
- 1478 396. D. Putland, W. Goldizen, Juvenile helping behaviour in the Dusky Moorhen, *Gallinula*
1479 *tenebrosa*. *The Emu* **101**, 265–267 (2001).
- 1480 397. S. Pywell, A. Lill, Breeding biology of the dusky moorhen in a suburban park. *Corella*
1481 **27**, 24–30 (2003).

- 1482 398. J. S. Quinn, G. E. Woolfenden, J. W. Fitzpatrick, B. N. White, Multi-locus DNA
1483 fingerprinting supports genetic monogamy in Florida scrub-jays. *Behavioral Ecology and*
1484 *Sociobiology* **45**, 1–10 (1999).
- 1485 399. K. Rabenold, “Campylorhynchus wrens: The ecology of delayed dispersal and
1486 cooperation in the Venezuelan savanna” in *Cooperative Breeding in Birds: Long-term Studies of*
1487 *Ecology and Behavior* (Cambridge: Cambridge University Press, 1990).
- 1488 400. K. N. Rabenold, [Cooperation in breeding by nonreproductive wrens: Kinship, reciprocity,](#)
1489 [and demography](#). *Behavioral Ecology and Sociobiology* **17**, 1–17 (1985).
- 1490 401. K. N. Rabenold, [Cooperative Enhancement Of Reproductive Success in Tropical Wren](#)
1491 [Societies](#). *Ecology* **65**, 871–885 (1984).
- 1492 402. K. N. Rabenold, S. N. Austad, Demography and the evolution of cooperative breeding in
1493 the bicolored wren, *Campylorhynchus griseus*. *Behaviour* **97**, 308–324 (1986).
- 1494 403. P. P. Rabenold, K. N. Rabenold, W. H. Piper, J. Haydock, S. W. Zack, [Shared paternity](#)
1495 [revealed by genetic analysis in cooperatively breeding tropical wrens](#). *Nature* **348**, 538–540
1496 (1990).
- 1497 404. J. Radford, “Conservation ecology and breeding biology of the White-browed
1498 Treecreeper *Climacteris affinis*,” thesis, University of Melbourne, Australia (2002).
- 1499 405. J. Ragusa-Netto, Nestling development, size and juvenile survival in *Donacobius*
1500 *atricapillus* (Passeriformes: Troglodytidae. *Ararajuba* **4**, 81–85 (1996).
- 1501 406. R. J. Raitt, S. R. Winterstein, J. W. Hardy, Structure and Dynamics of Communal Groups
1502 in the Beechey Jay. *The Wilson Bulletin* **96**, 206–227 (1984).
- 1503 407. S. Raj Pant, J. Komdeur, T. A. Burke, H. L. Dugdale, D. S. Richardson, [Socio-ecological](#)
1504 [conditions and female infidelity in the Seychelles warbler](#). *Behavioral Ecology* **30**, 1254–1264
1505 (2019).
- 1506 408. M. K. Rathburn, R. Montgomerie, [Breeding biology and social structure of White-winged](#)
1507 [Fairy-wrens \(*Malurus leucopterus* \): Comparison between island and mainland subspecies](#)
1508 [having different plumage phenotypes](#). *Emu - Austral Ornithology* **103**, 295–306 (2003).
- 1509 409. C. Restrepo, [Cooperative Breeding in the Frugivorous Toucan Barbet \(*Semnornis*](#)
1510 [ramphastinus](#)). *The Auk* **115**, 4–15 (1998).

- 1511 410. H.-U. Reyer, [Flexible helper structure as an ecological adaptation in the pied kingfisher](#)
1512 [\(*Ceryle rudis rudis* L.\)](#). *Behavioral Ecology and Sociobiology* **6**, 219–227 (1980).
- 1513 411. G. Reynolds, Golden Conure research will aid its survival. *PsittaScene* **15**, 10–13 (2003).
- 1514 412. J. F. Reynolds, Notes on birds observed in the vicinity of Tabora, Tanzania with special
1515 reference to breeding data. *Journal of East African Natural History*, 117–139 (1968).
- 1516 413. Â. M. Ribeiro, P. Lloyd, K. A. Feldheim, R. C. K. Bowie, [Microgeographic socio-genetic](#)
1517 [structure of an African cooperative breeding passerine revealed: Integrating behavioural and](#)
1518 [genetic data: Asymmetric dispersal in a cooperative breeding bird](#). *Molecular Ecology* **21**, 662–
1519 672 (2012).
- 1520 414. B. A. Ribeiro, L. A. Carrara, F. R. Santos, M. Rodrigues, Sex-biased help and possible
1521 facultative control over offspring sex ratio in the Rufous-fronted Thornbird, *Phacellodomus*
1522 *rufifrons*. *Revista Brasileira de Ornitologia* **15**, 561–568 (2007).
- 1523 415. D. S. Richardson, T. Burke, J. Komdeur, [Direct Benefits and the Evolution of Female-](#)
1524 [Biased Cooperative Breeding in Seychelles Warblers](#). *Evolution; international journal of organic*
1525 *evolution* **56**, 2313–2321 (2002).
- 1526 416. D. S. Richardson, F. L. Jury, K. Blaakmeer, J. Komdeur, T. Burke, [Parentage assignment](#)
1527 [and extra-group paternity in a cooperative breeder: The Seychelles warbler \(*Acrocephalus*](#)
1528 [sechellensis\)](#). *Molecular Ecology* **10**, 2263–2273 (2001).
- 1529 417. A. R. Ridley, N. J. Raihani, [Task partitioning increases reproductive output in a](#)
1530 [cooperative bird](#). *Behavioral Ecology* **19**, 1136–1142 (2008).
- 1531 418. C. Riehl, [Egg ejection risk and hatching asynchrony predict egg mass in a communally](#)
1532 [breeding cuckoo, the Greater Ani \(*Crotophaga major*\)](#). *Behavioral Ecology* **21**, 676–683 (2010).
- 1533 419. C. Riehl, [Mating system and reproductive skew in a communally breeding cuckoo: Hard-](#)
1534 [working males do not sire more young](#). *Animal Behaviour* **84**, 707–714 (2012).
- 1535 420. C. Riehl, L. Jara, [Natural History and Reproductive Biology of the Communally Breeding](#)
1536 [Greater Ani \(*Crotophaga major*\) at Gatún Lake, Panama](#). *The Wilson Journal of Ornithology* **121**,
1537 679–687 (2009).

- 1538 421. J. K. Robertson, J. R. Caldwell, L. A. Grieves, A. Samuelsen, G. S. Schmaltz, J. S. Quinn,
 1539 [Male parental effort predicts reproductive contribution in the joint-nesting, Smooth-billed Ani](#)
 1540 [\(Crotophaga ani\)](#). *Journal of Ornithology* **159**, 471–481 (2018).
- 1541 422. M. Rodrigues, L. Carrara, Co-operative breeding in the rufous-fronted thornbird
 1542 Phacellodomus rufifrons: A Neotropical ovenbird. *Ibis* **146**, 351–354 (2004).
- 1543 423. I. Rowley, E. Russell, Apostlebird (Struthidea cinerea) (2020).
- 1544 424. I. Rowley, “Co-operative breeding in Australian birds” in *Proceedings of the 16th*
 1545 *International Ornithological Congress* (Australian Academy of Science: Canberra, 1976), pp.
 1546 657–666.
- 1547 425. I. Rowley, Co-operative breeding by black-faced woodswallows. *Corella* **23**, 63–66
 1548 (1999).
- 1549 426. I. Rowley, [Communal Activities Among White-Winged Choughs Corcorax](#)
 1550 [Melanorhamphus](#). *Ibis* **120**, 178–197 (1978).
- 1551 427. I. Rowley, Cooperative breeding by dusky woodswallows. *Canberra Bird Notes* **25**, 49–
 1552 58 (2000).
- 1553 428. I. Rowley, E. Russell, Emperor Fairywren (Malurus cyanocephalus) (2020).
- 1554 429. I. Rowley, E. Russell, *Fairy-Wrens and Grasswrens: Maluridae* (Oxford University
 1555 Press: Oxford, 1997).
- 1556 430. I. Rowley, Nesting by black-faced woodswallows Artamus cinereus. *Corella*, 65–69
 1557 (2002).
- 1558 431. I. Rowley, E. Russell, [A population study of the Blue-breasted Fairy-wren, Malurus](#)
 1559 [pulcherrimus](#), at Dryandra, Western Australia. *Emu - Austral Ornithology* **102**, 127–135 (2002).
- 1560 432. I. Rowley, E. Russell, Red-winged Fairywren (Malurus elegans) (2020).
- 1561 433. I. Rowley, E. Russell, Splendid Fairywren (Malurus splendens) (2020).
- 1562 434. I. Rowley, E. Russell, Variegated Fairywren (Malurus lamberti) (2020).
- 1563 435. I. Rowley, E. Russell, White-shouldered Fairywren (Malurus alboscapulatus) (2020).
- 1564 436. I. Rowley, E. Russell, White-winged Chough (Corcorax melanorhamphos) (2020).

- 1565 437. D. R. Rubenstein, [Female extrapair mate choice in a cooperative breeder: Trading sex for](#)
1566 [help and increasing offspring heterozygosity](#). *Proceedings of the Royal Society B: Biological*
1567 *Sciences* **274**, 1895–1903 (2007).
- 1568 438. E. Russell, I. Rowley, D. Christie, Australian Magpie (*Gymnorhina tibicen*) (2020).
- 1569 439. E. Russell, I. Rowley, [Demography and social organisation of the red-winged fairy-wren,](#)
1570 [Malurus elegans](#). *Australian Journal of Zoology* **48**, 161–200 (2000).
- 1571 440. A. F. Russell, B. J. Hatchwell, [Experimental evidence for kin-biased helping in a](#)
1572 [cooperatively breeding vertebrate](#). *Proceedings of the Royal Society of London. Series B:*
1573 *Biological Sciences* **268**, 2169–2174 (2001).
- 1574 441. E. Russell, I. Rowley, Helper contributions to reproductive success in the splendid fairy-
1575 wren (*MMurus splendens*). *Behavioral Ecology and Sociobiology* **22**, 131–140 (1988).
- 1576 442. E. M. Russell, the late R. J. Brown, M. N. Brown, [Life history of the white-breasted](#)
1577 [robin, Eopsaltria georgiana \(Petroicidae\), in south-western Australia](#). *Australian Journal of*
1578 *Zoology* **52**, 111 (2004).
- 1579 443. E. Russell, I. Rowley, Pied Butcherbird (*Cracticus nigrogularis*) (2020).
- 1580 444. D. Saito, I. Nishiumi, M. Nakamura, [Characterization of nine polymorphic microsatellite](#)
1581 [loci from the alpine accentor Prunella collaris](#). *Molecular Ecology Notes* **1**, 258–259 (2001).
- 1582 445. W. Sankamethawee, B. D. Hardesty, G. A. Gale, [Sex-bias and timing of natal dispersal in](#)
1583 [cooperatively breeding Puff-throated Bulbuls Alophoixus pallidus](#). *Journal of Ornithology* **151**,
1584 779–789 (2010).
- 1585 446. L. R. D. Santos, “Biologia reprodutiva e comportamento cooperativo em ninhos de
1586 *Cypsnagra hirundinacea*,” (2008).
- 1587 447. E. S. A. Santos, L. L. S. Santos, M. Lagisz, S. Nakagawa, [Conflict and cooperation over](#)
1588 [sex: The consequences of social and genetic polyandry for reproductive success in dunnocks](#).
1589 *Journal of Animal Ecology* **84**, 1509–1519 (2015).
- 1590 448. V. Saracura, R. H. Macedo, D. Blomqvist, [GENETIC PARENTAGE AND VARIABLE](#)
1591 [SOCIAL STRUCTURE IN BREEDING SOUTHERN LAPWINGS](#). *The Condor* **110**, 554–558
1592 (2008).

- 1593 449. N. Seddon, J. A. Tobias, S. H. M. Butchart, [Group living, breeding behaviour and](#)
1594 [territoriality in the Subdesert Mesite *Monias benschi*](#). *Ibis* **145**, 277–294 (2003).
- 1595 450. N. Seddon, W. Amos, G. Adcock, P. Johnson, K. Kraaijeveld, F. J. L. Kraaijeveld-Smit,
1596 W. Lee, G. D. Senapathi, R. A. Mulder, J. A. Tobias, [Mating system, philopatry and patterns of](#)
1597 [kinship in the cooperatively breeding subdesert mesite *Monias benschi*](#). *Molecular Ecology* **14**,
1598 3573–3583 (2005).
- 1599 451. L. Severinghaus, Flocking and cooperative breeding of Formosan blue magpie. *Bulletin of*
1600 *the Institute of Zoology, Academia Sinica* **26**, 27–37 (1987).
- 1601 452. A. Sharma, Effect of helpers on breeding success of the Common Babbler (*Turdoides*
1602 *caudatus*). *Current Science* **82**, 391–392 (2002).
- 1603 453. P. Sherman, G. Kirwan, C. Sharpe, Grey-winged Trumpeter (*Psophia crepitans*) (2020).
- 1604 454. P. T. Sherman, [Reproductive biology and ecology of white-winged trumpeters \(*Psophia*](#)
1605 [leucoptera\) and recommendations for the breeding of captive trumpeters](#). *Zoo Biology* **19**, 65–84
1606 (2000).
- 1607 455. P. T. Sherman, [Social Organization of Cooperatively Polyandrous White-Winged](#)
1608 [Trumpeters \(*Psophia leucoptera*\)](#). *The Auk* **112**, 296–309 (1995).
- 1609 456. L. Short, J. Horne, *Toucans, Barbets and Honeyguides: Ramphastidae, Capitonidae and*
1610 *Indicatoridae* (Oxford University Press: Oxford, 2001).
- 1611 457. R. Silva e Silva, [Breeding behavior, distribution, and conservation of the Sharp-tailed](#)
1612 [Tyrant *Culicivora caudacuta* \(Vieillot, 1818\) \(Aves: Tyrannidae\), a South American grassland](#)
1613 [specialist](#). *Papéis Avulsos de Zoologia* **61**, e20216165 (2021).
- 1614 458. S. A. Sloane, [Incidence and Origins of Supernumeraries at Bushtit \(*Psaltriparus minimus*\)](#)
1615 [Nests](#). *The Auk* **113**, 757–770 (1996).
- 1616 459. S. Sridhar, K. Praveen Karanth, Helpers in cooperatively breeding small green bee-eater
1617 (*Merops orientalis*). *Current Science* **65**, 489–490 (1993).
- 1618 460. P. B. Stacey, [Kinship, promiscuity, and communal breeding in the acorn woodpecker](#).
1619 *Behavioral Ecology and Sociobiology* **6**, 53–66 (1979).

- 1620 461. T. Steeves, S. Kearney-McGee, M. Rubega, C. Cink, C. Collins, Chimney Swift
1621 (Chaetura pelagica) (2020).
- 1622 462. B. E. Storer, “Aspects of the breeding ecology of the pygmy nuthatch (Sitta pygmaea)
1623 and the foraging ecology of wintering mixed-species flocks in western Montana,” thesis, The
1624 University of Montana (1977).
- 1625 463. S. D. Strahl, [The social organization and behaviour of the Hoatzin Opisthocomus hoazin](#)
1626 [in central Venezuela](#). *Ibis* **130**, 483–502 (1988).
- 1627 464. D. Strickland, H. Ouellet, Canada Jay (Perisoreus canadensis) (2020).
- 1628 465. C. J. Stutterheim, [Breeding biology of the redbilled oxpecker in the Kruger National Park](#).
1629 *The Ostrich* **53**, 79–90 (1982).
- 1630 466. W. J. Sydeman, M. Güntert, R. P. Balda, [Annual Reproductive Yield in the Cooperative](#)
1631 [Pygmy Nuthatch \(Sitta pygmaea\)](#). *The Auk* **105**, 70–77 (1988).
- 1632 467. M. Taborsky, D. Limberger, [Helpers in fish](#). *Behavioral Ecology and Sociobiology* **8**,
1633 143–145 (1981).
- 1634 468. S. Tang, D. Ke, T. Yu, C. Wang, Q. Zhao, H. Fan, G. Zhang, C. Wang, X. Lu, [Social](#)
1635 [organization, demography and genetic mating system of a Tibetan cooperative breeder](#). *Ibis* **159**,
1636 687–692 (2017).
- 1637 469. Z. Tárano, Group territoriality and plural breeding in the Purple Gallinule (Porphyrola
1638 martinica) in a seasonally flooded Savanna in Venezuela. *Ornitologia neotropical* **19**, 43–53
1639 (2008).
- 1640 470. W. R. Tarboton, [Cooperative breeding and group territoriality in the black tit](#). *The Ostrich*
1641 **52**, 216–225 (1981).
- 1642 471. B. Taylor, Dusky Moorhen (Gallinula tenebrosa) (2020).
- 1643 472. B. Taylor, Ground Cuckooshrike (Coracina maxima) (2020).
- 1644 473. B. Taylor, C. Sharpe, Henderson Island Crake (Zapornia atra) (2020).
- 1645 474. B. Taylor, Tasmanian Nativehen (Tribonyx mortierii) (2020).

- 1646 475. J. Theuerkauf, S. Rouys, J. M. Mériot, R. Gula, R. Kuehn, [Cooperative breeding, mate](#)
1647 [guarding, and nest sharing in two parrot species of New Caledonia](#). *Journal of Ornithology* **150**,
1648 791–797 (2009).
- 1649 476. T. Thompson, “Breeding biology and the nature and importance of helper contributions in
1650 the cooperative breeding brown-headed nuthatch in a texas urban population,” thesis, Stephen F.
1651 Austin State University, United States (2000).
- 1652 477. R. Tingay, M. Culver, E. Hallerman, J. Fraser, R. Watson, Subordinate males sire
1653 offspring in Madagascar fish-eagle (*Haliaeetus vociferoides*) polyandrous breeding groups.
1654 *Journal of Raptor Research* **36**, 280–286 (2002).
- 1655 478. A. K. Townsend, R. Bowman, J. W. Fitzpatrick, M. Dent, I. J. Lovette, Genetic
1656 monogamy across variable demographic landscapes in cooperatively breeding Florida scrub-jays.
1657 *Behavioral Ecology* **22**, 464–470 (2011).
- 1658 479. A. K. Townsend, A. B. Clark, K. J. McGowan, I. J. Lovette, [Reproductive partitioning](#)
1659 [and the assumptions of reproductive skew models in the cooperatively breeding American crow](#).
1660 *Animal Behaviour* **77**, 503–512 (2009).
- 1661 480. C. A. Ursino, M. C. De Mársico, M. Sued, A. Farall, J. C. Reboreda, [Brood parasitism](#)
1662 [disproportionately increases nest provisioning and helper recruitment in a cooperatively breeding](#)
1663 [bird](#). *Behavioral Ecology and Sociobiology* **65**, 2279–2286 (2011).
- 1664 481. C. A. Ursino, M. C. De Mársico, J. C. Reboreda, C. Riehl, [Kinship and genetic mating](#)
1665 [system of the Grayish Baywing \(*Agelaioides badius* \), a cooperatively breeding Neotropical](#)
1666 [blackbird](#). *The Auk* **134**, 410–420 (2017).
- 1667 482. J. Valencia, C. de la Cruz, B. González, [Flexible Helping Behaviour in the Azure-Winged](#)
1668 [Magpie: Helping in the Azure-Winged Magpie](#). *Ethology : formerly Zeitschrift für*
1669 *Tierpsychologie* **109**, 545–558 (2003).
- 1670 483. D. Van de Loock, “Life-history strategies of a facultative cooperative breeder in a
1671 fragmented Afrotropical cloud forest,” thesis, Ghent University, Ghent, Belgium (2019).
- 1672 484. J. Vargas-Soriano, J. S. Ortiz, G. E. Segura, [Breeding Phenology and Nesting Success of](#)
1673 [the Yucatan Wren in the Yucatan Peninsula, Mexico](#). *The Wilson Journal of Ornithology* **122**,
1674 439–446 (2010).

- 1675 485. C. W. Varian-Ramos, W. R. Lindsay, J. Karubian, M. S. Webster, [Female Red-backed](#)
1676 [Fairy-Wrens \(*Malurus melanocephalus* \) do not appear to pay a cost for high rates of](#)
1677 [promiscuity](#). *The Auk* **129**, 529–536 (2012).
- 1678 486. C. W. Varian-Ramos, J. Karubian, V. Talbott, I. Tapia, M. S. Webster, [Offspring sex](#)
1679 [ratios reflect lack of repayment by auxiliary males in a cooperatively breeding passerine](#).
1680 *Behavioral Ecology and Sociobiology* **64**, 967–977 (2010).
- 1681 487. S. L. Vehrencamp, [The adaptive significance of communal nesting in Groove-billed anis](#)
1682 [\(*Crotophaga sulcirostris*\)](#). *Behavioral Ecology and Sociobiology* **4**, 1–33 (1978).
- 1683 488. S. L. Vehrencamp, B. S. Bowen, R. R. Koford, [Breeding roles and pairing patterns within](#)
1684 [communal groups of groove-billed anis](#). *Animal Behaviour* **34**, 347–366 (1986).
- 1685 489. C. J. Vernon, [Observations on the winter behaviour of the white helmet shrike, *Prionops*](#)
1686 [plumata](#). *The Ostrich* **37**, 3–5 (1966).
- 1687 490. P. Vickery, Grasshopper Sparrow (*Ammodramus savannarum*) (2020).
- 1688 491. T. A. Waite, D. Strickland, [Cooperative Breeding in Gray Jays: Philopatric Offspring](#)
1689 [Provision Juvenile Siblings](#). *The Condor* **99**, 523–525 (1997).
- 1690 492. J. Walters, B. F. Walters, [Co-Operative Breeding by Southern Lapwings Vanell Us](#)
1691 [Chilensis](#). *Ibis* **122**, 505–509 (1980).
- 1692 493. J. R. Walters, P. D. Doerr, J. H. Carter III, [The Cooperative Breeding System of the Red-](#)
1693 [cockaded Woodpecker](#). *Ethology : formerly Zeitschrift für Tierpsychologie* **78**, 275–305 (1988).
- 1694 494. J. Walters, “Red-cockaded Woodpeckers: A ‘primitive’ cooperative breeder” in
1695 *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Cambridge:
1696 Cambridge University Press, 1990).
- 1697 495. C. Wang, X. Lu, [Extra-pair paternity in relation to breeding synchrony in ground tits: An](#)
1698 [individual-based approach](#). *Journal of Avian Biology* **45**, 561–565 (2014).
- 1699 496. C. C. Warren, P. J. Motyka, H. L. Mounce, [Home range sizes of two Hawaiian](#)
1700 [honeycreepers: implications for proposed translocation efforts](#). *Journal of Field Ornithology* **86**,
1701 305–316 (2015).

- 1702 497. M. H. Warrington, L. A. Rollins, A. F. Russell, S. C. Griffith, [Sequential polyandry](#)
1703 [through divorce and re-pairing in a cooperatively breeding bird reduces helper-offspring](#)
1704 [relatedness](#). *Behavioral Ecology and Sociobiology* **69**, 1311–1321 (2015).
- 1705 498. R. T. Watson, S. Razafindramanana, R. Thorstrom, S. Rafanomezantsoa, [Breeding](#)
1706 [biology, extra-pair birds, productivity, siblicide and conservation of the Madagascar Fish Eagle](#).
1707 *The Ostrich* **70**, 105–111 (1999).
- 1708 499. M. S. Webster, C. W. Varian, J. Karubian, [Plumage color and reproduction in the red-](#)
1709 [backed fairy-wren: Why be a dull breeder?](#) *Behavioral Ecology* **19**, 517–524 (2008).
- 1710 500. M. S. Webster, K. A. Tarvin, E. M. Tuttle, S. Pruett-Jones, [Reproductive promiscuity in](#)
1711 [the splendid fairy-wren: Effects of group size and auxiliary reproduction](#). *Behavioral Ecology* **15**,
1712 907–915 (2004).
- 1713 501. L. A. Whittingham, P. O. Dunn, R. D. Magrath, [Relatedness, polyandry and extra-group](#)
1714 [paternity in the cooperatively-breeding white-browed scrubwren \(*Sericornis frontalis* \)](#).
1715 *Behavioral Ecology and Sociobiology* **40**, 261–270 (1997).
- 1716 502. R. Wilkinson, A. E. Brown, [Effect of Helpers on the Feeding Rates of Nestlings in the](#)
1717 [Chestnut-Bellied Starling *Spreo pulcher*](#). *The Journal of Animal Ecology* **53**, 301 (1984).
- 1718 503. R. Wilkinson, [Social organization and communal breeding in the chestnut-bellied starling](#)
1719 [\(*Spreo pulcher*\)](#). *Animal Behaviour* **30**, 1118–1128 (1982).
- 1720 504. D. A. Williams, [Female control of reproductive skew in cooperatively breeding brown](#)
1721 [jays \(*Cyanocorax morio* \)](#). *Behavioral Ecology and Sociobiology* **55**, 370–380 (2004).
- 1722 505. D. A. Williams, A. M. Hale, Helper effects on offspring production in cooperatively
1723 breeding brown jays (*Cyanocorax morio*). *The Auk* **123**, 847–857 (2005).
- 1724 506. D. Williams, “Routes to fitness in cooperatively breeding brown jays,” thesis, Purdue
1725 Univeristy (2000).
- 1726 507. E. Willis, [A Study of Nesting Ant-Tanagers in British Honduras](#). *The Condor* **63**, 479–
1727 503 (1961).
- 1728 508. M. Winterbottom, T. Burke, T. Birkhead, [The phalloid organ, orgasm and sperm](#)
1729 [competition in a polygynandrous bird: The red-billed buffalo weaver \(*Bubalornis niger* \)](#).
1730 *Behavioral Ecology and Sociobiology* **50**, 474–482 (2001).

- 1731 509. M. Winterbottom, T. Birkhead, [The Red-billed Buffalo-Weaver: Observations of anatomy](#)
1732 [and behaviour](#). *The Ostrich* **74**, 237–240 (2003).
- 1733 510. S. R. Winterstein, R. J. Raitt, Nestling Growth and Development and the Breeding
1734 Ecology of the Beechey Jay. *The Wilson Bulletin* **95**, 256–268 (1983).
- 1735 511. P. Woodall, Blue-winged Kookaburra (*Dacelo leachii*) (2020).
- 1736 512. P. Woodall, “Family Alcedinidae (Kingfishers)” in *Handbook of the Birds of the World*.
1737 *Vol. 6. Mousebirds to Hornbills* (Lynx edicions: Barcelona, 2001), pp. 130–249.
- 1738 513. P. Woodall, Pied Kingfisher (*Ceryle rudis*) (2020).
- 1739 514. G. Woolfenden, J. Fitzpatrick, “Florida Scrub Jays: A synopsis after 18 years of study” in
1740 *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior*. (Cambridge:
1741 Cambridge University Press, 1990).
- 1742 515. I. A. Woxvold, [Breeding ecology and group dynamics of the apostlebird](#). *Australian*
1743 *Journal of Zoology* **52**, 561–581 (2004).
- 1744 516. I. A. Woxvold, R. A. Mulder, [Mixed mating strategies in cooperatively breeding](#)
1745 [apostlebirds *Struthidea cinerea*](#). *Journal of Avian Biology* **39**, 50–56 (2008).
- 1746 517. P. H. Wrege, S. T. Emlen, [Biochemical determination of parental uncertainty in white-](#)
1747 [fronted bee-eaters](#). *Behavioral Ecology and Sociobiology* **20**, 153–160 (1987).
- 1748 518. J. Wright, [Helping-at-the-Nest and Group Size in the Arabian Babbler *Turdoides*](#)
1749 [squamiceps](#). *Journal of Avian Biology* **29**, 105 (1998).
- 1750 519. Y. Xu, N. Yang, K. Zhang, B. Yue, J. Ran, [Cooperative breeding by Buff-throated](#)
1751 [Partridge *Tetraophasis szechenyii*: A case in the Galliformes](#). *Journal of Ornithology* **152**, 695–
1752 700 (2011).
- 1753 520. S. Yamagishi, E. Urano, K. Eguchi, [Group composition and contributions to breeding by](#)
1754 [Rufous Vangas *Schetba rufa* in Madagascar](#). *Ibis* **137**, 157–161 (1995).
- 1755 521. S. Yamagishi, M. Nakamura, Sickie-billed Vanga (*Falcula palliata*) (2020).
- 1756 522. E. C. Young, [Dispersal from Natal Territories and the Origin of Cooperatively](#)
1757 [Polyandrous Breeding Groups in the Brown Skua](#). *The Condor* **100**, 335–342 (1998).

- 1758 523. L. C. Young, B. J. Zaun, E. A. VanderWerf, [Successful same-sex pairing in Laysan](#)
 1759 [albatross](#). *Biology Letters* **4**, 323–325 (2008).
- 1760 524. S. Zack, [Behaviour and breeding biology of the cooperatively breeding Grey-backed](#)
 1761 [Fiscal Shrike Lanius excubitorius in Kenya](#). *Ibis* **128**, 214–233 (1986).
- 1762 525. S. Zack, J. D. Ligon, Cooperative Breeding in Lanius Shrikes. II. Maintenance of Group-
 1763 Living in a Nonsaturated Habitat. *The Auk* **102**, 766–773 (1985).
- 1764 526. A. Zahavi, “Arabian Babblers: The quest for social status in a cooperative breeder” in
 1765 *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior* (Cambridge:
 1766 Cambridge University Press, 1990).

1767 **Session information**

```

1768 R version 4.5.1 (2025-06-13)
1769 Platform: aarch64-apple-darwin20
1770 Running under: macOS Tahoe 26.4.1
1771
1772 Matrix products: default
1773 BLAS: /Library/Frameworks/R.framework/Versions/4.5-arm64/Resources/lib/libRblas.0.dylib
1774 LAPACK: /Library/Frameworks/R.framework/Versions/4.5-arm64/Resources/lib/libRlapack.dyli
1775 b; LAPACK version 3.12.1
1776
1777 locale:
1778 [1] C.UTF-8/C.UTF-8/C.UTF-8/C/C.UTF-8/C.UTF-8
1779
1780 time zone: Europe/Stockholm
1781 tzcode source: internal
1782
1783 attached base packages:
1784 [1] stats graphics grDevices utils datasets methods base
1785
1786 other attached packages:
1787 [1] corpcor_1.6.10 ggrepel_0.9.6 GGally_2.4.0 treeio_1.32.0
1788 [5] ggsci_3.2.0 stringdist_0.9.15 openxlsx_4.2.8 car_3.1-3
1789 [9] carData_3.0-5 reshape2_1.4.4 sf_1.0-21 raster_3.6-32
  
```

```

1790 [13] sp_2.2-0      terra_1.8-72  officer_0.7.0  flextable_0.9.10
1791 [17] magrittr_2.0.4 kableExtra_1.4.0 corrplot_0.95  MCMCglmm_2.36
1792 [21] coda_0.19-4.1 Matrix_1.7-4  magick_2.8.7  TreeTools_1.16.1
1793 [25] psych_2.5.6   ggnewscale_0.5.2 ggtreeExtra_1.18.0 ggtree_3.16.3
1794 [29] tidytree_0.4.6 RColorBrewer_1.1-3 ape_5.8-1      scatterpie_0.2.5
1795 [33] ggmap_4.0.1   cowplot_1.2.0  lubridate_1.9.5 forcats_1.0.0
1796 [37] stringr_1.6.0 purrr_1.2.1   readr_2.1.6   tidyr_1.3.2
1797 [41] tibble_3.3.1  ggplot2_4.0.2 tidyverse_2.0.0 dplyr_1.2.0
1798
1799 loaded via a namespace (and not attached):
1800 [1] tensorA_0.36.2.1  rstudioapi_0.17.1  jsonlite_2.0.0
1801 [4] farver_2.1.2      rmarkdown_2.29     fs_1.6.7
1802 [7] ragg_1.5.0        vctrs_0.7.1       RCurl_1.98-1.17
1803 [10] askpass_1.2.1     htmltools_0.5.8.1 Formula_1.2-5
1804 [13] gridGraphics_0.5-1 KernSmooth_2.23-26 pdftools_3.5.0
1805 [16] plyr_1.8.9        uuid_1.2-1         lifecycle_1.0.5
1806 [19] pkgconfig_2.0.3   R6_2.6.1           fastmap_1.2.0
1807 [22] rbitutils_2.3     digest_0.6.39     aplot_0.2.8
1808 [25] colorspace_2.1-1 patchwork_1.3.2    textshaping_1.0.3
1809 [28] labeling_0.4.3    timechange_0.4.0  mgcv_1.9-3
1810 [31] abind_1.4-8       htr_1.4.8          polyclip_1.10-7
1811 [34] compiler_4.5.1    proxy_0.4-27      bit64_4.6.0-1
1812 [37] fontquiver_0.2.1  withr_3.0.2       S7_0.2.1
1813 [40] DBI_1.3.0         ggstats_0.10.0    ggforce_0.5.0
1814 [43] R.utils_2.13.0    MASS_7.3-65       openssl_2.3.5
1815 [46] rappdirs_0.3.4    classInt_0.4-11   tools_4.5.1
1816 [49] units_0.8-7       zip_2.3.3          R.oo_1.27.1
1817 [52] glue_1.8.0        nlme_3.1-168      R.cache_0.17.0
1818 [55] grid_4.5.1        PlotTools_0.3.1   generics_0.1.4
1819 [58] gtable_0.3.6      tzdb_0.5.0        R.methodsS3_1.8.2
1820 [61] class_7.3-23      data.table_1.17.8 hms_1.1.4
1821 [64] xml2_1.4.0        pillar_1.11.1     yulab.utils_0.2.1
1822 [67] splines_4.5.1     tweenr_2.0.3      lattice_0.22-7
1823 [70] bit_4.6.0         tidyselect_1.2.1  fontLiberation_0.1.0
1824 [73] knitr_1.51        fontBitstreamVera_0.1.1 svglite_2.2.1
1825 [76] xfun_0.56         stringi_1.8.7     qpdf_1.4.1

```

1826	[79] lazyeval_0.2.2	ggfun_0.2.0	yaml_2.3.12
1827	[82] pacman_0.5.1	evaluate_1.0.5	codetools_0.2-20
1828	[85] gdttools_0.4.3	ggplotify_0.1.2	cli_3.6.5
1829	[88] systemfonts_1.2.3	Rdpack_2.6.4	dichromat_2.0-0.1
1830	[91] Rcpp_1.1.1	png_0.1-8	parallel_4.5.1
1831	[94] cubature_2.1.4-1	jpeg_0.1-11	bitops_1.0-9
1832	[97] viridisLite_0.4.2	scales_1.4.0	e1071_1.7-16
1833	[100] rlang_1.1.7	fastmatch_1.1-8	mnormt_2.1.2