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Group formation and the evolutionary pathway to complex sociality in birds

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Group-living species show a diversity of social organization, from simple mated pairs to complex communities of interdependent individuals performing specialized tasks. The advantages of living in cooperative groups are well understood, but why some species breed in small aggregations while others evolve large, complex groups with clearly divided roles is unclear. We address this problem by reconstructing the evolutionary pathways to cooperative breeding across 4,730 bird species. We show that differences in the way groups form at the origin of cooperative breeding predicts the level of group complexity that emerges. Groups that originate through the retention of offspring have a clear reproductive divide with distinct breeder and helper roles. This is associated with reproductive specialization, where breeders invest more in fecundity and less in care. In contrast, groups formed through the aggregation of unrelated adults are smaller and lack specialization. These results help explain why some species have not transitioned beyond simple groups while others have taken the pathway to increased group complexity.

Cooperatively breeding animals have provided us with profound insights into the evolution of cooperation and group living[1–3]. Decades of research has shown that breeding in cooperative groups can increase reproductive success[4,5], especially under conditions where independent breeding is difficult[6–8]. This has allowed species to expand into new ecological niches and persist in environments uninhabitable for less social species[9–11]. Detailed accounts of cooperative breeders have also revealed that there is remarkable unexplained variation in the complexity of social groups across species[12,13]. Complex groups are defined here as those in which there is a clear division of reproduction, group members are specialized in breeding and helping roles and groups are large[2]. Why do animal societies vary dramatically in group size, and why are tasks such as reproduction and offspring care partitioned amongst group members in some species but not in others[5,14–18] (Fig. 1)?

Evolutionary theory predicts that differences in the complexity of social groups can arise because of differences in the way groups form[19]. Groups formed by offspring staying with their parents (family groups) have relatively high average relatedness between individuals, creating the potential for helping to increase fitness indirectly via kin selection[20]. Relaxing the need to reproduce as a route to fitness is important because it allows some individuals to specialize in helping while others specialize in reproduction. This can increase fecundity and lead to larger, more productive, groups[21]. Consistent with this prediction, highly complex groups such as social insect colonies and multicellular organisms consist of related individuals[22,23]. In contrast, when groups form by unrelated individuals aggregating after dispersal from their natal unit (non-family groups), relatedness can be low (Fig. 1). Under these circumstances, individuals must reproduce to pass on their genes, which can generate competition over breeding and limit investment in other tasks that may constrain group size[24–26]. More complex social groups are therefore predicted to evolve when groups originate from family rather than from non-family units.

To test whether group formation determines the level of group complexity that can evolve, we need to: (1) reconstruct the evolutionary origins of group formation; (2) examine whether this is associated with how reproduction is divided amongst group members; and (3) assess whether this explains the evolution of larger, more productive, groups with specialized breeders and helpers. This is challenging because it requires detailed information on the reproductive and helping behaviour of individuals in a clade of animals where there are multiple independent evolutionary transitions to cooperative breeding in family and non-family groups. This is possible in birds because there are many well-studied family and non-family cooperative breeders across the phylogeny, genetic parentage has been measured in diverse species and the phylogenetic relationships among species are well characterized[3,10,27–30]. We use data across 4,730 bird species to first ask how different types of cooperative groups evolved. Do family and non-family groups represent distinct evolutionary pathways to cooperative breeding, or is one a necessary precursor for the evolution of the other?

Results

Reconstructing the origins of family ($n_{species}=140$) and non-family groups ($n_{species}=32$) revealed that they have distinct evolutionary origins (Fig. 2a). Independent breeding was estimated to be ancestral to all 132 origins of family groups (range, 58–254 origins sampled across 1,000 phylogenies using a Bayesian phylogenetic mixed model (BPMM); Fig. 2b) and all 14 origins of non-family groups (range, 1–228 origins sampled across 1,000 phylogenies). This finding was confirmed using stochastic character mapping: 88/89 family origins were from non-cooperative ancestors (one origin was from a non-family cooperative breeder) and 27/27 non-family origins were from non-cooperative ancestors. Classifying species as family or non-family does not capture instances where family groups contain unrelated helpers. Using more fine-grained classifications of cooperative breeding systems, we found that groups containing unrelated helpers originate from family groups and do not transition to non-family groups (Supplementary Table 6). These results demonstrate that superficially similar breeding systems in birds have separate evolutionary origins, as found in snapping shrimp where eusocial and communal breeding systems have distinct origins[31].

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Fig. 1 | The diversity of social group complexity across cooperative birds. a,**b**, Reproduction is monopolized by a dominant pair, and fecundity increases with group size in white-winged choughs (**a**)[5,14] whereas reproduction is shared among group members in Guira cuckoos and per capita fecundity decreases with group size (**b**)[15,16]. **c**,**d**, Groups form through the retention of offspring in grey-crowned babblers and may reach up to 13 individuals (**c**)[17], while groups form through the aggregation of unrelated individuals after they disperse from their natal units in groove-billed anis and typically contain four individuals (**d**)[18]. Credit: Patrick Kavanagh (a), Bob Brewer (b), Graham Lee (c) and Andy Reago and Chrissy McClarren (d)

Why some species form cooperative groups with family members whereas others aggregate with unrelated individuals is poorly understood. One factor predicted to influence the route to group formation is the mating behaviour of founding females[32]. Cooperative family groups are expected to evolve more frequently from ancestral species with monogamous females, as this provides the opportunity for retained offspring to raise full siblings ($r=0.5$), for which there is support in birds[33]. In contrast, polyandry may increase the likelihood that non-family groups evolve if it incentivizes males to provide offspring care. For example, in the dunnock (*Prunella modularis*), females mate with multiple males, which increases the likelihood that they provide offspring care[34]. Whether the mating behaviour of the ancestors of non-family and family cooperative breeders differs is unknown.

We tested whether differences in group formation were associated with the mating behaviour of ancestral species by reconstructing patterns of genetic parentage. We found that non-family groups originated from species with higher rates of female polyandry compared to family groups (BPMM; non-family group ancestral polyandry: $\beta=41\%$, credible interval (CI) = 14–93%; family group ancestral polyandry: $\beta=17\%$, CI = 4–50%; $P_{\text{family versus non-family}}=0.05$; Fig. 2c). In fact, in the ancestors of non-family groups, females were estimated to be more polyandrous than those that remained as independent breeders (BPMM; non-cooperative ancestral polyandry: $\beta=20\%$, CI = 7–50%; $P_{\text{non-family versus non-cooperative}}=0.05$). These results were robust to different breeding system classifications of species where there is ambiguity over whether they are cooperative breeders (Supplementary Table 10).

The difference in polyandry rates between the ancestors of family and non-family groups clarifies the role of female mating behaviour in the evolution of cooperative breeding. Monogamy is predicted to favour cooperative breeding only where offspring are retained as helpers[32], as demonstrated in previous analyses restricted to family groups[22,33,35]. Failure to distinguish between family and non-family cooperative breeders, and combining their different rates of polyandry, leads to variable and ambiguous associations with female mating behaviour. Our analysis shows that high rates of polyandry do not preclude group formation, but set non-family groups on a different evolutionary pathway to that taken by family groups. The factors that align fitness interests in the absence of relatedness in non-family groups remain understudied, but it is logical that a large ecological benefit to cooperation is required.

Next, we examined whether variation in group complexity across cooperative breeders can be explained by their different evolutionary origins of group formation. In line with the prediction that high relatedness enables reproduction to be divided among group members, we found that the percentage of groups with more than one reproductive female was higher in non-family than in family groups (BPMM; non-family: $\beta=95\%$, CI = 73–99%; family: $\beta=6\%$, CI = 0–24%; $n_{\text{species}}=23$; $P_{\text{family versus non-family}}<0.001$; Fig. 3a). Similarly, non-family groups were significantly more likely than family groups to have multiple male breeders (BPMM; non-family: $\beta=83\%$, CI = 57–95%; family $\beta=7\%$, CI = 1–17%; $n_{\text{species}}=44$; $P_{\text{family versus non-family}}<0.001$; Fig. 3b). Therefore, family living is necessary for division of reproduction within groups, consistent with concessions models of reproductive skew[24,36,37].

One consequence of dividing reproduction is that different group members can specialize in breeding and helping roles, potentially leading to increased fecundity. To examine whether females in family and non-family groups differ in their reproductive specialization, we collected data on changes in fecundity and offspring care as group size increased. If living in family groups allows reproductive specialization, then we expect female fecundity to increase with group size and to be associated with a corresponding decrease in offspring care.

We found that breeding females in family groups increased their investment in fecundity as groups became larger (BPMM; Fisher's Z-transformed correlation (Zr) between fecundity and group

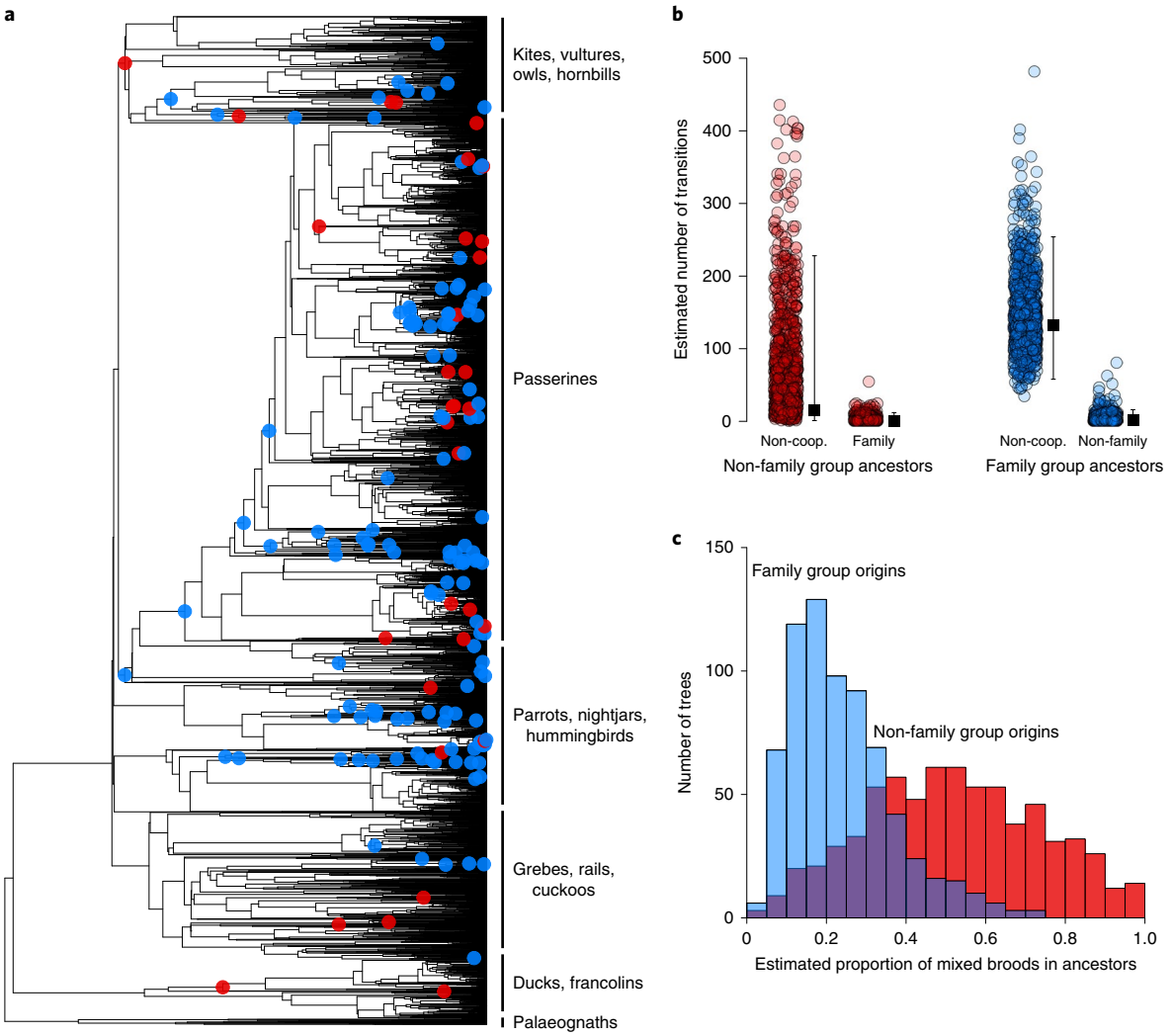

Fig. 2 | The evolutionary origins of group formation. a, Origins of cooperative breeding in family (blue) and non-family (red) groups ($n_{species}$ = 4,730). **b**, The number of origins of family and non-family cooperative (coop.) breeding from different types of ancestors estimated across 1,000 phylogenetic trees (back-transformed mode and 95% CI estimated using a BPMM are shown—see Methods for further details). **c**, Polyandry rates in ancestral independently breeding species that made the transition to breed cooperatively in family and non-family groups, estimated across 700 phylogenetic trees. Ancestral traits estimated using BPMMs.

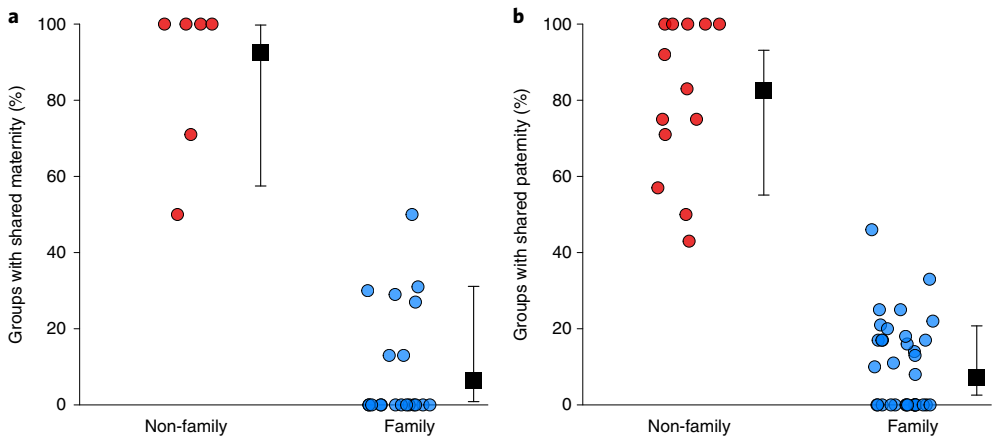

Fig. 3 | Evolution of divided reproduction. a, Percentage of multi-female groups with shared maternity in family ($n_{species}$ = 17) and non-family ($n_{species}$ = 6) cooperative breeders. **b**, Percentage of multi-male groups with shared paternity in family ($n_{species}$ = 31) and non-family ($n_{species}$ = 13) cooperative breeders. Dots represent raw data for individual species, with the back-transformed mode and 95% CI estimated using a BPMM.

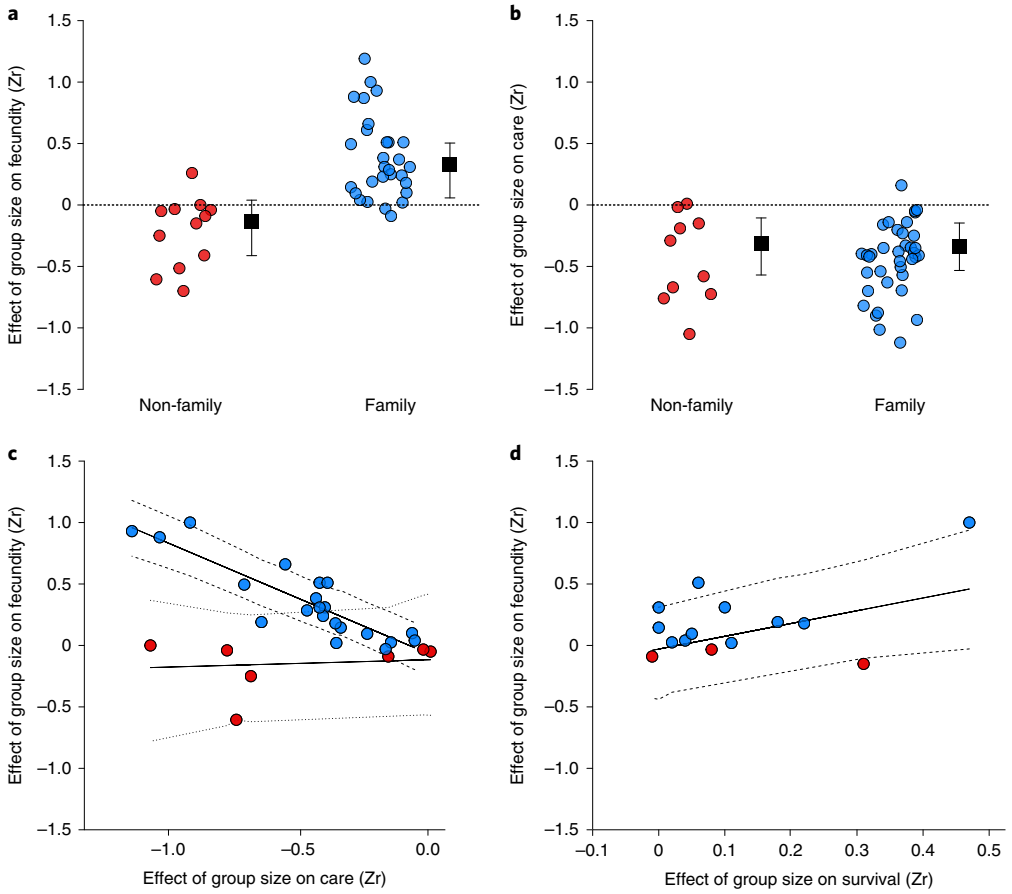

Fig. 4 | Evolution of task specialization. a, The correlation between maternal fecundity and group size (Zr) was positive in family groups ($n_{species}=29$) but negative in non-family groups ($n_{species}=12$). **b**, The correlation between maternal care and group size was negative in family ($n_{species}=37$) and non-family ($n_{species}=10$) groups. Dots represent raw data for individual species, with the mode and 95% CI estimated using BPMMs. **c**, There was a negative relationship between how maternal fecundity and maternal care change with group size in family groups (blue, $n_{species}=21$), but no relationship in non-family groups (red, $n_{species}=7$). **d**, Increased fecundity was not offset by decreased survival in family groups (blue, $n_{species}=11$). Raw data are plotted with regression lines (solid) and 95% CI (broken) estimated from BPMMs.

size = 0.33, CI = 0.06–0.50, $n_{species}=29$), whereas the fecundity of breeding females in non-family groups decreased with group size (Zr = −0.14, CI = −0.41 to 0.04, $n_{species}=12$, $P_{family\ versus\ non\text{-}family}<0.001$; Fig. 4a). In all species, breeding females reduced investment in care as group size increased (BPMM; family Zr = −0.34, CI = −0.53 to −0.15; non-family Zr = −0.32, CI = −0.57 to −0.11; $n_{species}=47$; $P_{family\ versus\ non\text{-}family}=0.60$; Fig. 4b). However, only in family groups were reductions in offspring care related to increases in fecundity (BPMM; slope (β) = −1.02, CI = −1.42 to −0.62, $n_{species}=21$; Fig. 4c). The data for non-family groups, although limited ($n_{species}=7$), showed that reduced care was not associated with fecundity benefits in larger groups ($\beta=0.11$, CI = −0.36 to 0.41; $P_{family\ versus\ non\text{-}family}<0.001$). More data are needed to confirm the pattern in non-family groups, but the difference in the relationship between fecundity and care in family and non-family groups remained significant even when we down-sampled the number of family group species to be the same as non-family groups (seven family group species: $\beta=-0.84$, CI = −1.62 to −0.35; $P_{family\ versus\ non\text{-}family}<0.01$). This suggests that the difference observed between family and non-family groups is not an artefact of sample size differences.

The fecundity benefits associated with larger groups in families support the hypothesis that non-breeding helpers are crucial for alleviating the costs of offspring care, enabling breeders to specialize in reproduction. Evidence from experimental field studies of family group cooperative breeders supports a causal role for helpers in reducing breeder care and increasing fecundity (Supplementary Table 9). In contrast, extra group members in non-family groups have a negative effect on fecundity. Empirical studies have demonstrated that this can be due to reproductive competition[38,39]—for example, in the groove-billed ani (*Crotophaga sulcirostris*) >30% of eggs are destroyed by co-breeding females[40].

The contrasting effect of group size on fecundity in family and non-family cooperative species is expected to influence how large groups can become. Consistent with this prediction, maximum group size was nearly twice as high in family groups compared to non-family groups (BPMM; maximum group sizes: non-family $\beta=4.6$, CI = 2.7–7.2; family $\beta=7.0$, CI = 4.4–11.4; $n_{species}=123$; $P_{family\ versus\ non\text{-}family}<0.001$; Extended Data Fig. 1a). In fact, the frequency of species that formed groups of ten or more individuals was three times higher in family (29/95 = 31%) relative to non-family cooperative breeders (3/28 = 11%). Species living in family groups are also larger on average than those living in non-family groups, but this difference is less pronounced (BPMM; mean group size: non-family $\beta=2.5$, CI = 1.8–4.2; family $\beta=3.4$, CI = 2.1–5.0; $n_{species}=113$; $P_{family\ versus\ non\text{-}family}=0.04$; Extended Data Fig. 1b). Taken together, these results suggest that family groups have the potential to be much larger than non-family groups but that other factors, such as ecological conditions, may determine typical group sizes.

The positive association between the number of helpers and fecundity in family groups highlights an important advantage of the

reproductive division of labour—higher productivity. High fecundity may, however, come at a cost to survival, with females investing more in current versus future reproduction that can offset the productivity advantages of dividing reproduction[41]. This was not the case. The survival of breeding females in family groups typically increased with the number of helpers (BPMM; Zr = 0.06, CI = −0.09 to 0.21; $n_{species}$ = 17; Extended Data Fig. 2a) and was positively, not negatively, related to fecundity (BPMM; β = 1.15, CI = −0.11 to 2.17, $n_{species}$ = 11; Fig. 4d).

Given that the fecundity of breeding females in non-family groups decreases with group size, there must be other fitness benefits to living in groups that favour this strategy. One possibility is that survival is higher in larger groups, resulting in future breeding opportunities. The relationship between group size and breeding female survival has been quantified in only three species that form non-family groups, and in two of these species females typically live longer in larger groups (Extended Data Fig. 2a). More data are needed to identify the fitness benefits that favour cooperative breeding in non-family groups over independent reproduction.

Discussion

The trade-off between fecundity and survival is fundamental to shaping life-history strategies across divergent taxa[41]. Our results suggest that the reproductive division of labour, which enables breeding females to reduce maternal care, can relax such life-history trade-offs. Similar patterns are observed in eusocial insects where queens in family groups can live for more than a decade and produce thousands of eggs per day[42,43]. The escape from life-history trade-offs may be a crucial and general advantage to breeding cooperatively in family relative to non-family groups.

Even birds with complex social groups, however, differ fundamentally from eusocial insects, where reproductive specialization has led to the evolution of sterile workers and morphological castes[32,44]. Certain life-history characteristics of social insects, such as strict lifetime monogamy and greater longevity of breeders than helpers, ensure that within-group relatedness remains high for the entirety of a helper's lifespan[45,46]. In contrast, birds living in family groups often contain a mix of kin and non-kin due to breeder turnover, polyandry, co-breeding and unrelated immigrant helpers. Defining species as family and non-family does not capture such sources of variation in relatedness, which remains challenging, but these factors are probable explanations for why birds have not undergone the major evolutionary transition to eusociality. The clear effect of group formation on group complexity in cooperative birds, nevertheless, supports the hypothesis that the formation of family groups is a necessary, though insufficient, step towards eusociality[32].

Our analyses show that variation in the complexity of social groups in birds is, in part, explained by species characteristics present before the emergence of sociality. The mating behaviour of ancestral females appears to set species on an evolutionary pathway to forming groups with either family or non-family members. How groups form is crucial for the division of reproduction among group members, which leads to the evolution of reproductive specialization and larger, more productive, groups. The evolution of group complexity revealed by our analyses therefore suggests that family and non-family groups do not form a continuum of social complexity, as is often argued[47–49]. Instead, species that live in non-families have distinct evolutionary origins and appear limited in their potential to evolve complex social groups. Cooperative breeders, as defined by multiple adults caring for offspring, therefore contain species that have arisen through different evolutionary processes that have distinct and non-overlapping evolutionary histories.

Methods

Data on breeding systems. We classified species as either non-cooperative ($n_{species}$ = 4,558) or cooperative ($n_{species}$ = 172) based on information published in major review articles of avian breeding systems[3,10,27,28,30]. Cooperatively breeding species are those in which more than two adults contribute to offspring care[25]. We categorized cooperative species as either breeding in family ($n_{species}$ = 140) or non-family groups ($n_{species}$ = 32) using the most recent review of the kin relationships in social groups of avian cooperative breeders[30]. Riehl's review assigned cooperatively breeding species into one of four categories: (1) 'pair-nesting with related helpers only' ($n_{species}$ = 118); (2) 'pair-nesting with unrelated helpers only, or with both related and unrelated helpers' ($n_{species}$ = 40); (3) 'groups containing only unrelated co-breeders' ($n_{species}$ = 31); and (4) 'groups containing both related and unrelated co-breeders and/or helpers' ($n_{species}$ = 24). We assigned species in categories 1, 2 and 4 in Riehl's system as family groups, and assignments in category 3 as non-family groups. We assigned species in categories 2 and 4 as family group cooperative breeders because, in these species, most groups form as family units and are subsequently joined by immigrant birds that either attempt to co-breed or act as non-breeding helpers (Supplementary Table 1)[50]. We explored the sensitivity of our results to differences in categorization and found that it does not alter our conclusions (see Section 2.1 of the Supplementary Methods). In addition, some species are difficult to classify because of intraspecific variation, both across populations and through time, leading to differences amongst published studies in estimates of group relatedness and dispersal. For example, the stitchbird (*Notiomystis cincta*) was observed to breed in groups at one study location[51] but not at another[52]. We examined the sensitivity of our results to the different breeding system classifications reported in the literature for this species and found that our conclusions were unaffected (Supplementary Table 10)[50].

Riehl's review identified 213 cooperatively breeding bird species. For 45/213 species, either helpers were juveniles or the information presented in the original description of the breeding system was unclear regarding the relatedness of helpers. Because we test hypotheses about why individuals help others reproduce instead of breeding independently in family and non-family groups, these species were excluded from our analyses. In addition, we identified four cooperatively breeding species not included in Riehl's review. Full details of the breeding system classifications used are provided in Supplementary Table 1.

Data on female polyandry rates. We compiled data from Cornwallis et al.[10] and Brouwer and Griffith[53] and updated these to include any data published on polyandry in birds estimated using molecular methods up to and including 21 November 2018. We used the following topic search term in Web of Science: 'extra-pair paternity OR extra pair paternity OR extra-pair fertilization OR extra pair fertilization OR extra-pair fertilization OR extra pair fertilization OR extrapair'. Our measure of female polyandry was the percentage of broods that contained one or more chicks sired by multiple males. For socially monogamous non-cooperative species, this was the percentage of broods that contained chicks sired by males other than the pair-bonded male. In species in which a single parent cares for the offspring or in those lacking parental care, this was the proportion of broods with multiple paternity. For cooperatively breeding species, this was the percentage of broods that contained chicks sired by multiple males inside or outside the group. In total, we obtained polyandry estimates for 352 species (Supplementary Table 1). When multiple polyandry estimates from different populations of the same species were available, we took weighted means.

Data on group size, division of reproduction and specialization. We searched the primary literature for data on group size, division of reproduction and reproductive specialization using species-specific searches in Web of Science for each cooperative species included in our sample ($n_{species}$ = 172). We searched both common and scientific species names, including known synonyms, up to and including 22 February 2019. In addition, we consulted two edited volumes on cooperatively breeding birds[3,27] that contain species-specific accounts of 14 and 20 species, respectively.

For each species, we measured division of reproduction as the percentage of multi-female groups with mixed within-group maternity and the percentage of multi-male groups with mixed within-group paternity. We considered only groups that contained multiple females or multiple males for each species, because we are interested in how reproduction is divided among same-sex group members. Our measure of reproductive specialization was Fisher's Z transformation of the statistical correlation between fecundity and group size (Zr fecundity). Fecundity was measured either as clutch size, number of clutches or egg volume. We also calculated the effect size between the amount of care provided by breeding females to offspring and group size (Zr care). Maternal care was measured either as provisioning, brooding or incubation. We explored the sensitivity of our results to how variables were measured, and found no significant effects of the different measures of fecundity and maternal care (see Section 2.2 of the Supplementary Methods). Finally, we calculated the effect size between the survival probability of breeding females and group size (Zr survival) to examine the potential for trade-offs between fecundity, care and survival across different group sizes. When multiple effect sizes from different populations of the same species were available, we took weighted means. We obtained data on group size for 127 species (Supplementary Table 2), division of reproduction for 46 species (Supplementary Table 3), Zr fecundity for 41 species, Zr care for 47 species and Zr survival for 20 species (Supplementary Table 4). Not all data were available for each species,

so sample sizes vary between analysis. Full details are provided in Supplementary Tables 2–4 (ref. [50]).

Phylogenetic trees. We downloaded a sample of 1,300 phylogenetic trees from the birdtree.org website published by Jetz et al.[29] from the Hackett backbone, and trimmed them to the 4,730 species for which we had breeding system data.

Statistical analyses. We used BPMMs fitted in the MCMCglmm R package[54,55] for our analyses unless otherwise specified. Parameters were estimated using the mode (β) and CI of posterior distributions; *P* values derived from the Markov Chain (pMCMC) are either the proportion of samples greater or less than 0 or, where two parameter estimates are compared, the proportion of posterior samples where one parameter is greater than the other. We assessed model convergence by inspecting traces of posterior distributions to evaluate chain mixing, by calculating the degree of auto-correlation between successive iterations in each chain and by running each model three times and then using Gelman and Rubin's convergence test to compare within- and between-chain variance[56].

All BPMMs included a phylogenetic (co)variance matrix fitted as a random effect to account for non-independence between species due to shared evolutionary history. We accounted for phylogenetic uncertainty in each BPMM by marginalizing over our sample of 1,300 bird trees—see the supplementary material in ref. [57] for full details. We did this by sequentially including each of the 1,300 phylogenetic (co)variance matrices in our BPMMs at successive iterations of the Markov chain, using the variance components and latent variables from the previous tree in the sequence as starting values for the next tree in the sequence. For all BPMMs except those used for ancestral state estimation, models were run for 1,000 iterations per tree with only the last iteration from each tree being saved. This gave a total of 1,300,000 iterations for each model. The first 300 trees from each BPMM were discarded as a burn-in, giving a total of 1,000 saved iterations. For all parameters, this gave an effective sample size of 1,000 or higher. In each of these BPMMs we used inverse-Wishart priors (variance = 1 and belief parameter = 0.002) for the random effects. When estimating ancestral breeding systems and ancestral polyandry rates we used a similar approach to account for phylogenetic uncertainty, but varied the priors and the number of iterations per tree (see Estimation of ancestral breeding systems for further details).

Specific analyses are described below. Full details of statistical model specification, including priors, run length and burn-in periods, are provided in Supplementary Data 1 (R code)[50]. All parameter estimates are reported in Supplementary Table 5 (ref. [50]).

Estimation of ancestral breeding systems. We estimated ancestral breeding systems using a BPMM with a multinomial response variable (1 = family cooperative breeder, 2 = non-cooperative breeder, 3 = non-family cooperative breeder) with a logit link function. This estimates the probability that each node in the phylogeny is either a family group cooperative breeder, a non-cooperative breeder or a non-family group cooperative breeder. We fixed the residual variance and covariance at 6.67 and 3.33, respectively, and used a flat prior on the logit scale (mean = 0, variance = residual variance $\times \pi^{2/3}$) for the intercept to improve chain mixing. We used a parameter-expanded prior for the random effects, with variance and covariance set as 6.67 and 3.33, respectively, and a prior mean of 0 and covariance matrix of 25^2. We used 100,000 iterations for each tree and discarded the first 99,999 samples from each, with the first 300 trees also discarded as a burn-in. This gave a total of 13×10^7 iterations with 1,000 saved. We assigned each node in each tree to a given ancestral state (family, non-family, non-cooperative) if that state had posterior probability >0.67 (that is, if it was twice as likely as the other states). Any nodes having similar posterior probabilities for each state (that is, <0.67) were classified as unknown. This allowed us to estimate the number of origins of cooperative breeding in family and non-family groups, and to determine whether transitions between family and non-family cooperative breeding systems are possible or whether these breeding systems always evolve from non-cooperative ancestors.

We confirmed these results using transition rate models fitted with two further techniques: reverse jump Markov chain Monte Carlo (rjMCMC) and stochastic character mapping. First, we used the multi-state module in BayesTraits (v.3) with rjMCMC estimation[58]. We constructed two models. In the first, we used an all-rates-different *Q* matrix to estimate transition rates between family, non-family and non-cooperative states. We resampled across the same 1,000 phylogenies used to estimate ancestral breeding systems in our multinomial BPMM (that is, those not discarded as a burn-in). In the second model, we restricted transitions between family and non-family cooperative breeders in our *Q* matrix, which forces these breeding systems to evolve from non-cooperative ancestors. Again, we resampled across the 1,000 phylogenies not discarded as a burn-in in our multinomial BPMM. Each model was run for 4,000,000 iterations with the first 1,000,000 discarded as a burn-in, and we used hyper priors to reduce uncertainty over prior selection[59]. Model convergence was assessed by inspecting traces of posterior distributions to evaluate chain mixing, by calculating the degree of auto-correlation between successive iterations in each chain and by running each model three times and then using Gelman and Rubin's convergence test to compare within- and between-chain variance. In our first model, transitions between family and non-family cooperative breeding systems were estimated to be zero and we found little evidence of a difference between this model and our second model, where transitions were restricted to be zero (Bayes factor = −0.1). This supports our finding using multinomial BPMMs that family and non-family cooperative breeding systems evolve from non-cooperative ancestors.

We then simulated character histories (family, non-family and non-cooperative states) across the 1,000 phylogenies not discarded as a burn-in in our multinomial BPMM, with ten simulations per tree using the *phytools* R package[60]. We used an equal-rates *Q* matrix with empirical Bayes estimation. We found that family and non-family cooperative breeding systems evolved from non-cooperative ancestors: 88/89 family origins were non-cooperative ancestors (one origin was from a non-family cooperative breeder) and 27/27 non-family origins were from non-cooperative ancestors. This is consistent with results found using the multinomial BPMM and rjMCMC. Note that using an all-rates-different *Q* matrix gave similar results: 71/71 family origins were from non-cooperative ancestors and 29/29 non-family origins were non-cooperative species. However, this *Q* matrix suggested that family group cooperative breeding has been lost 219 times (reverting to non-cooperative systems), which is unlikely given the number of family group species within our dataset and given the 33 losses estimated by our multinomial MCMCglmm. Using an equal-rates *Q* matrix estimated seven loses of family cooperative breeding.

Estimation of ancestral polyandry rates. We used the results from our multinomial BPMM ancestral state estimations to test whether differences in group formation were associated with the mating behaviour of ancestral species. We assigned each node on each phylogeny (1,000, of which 300 were discarded as a burn-in) to the following transition categories based on the breeding system of its descendants: (1) family group origin, (2) family group to family group transition, (3) non-family group origin, (4) non-family group to non-family group transition, (5) non-cooperative to non-cooperative transition and (6) 'other' (all unknown transitions due to uncertainty in ancestral state estimation). These transition categories were then included as a fixed effect (a factor with six levels) in a BPMM with ancestral polyandry as the response variable (number of broods with and without extra-pair paternity, modelled using a binomial distribution with a logit link function) and a phylogenetic (co)variance matrix fitted as a random term. This estimates the polyandry rates for each level of our fixed effect, allowing us to compare the mating behaviour of females prior to the origin of cooperative breeding in family and non-family groups. We used an inverse-Wishart prior for the random term and allowed 50,000 iterations per tree, saving only the last iteration and discarding the first 300 trees as a burn-in. We used the last 1,000 trees in our sample of 1,300 because the first 300 had previously been discarded as the burn-in from our BPMM used to estimate ancestral states (see Estimation of ancestral breeding systems). This gave a total of 3.5×10^7 iterations with 700 saved. We explored the sensitivity of these results to uncertainty in our estimations of ancestral breeding systems, and also to whether polyandry was measured as the percentage of broods that contained chicks sired by multiple males inside or outside the group or the percentage of broods that contained chicks sired by males outside the group only (see Section 2.3 of the Supplementary Methods).

Group formation and division of reproduction. To test whether family and non-family group cooperative breeders differ in how reproduction is divided among group members, we constructed a multi-response BPMM with the number of multi-female groups with and without mixed maternity and the number of multi-male groups with and without mixed paternity as response variables (modelled using binomial distributions with logit link functions). Group formation (two-level factor: family versus non-family) was included as a fixed effect, and the global intercept was removed to estimate intercepts for each trait separately. We estimated the residual and phylogenetic variances in each trait by fitting two 2×2 unstructured variance–covariance matrices as random effects. We used an inverse-Wishart prior for the random effect and allowed 1,000 iterations per tree across 1,300 trees, with the first 300 discarded as a burn-in. Note that the number of multi-female and multi-male groups studied varied considerably between species, ranging from 2 to 35 groups. Using a binomial distribution weights the model in favour of species with larger sample sizes.

Group formation and group size. We constructed two separate BPMMs to test whether family and non-family groups differed in mean and maximum group size. First, we modelled mean group size (log transformed with a Gaussian distribution) as a function of group formation (two-level fixed effect: family versus non-family). We then modelled maximum group size (using a Poisson distribution with a log-link function) as a function of group formation (two-level fixed effect: family versus non-family). We suppressed the global intercept in each model to estimate group sizes for family and non-family groups separately. In each model a phylogenetic (co)variance matrix was included as a random effect. We used an inverse-Wishart prior for the random effect and allowed 1,000 iterations per tree (1,300 trees used in total). We chose mean group size because this was the measure of central tendency available for most species in our sample, and maximum group size to determine whether group formation sets an upper limit on the number of individuals in cooperative groups.

Testing for publication bias. Publication bias occurs when results published in the literature are systematically different from those that are not published, meaning that the effect sizes included in a meta-analysis are not representative of the 'true' relationship between two variables[61]. This can occur, for example, when the chances of publication vary with the direction of the effect size. We did not expect publication bias in our sample of effect sizes, for two reasons. First, many of the studies from which our effect sizes were calculated are observational and thus descriptive, giving no reason to expect relationships in a specific direction not to be reported. Second, both negative and positive values of our effect sizes have a history of being published in high-impact journals[4,38,40], again suggesting that the direction of the relationship does not influence the likelihood of publication. Nevertheless, publication bias was assessed in each of our effect sizes (Zr fecundity, Zr care and Zr survival) by visualizing funnel plots, by conducting trim-and-fill analyses and by regressing the standardized normal deviates of each effect size against the inverse of their standard errors.

Overall, we detected little evidence of publication bias in our effect sizes (Extended Data Fig 3). For Zr care, the results from the trim-and-fill analyses suggested that 17 positive effect sizes were missing. However, the lack of positive effect sizes for the relationship between maternal care and group size is more likely to reflect the underlying biology of cooperatively breeding systems than publication bias: in both family and non-family groups, females typically reduce investment in care when in larger groups. This is reflected by the change in between-study variance across effect sizes when we included group formation (two-level fixed effect: family versus non-family) as a moderator. For Zr care, group formation did not account for any of the between-study variance (I^2 remained 34%) whereas for Zr fecundity, inclusion of group formation as a moderator explained some of the heterogeneity in effect sizes (I^2 was reduced from 87 to 73%), as expected given that relatedness is predicted to influence competition between females within groups. In general, heterogeneity among species is thought to make it difficult to detect publication bias in evolutionary biology[61].

Changes in fecundity, care and survival with group size. We simultaneously tested for differences between family and non-family groups in Zr fecundity, Zr care and Zr survival size by treating these three correlations as a single response variable in a BPMM modelled using a Gaussian distribution. We indexed each observation by the type of correlation it measured (three levels: Zr fecundity versus Zr care versus Zr survival) and included the interaction between this index and group formation (two levels: family vsersus non-family) as a fixed effect in the model. We removed the global intercept to estimate separate intercepts for each type of correlation for family and non-family groups (giving six main effect estimates in total). We accounted for differences between studies in sample size by weighting each effect size by its sampling variance, which was calculated as $1/(n-3)$ where n is the number of groups studied[62]. There are also potentially unknown sources of variation between studies that cannot be explicitly included in analyses. However, this is expected to increase noise in the data, reducing the ability to detect significant relationships[61]. We estimated the residual and phylogenetic variance in each trait separately, by fitting two 3×3 unstructured variance–covariance matrices as random effects. We used an inverse-Wishart prior for the random effect and allowed 1,000 iterations per tree (1,300 trees used in total).

Relationship between fecundity and care in family and non-family groups. We tested whether changes in breeder fecundity in response to having more helpers were correlated with changes in care, using a BPMM with Zr fecundity as the response variable (modelled using a Gaussian distribution) and Zr care (continuous) and group formation (two-level factor: family versus non-family) and their interaction included as fixed effects. Each observation in our response variable was weighted by its inverse sampling variance, and the effect of shared ancestry was modelled by fitting a phylogenetic (co)variance matrix as a random effect. We also fitted sample size (log transformed) associated with Zr care as a fixed effect to account for differences in sampling effort across studies. We used an inverse-Wishart prior for the random effect and allowed 1,000 iterations per tree (1,300 trees used in total). We repeated this analysis, randomly sampling seven family group cooperative breeders from the 21 species available, to explore the sensitivity of our results to the low sample size for non-family groups ($n_{species}=7$).

Relationship between fecundity and survival in family groups. For family groups, we tested whether changes in fecundity with group size were offset by changes in survival by modelling Zr fecundity (Gaussian distribution) as the response variable and Zr survival (continuous) and the log sample size associated with each Zr survival observation as fixed effects using a BPMM. Each Zr fecundity effect size was weighted by its inverse sampling variance, and we included a phylogenetic (co)variance matrix as a random effect. We used an inverse-Wishart prior for the random effect and allowed 1,000 iterations per tree (1,300 trees used in total). It was not possible to examine the same relationship for non-family groups, due to limited data ($n_{species}=3$).

Relationship between survival and care in family groups. Finally, we explored whether changes in maternal survival with group size were associated with changes in maternal care in family groups, using a BPMM with Zr survival as the response variable (Gaussian distribution) and Zr care (continuous) and the log sample size associated with each Zr care observation included as fixed effects. Each Zr survival effect size was weighted by its inverse sampling variance, and a phylogenetic (co) variance matrix was included as a random effect. We used an inverse-Wishart prior for the random effect and allowed 1,000 iterations per tree (1,300 trees used in total). Again, it was not possible to examine the same relationship for non-family groups due to limited data ($n_{species}=2$). We found a negative relationship between Zr survival and Zr care (slope estimate $=-0.37$, CI $=-0.72$ to -0.05, $n_{species}=17$; Extended Data Fig. 2b), which suggests that the reduced costs of care associated with having helpers leads to increased survival of breeding females.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All data generated and analysed during in this study are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.sn02v6x11.

Code availability

The R code detailed all analyses in this study is available via the Dryad Digital Repository https://doi.org/10.5061/dryad.sn02v6x11.

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Author contributions

A.S.G., C.K.C. and P.A.D. conceived the study. P.A.D. designed the study and collected the data. P.A.D. and C.K.C. analysed the data. All authors contributed to writing the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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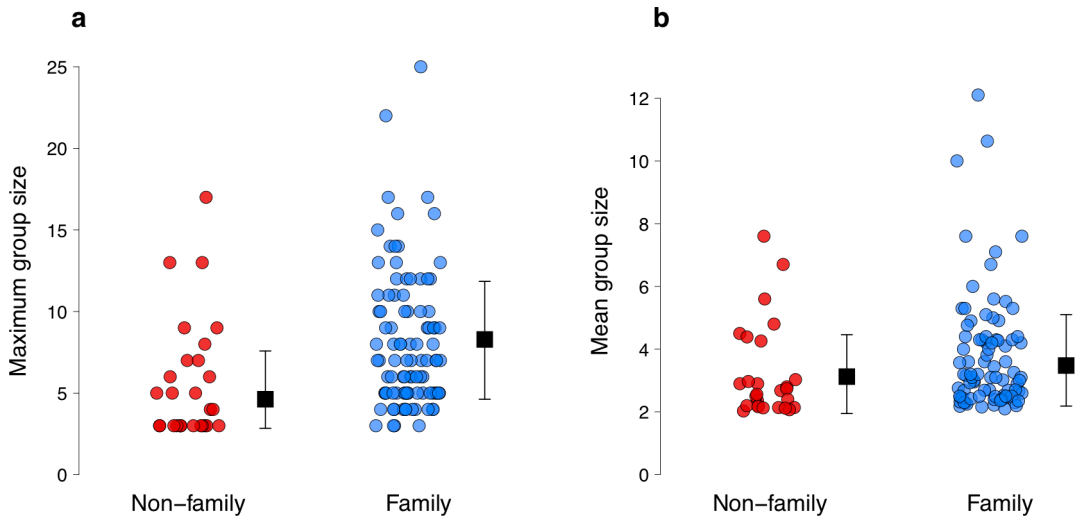
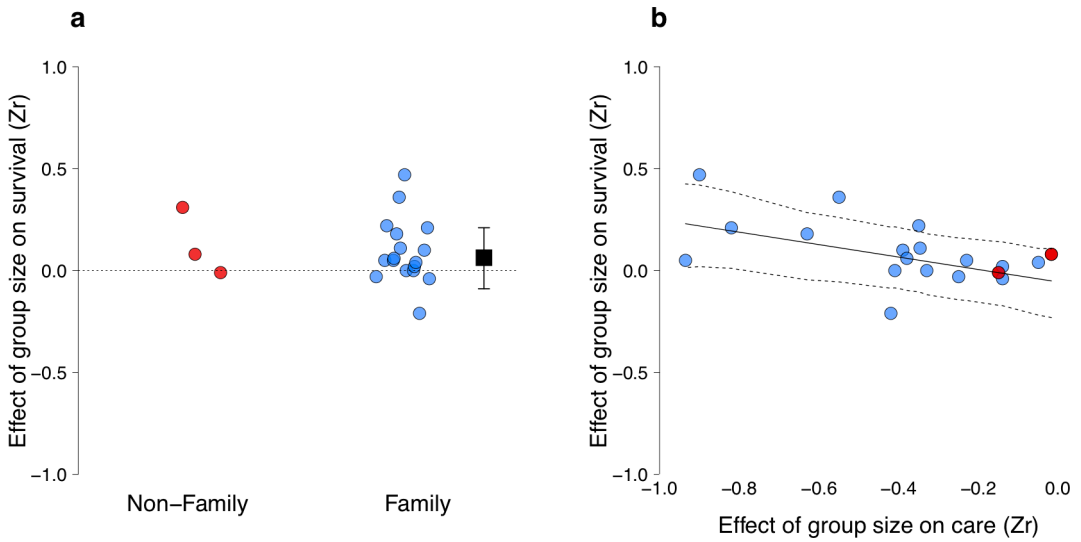


Extended Data Fig. 1 | The evolution of group size. Differences in the maximum (**a**) and mean (**b**) group sizes of family and non-family groups. Dots represent raw data for individual species with the back transformed mode and 95% CI estimated using a BPMM.



Extended Data Fig. 2 | Patterns of survival in groups. (**a**) The change in survival in relation to group size (Zr) in family and non-family groups. (**b**) The relationship between the change in survival in relation to group size (Zr) and how maternal care changes with group size (Zr). In larger family groups (blue dots) survival increases and maternal care decreases. Dots represent raw data for individual species and parameter estimates are the back transformed posterior mode and 95% CI estimated using BPMMs.

	Heterogeneity*	Trim and Fill	Egger's Regression**				
Effect Size	I^2	*N* missing studies	parameter	estimate	se	*t*	*P* value
Zr fecundity	87%	8	intercept	0.31	0.25	1.24	0.22
			slope	-0.05	0.03	-1.58	0.12
Zr care	34%	17	intercept	-0.70	0.27	-2.56	0.01
			slope	0.16	0.06	2.94	0.01
Zr survival	65%	0	intercept	0.29	0.35	0.81	0.43
			slope	-0.02	0.02	-1.05	0.31

* I^2 = between-study variability / total variability

** standard normal deviate of effect sizes ~ 1/se of effect sizes

Extended Data Fig. 3 | Publication bias tests and heterogeneity for each of the Fisher *Z* transformed correlation coefficients used as effect sizes in our study.

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Study description	Comparative analysis across 4731 bird species. Species level data are not independent due to shared evolutionary history therefore phylogenetic regression was used. Sample sizes vary between analyses depending on the data available for each species.
Research sample	4730 bird species - the number of species for which we have breeding system data.
Sampling strategy	We used the maximum amount of data available.
Data collection	P.A.D. collected the data from published sources which were identified using Web of Science.
Timing and spatial scale	Data collection started in January 2015 and lasted until February 2019. Data for individual species are from study populations found across the globe.
Data exclusions	No data were excluded from the analyses.
Reproducibility	We conducted sensitivity analyses to verify that our results are not an artefact of differences in the type of data available for our two main treatments (family and non-family group cooperatively breeding species).
Randomization	Our study is not experimental.
Blinding	Our study is not experimental.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	The study did not involve laboratory animals.
Wild animals	Our study is comparative and uses previously published data and therefore does not involve collecting raw data on wild animals.
Field-collected samples	The study did not involve samples collected from the field.
Ethics oversight	No ethical approval or guidance was required since the study uses previously published data.

Note that full information on the approval of the study protocol must also be provided in the manuscript.