Fluctuating environments favour cooperation among non-kin in birds

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Cooperative groups are highly variable in relatedness and size, but whether this influences the environments where species live remains unclear. We test the prediction that cooperation among nonkin occurs in extreme environments where the mutual benefits of helping are high. This contrasts to family groups where high relatedness reduces the direct benefits required for helping to be favoured, increasing the environments where cooperation persists. Using phylogenetic analyses of birds, we found that the frequency of cooperation (% nests with 3+ adults) and group size across nonfamily breeders ($n_{species}$=39) increased with fluctuations in precipitation across years. In contrast, cooperative breeding in families ($n_{species}$=128) increased in stable, hot environments and group size did not change with climate. Nonfamily and family cooperative breeders inhabited more extreme environments than phylogenetically matched pair breeders. This shows that cooperative breeding is associated with ecological shifts and that fluctuating climates favour cooperation among nonkin, a pattern not seen in family groups.

Introduction

Cooperation over offspring care occurs across the animal radiation from meerkats, *Suricata suricatta*[1], and ants[2] to African wild dogs, *Lycaon pictus*[3] and cichlid fish, *Lamprologus brichardi*[4]. Ecology has long been hypothesized to play an essential role in the evolution of cooperative breeding in animals[5]. This includes a range of environmental conditions[6–9], for example, cooperative breeding has been associated with temperature[10–13] and precipitation[10,11,13,14]. However, cooperative breeding systems are highly variable in the way groups form, their genetic structure, group sizes and how frequent cooperation is relative to pair breeding[15–19]. It is currently unclear whether this variation in cooperative behaviour is linked to the environments species inhabit, which is important for understanding why cooperation evolves and what strategies species use to cope with environmental change.

Cooperative breeding has been shown to evolve via two main routes[20]. First, cooperation may involve family groups that form when offspring remain in their natal territory or dispersal is restricted[21,22]. As individuals in family groups are related, kin selection has been the main explanation for these cooperative breeding systems[17,23,24]. Second, there are species where groups mainly consist of nonfamily members that aggregate after dispersing from their natal area[16,25,26]. Nonfamily groups typically consist of unrelated individuals who all attempt to breed at some point during their life and mutually benefit from cooperative care[2,16,26–28].

The different levels of relatedness in family and nonfamily groups are expected to change the relative importance of environmental conditions in selecting for cooperative behaviour[23]. Low relatedness in nonfamily groups means that the benefits of breeding in a group must be higher than breeding independently for cooperation to be favoured[23,29,30]. Consequently, nonfamily groups are expected to occur in extreme environments where breeding is not possible without help, at least in some years, or where mortality is so high it erodes options for cooperating with kin[5,10,15,28,31,32]. In contrast, family groups most likely evolved under relatively benign conditions, where the costs to independent reproduction are offset by helping relatives, and later colonised more extreme environments[13,33].

It is currently unclear if different evolutionary routes to cooperative breeding are associated with different ecological conditions. This is primarily because the environments where nonfamily cooperative breeders occur have not been quantified and formally compared to family cooperative breeders and pair breeders. As a result, it also remains unclear if environmental conditions explain variation in the size of groups and the frequency of cooperative breeding relative to pair breeding in species that form nonfamily groups[34–38].

Here we use data across birds to test if species that breed in nonfamily and family groups live in environments with different climatic conditions (Supplementary table 1 & 2). The breeding systems of cooperative species were classified using data on the presence of cobreeders (pairs versus multiple breeders) and the relatedness of helpers (presence of nonbreeding related, unrelated or both related and unrelated adults. Methods section ‘Classification of breeding systems’. Table 1). The climatic niches of species were characterized by intersecting range maps with a global climate database to calculate average, within-breeding season variation and between-breeding season variation in temperature and precipitation. Using Bayesian phylogenetic mixed models (BPMM) we first examined if the environments that nonfamily cooperative breeders inhabit differ from family cooperative breeders and phylogenetically matched pair breeding species (five most closely related species: $n_{species}$=460). Second, we tested whether variation in rates of cooperation (% nests with 3+ adults) and group size were related to climate, and if this differed between nonfamily and family groups.

Results

Cooperative breeders occupy more arid environments than pair breeders

Cooperative breeding species inhabit drier environments than pair breeding species (Fig. 1. Fig. S1). Specifically, nonfamily cooperative breeders experience significantly less variation in precipitation during their breeding seasons and tend to be in drier habitats than pair breeders (Fig. 1. Precipitation: BPMM 95% credible interval (CI) = 0.43 (0.06, 0.83), pMCMC = 0.026. Within-year variation in precipitation: BPMM (CI) = 0.54 (0.26, 0.99), pMCMC = 0.001. Supplementary table 3). Similarly, family cooperative breeders occupy areas with lower and less variable precipitation during the breeding season than pair breeders (Fig. 1. Precipitation: BPMM (CI) = 0.33 (0.04, 0.61), pMCMC = 0.034. Within-year variation in precipitation: BPMM (CI) = 0.33 (0.1, 0.63), pMCMC = 0.006. Supplementary table 3).

Nonfamily and family cooperative breeders occupy similar environments

Contrary to expectation, nonfamily and family cooperative breeders inhabited similar climatic niches (Supplementary table 3). These results were consistent across different classifications of cooperative breeding, for example, sub-setting family cooperative breeders according to the numbers of breeders, if helpers were a mix of family and nonfamily members, and which cutoff was used to assign species to breeding categories (e.g. any evidence of cobreeding and helping and 30% nests with cobreeding and helping. See methods 'Sensitivity to breeding system classifications' and 'Specific analyses' sections. Supplementary table 4-8).

It is possible that nonfamily and family cooperative breeders do live in different environments, but this is only evident when examining interactions between climate variables. For example, the benefits of helping when precipitation is low due to reduced food supplies may only materialise when temperatures are high and foraging for long periods in challenging. Comparing only relationships between precipitation or temperature will not detect such effects. We therefore tested if the relationships between climatic variables differ across nonfamily, family and pair breeders.

The direction of correlations between climatic variables was generally similar across nonfamily, family and pair breeding species (Fig. 2. Fig. S3. Supplementary table 9). However, correlations were much stronger in pair breeders compared to both nonfamily and family group cooperative breeders (Fig. 2). In particular, precipitation was more negatively related to temperature within and between breeding seasons in pair breeders compared to cooperative breeders (BPMM phylogenetic correlations of temperature variation between-years versus precipitation (CI): family vs pair = -0.31 (-0.72, 0.18), pMCMC = 0.234; nonfamily vs pair = -0.32 (-0.86, 0.15), pMCMC = 0.126). Similar correlations were observed for temperature variation within breeding seasons (Supplementary table 9). Therefore, pair breeding species living in wet environments experience less variation in temperature than either family or nonfamily cooperative breeders. These results suggest that cooperative breeders inhabit a greater range of environments than pair breeders, and this does not depend on whether groups consist of family or nonfamily members (Fig. 2).

Cooperative breeders have broader climate niches than pair breeders

To further examine the climates that nonfamily, family and pair breeding species are adapted to, we analysed differences in the correlation structure between climate variables across breeding systems. This was done by estimating the proportion of variance in eigenvalues explained by each eigenvector. The eigenvectors describe the axes of variation across the matrix of correlations between climate variables and the eigenvalues indicate the amount of variation in each direction. If the first eigenvector explains a greater proportion of variation in the eigenvalues for a particular group of species, such as pair breeders, this indicates that more variation is aligned along a single axis of climatic variation. This showed that a greater proportion of variation in eigenvalues was explained by eigenvector one in pair breeders compared to nonfamily and family cooperative breeders (Fig 2). Eigenvector one was strongly related to temperature and precipitation, showing that pair breeders live in hot, wet areas and cold, dry areas but not hot and dry, which cooperative breeders amanged to inhabit (Fig 2). This is consistent with cooperative breeders having broader climatic niches than pair breeders, irrespective of whether they form nonfamily or family groups (Fig. 2).

Contrasting effects of climate on cooperation and group sizes in nonfamily and family groups

Despite the climatic niches of nonfamily and family cooperative breeders generally being similar, the associations between climate and rates of cooperation and group sizes were quite different. Cooperative breeding in nonfamily groups significantly increased with variation in precipitation between breeding seasons and with average temperatures (Fig. 3. Fig. S4. % cooperative nests (CI): variation in precipitation between years = 0.35

(0.13, 0.55), pMCMC = 0.002; temperature = 0.31 (0.1, 0.52), pMCMC = 0.004. Supplementary table 11). Similarly, the size of nonfamily groups increased with variation in precipitation across breeding seasons and average temperatures (Fig. 4. Fig. S5. group size (CI): variation in precipitation between years = 1.73 (0.35, 3.53), pMCMC = 0.022; temperature = 2.26 (0.42, 3.45), pMCMC = 0.01. Supplementary table 12). In contrast, in family groups cooperative breeding increased in hotter environments with low variation in temperatures across years (Fig. 3. Fig. S4. BPMM (CI): temperature 0.13 (0.05, 0.28), pMCMC = 0.006; variation in temperature between years -0.17 (-0.27, -0.02), pMCMC = 0.032. Supplementary table 11). Furthermore, group size in family groups did not vary with any climate variables (Fig. 4. Fig. S5. Supplementary table 12).

Discussion

Cooperative breeding systems are highly variable, but whether this is linked to the environments where species live has been unclear. Our results show that the formation of nonfamily cooperative groups is associated with climates where fluctuating precipitation is combined with high temperatures, and these conditions lead to larger group sizes. In contrast, cooperative breeding in family groups is associated with stable hot environments and group sizes are largely decoupled from climatic variation. Compared to pair breeders, both nonfamily and family cooperative breeders occupy a wider range of environments, in particular more arid environments. Together these results illustrate the importance of social behaviour in understanding the environments where species occur.

It has previously been shown that family and nonfamily cooperative breeding species evolved independently with important consequences for the reproductive divison of labour[19,20,24,39]. Our results now indicate that different mechanisms of group formation may also influence the ecological niches of species. Cooperative breeding in nonfamily groups was more prevalent in environments with fluctuating precipitation and high temperatures, whereas family groups were more prevalent in stable, hot environments. Cooperative breeding in vertebrates has repeatedly been associated with high temperatures and variable rainfall, but previous analyses have either considered only family groups or combined family and nonfamily group species[8–14]. Our results are partly aligned with this work, showing that high temperatures are consistently associated with cooperative breeding in both nonfamily and family groups. Independent reproduction can be difficult in hot environments where extended periods of foraging are required to gain enough food for offspring and offspring need protecting from thermal stress and predators[5,32,40–42]. Consequently, both the mutual benefits of cooperating with nonkin and the indirect benefits of helping kin are likely high, leading to consistent selection across different cooperative breeding systems[28].

The increase in nonfamily cooperative breeding with environmental fluctuations, but not family groups, offers insights into the evolution of these different systems. Fluctuating environmental conditions can erode population genetic structure by increasing mortality and dispersal, and with it opportunities for cooperating with kin[43,44]. Data is limited on nonfamily cooperative breeders, but in white-winged choughs, *Corcorax melanorhamphos*, and pied babblers, *Turdoides bicolor*, dispersal increases during periods of high rainfall, presumably because of increased breeding opportunities and lower dispersal costs[45,46]. In pied babblers, dispersal also increases in drought years, potentially due to individuals being forced to find more habitable areas[46]. Consequently, nonfamily cooperative breeding systems may evolve in different environments to family cooperative breeding, not because the benefits of cooperation are different, but because opportunities of associating with kin are.

Similar to frequencies of cooperative breeding, the size of nonfamily groups was linked to hot climates with fluctuating precipitation, whereas family group size varied independently of climate. In nonfamily groups of the greater ani, *Crotophaga major* (one of the species in our dataset with average group sizes), it has been shown that dry years favour small groups because of competition over food, whereas in wet years larger groups are more successful because of better protection against predators[40]. The benefits of cooperation among nonkin in hot environments with variable precipitation may therefore lead to increased groups sizes[40,47]. Alternatively, group sizes may be determined by dispersal, dictated by variation in precipitation in a similar fashion to frequencies of cooperative breeding. In contrast, family group sizes are rarely found to vary with environmental conditions(e.g.[32,44]) and may instead be regulated by diminishing indirect fitness returns as groups get larger and reproductive output is capped by the number of breeders[15,48].

Extreme climatic conditions, where high temperatures are combined with periods of drought, increase reproductive failure and have been linked to the collapse of entire communities[32,44,49]. Cooperative breeding is one way species may cope with such adverse climates[46,50]. Climate change is expected to magnify environmental variation and it has been proposed that cooperative breeding can help reduce the impact of such variation on reproductive success[51]. Recent work shows, however, that variable environments may not consistently select for cooperative behaviour[52]. In line with this, our results show that cooperative breeders are not always in more variable environments, but that variable environments may disrupt family associations changing opportunities for cooperating with kin.

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Figures

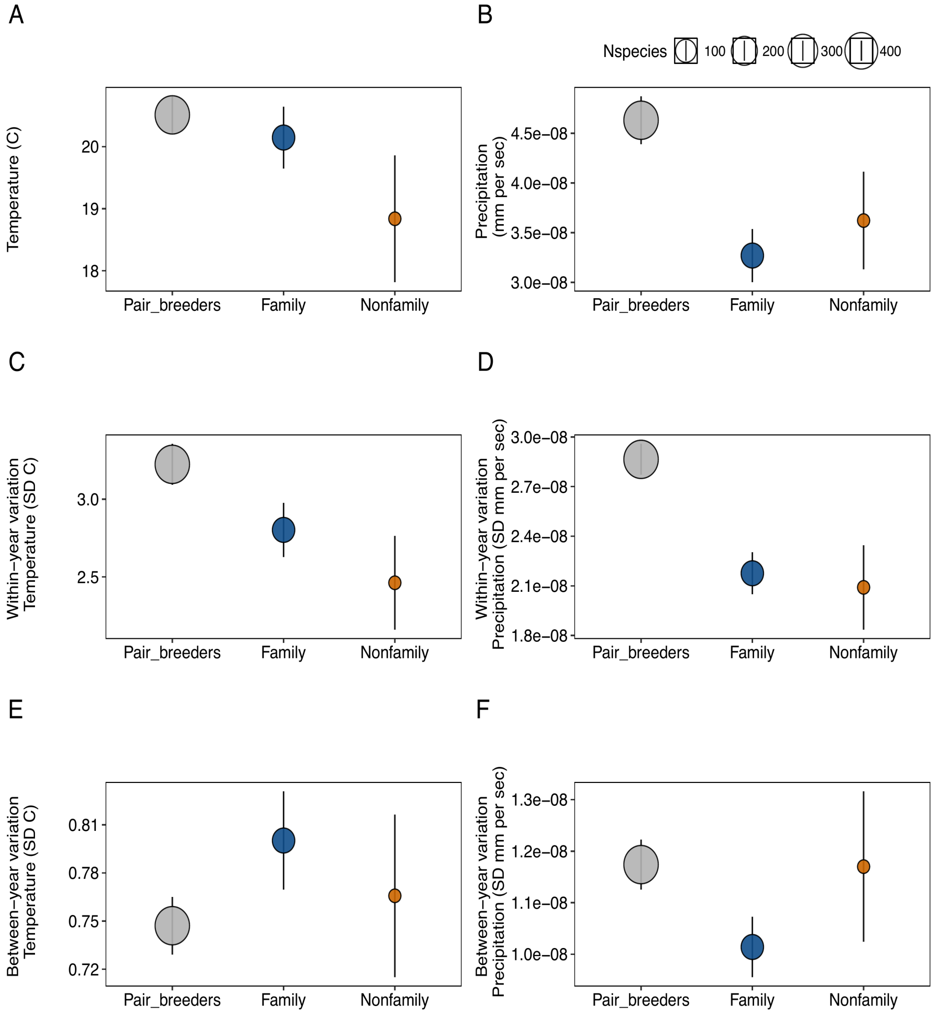

Figure 1: The environments where nonfamily group, family group and pair breeding species occur. Different breeding systems in relation to (A) median temperature, (B) median precipitation (mm per second), (C) temperature variation within years (SD), (D) precipitation variation within years (SD), (E) temperature variation between years (SD), (F) precipitation variation between years (SD). Nonfamily and family cooperative breeders occur in environments with significantly less precipitation and significantly less within-year variation in precipitation than pair breeders. Points are means ± SEs and the size represents the number of species in each category. For plots with more breeding system classifications that distinguish between species with multiple breeders and a combination of family and nonfamily members see figure S2 and S3.

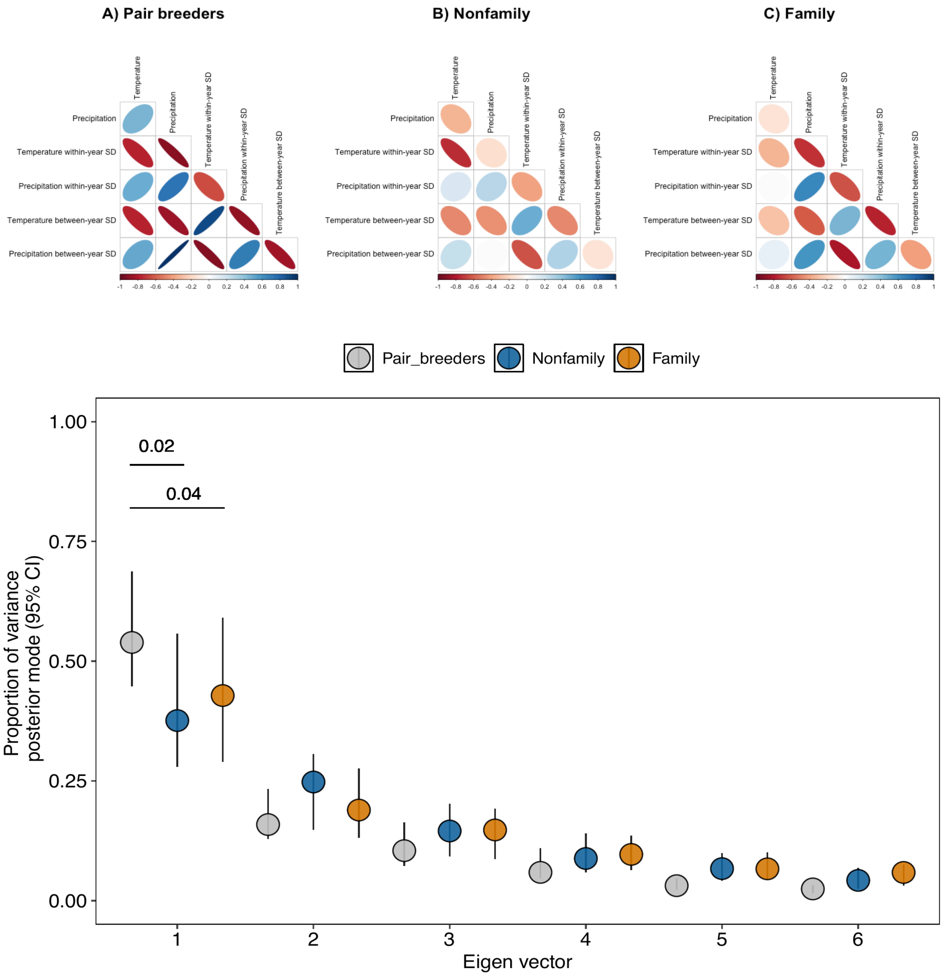

Figure 2: Nonfamily and family cooperative breeders occupy a broader range of climates than pair breeding species. (A-C) The correlational structure of climate variables across the different breeding systems. Ellipses show the direction and strength of correlations (tighter ellipses represent stronger correlations) with more intense blue colours indicating stronger positive correlations and more intense red colours indicating stronger negative correlations. D) The proportion of variation in eigenvalues explained by each eigenvector across breeding systems. If the first eigenvector explains a greater proportion of variation in the eigenvalues for a particular group of species (e.g. pair breeders, family cooperative breeders or nonfamily cooperative breeders) this indicates that more variation is aligned along a single axis of climatic variation. Lines represent significant differences (95% CI of difference does not included 0) with pMCMC values (proportion of iterations greater or less than 0).

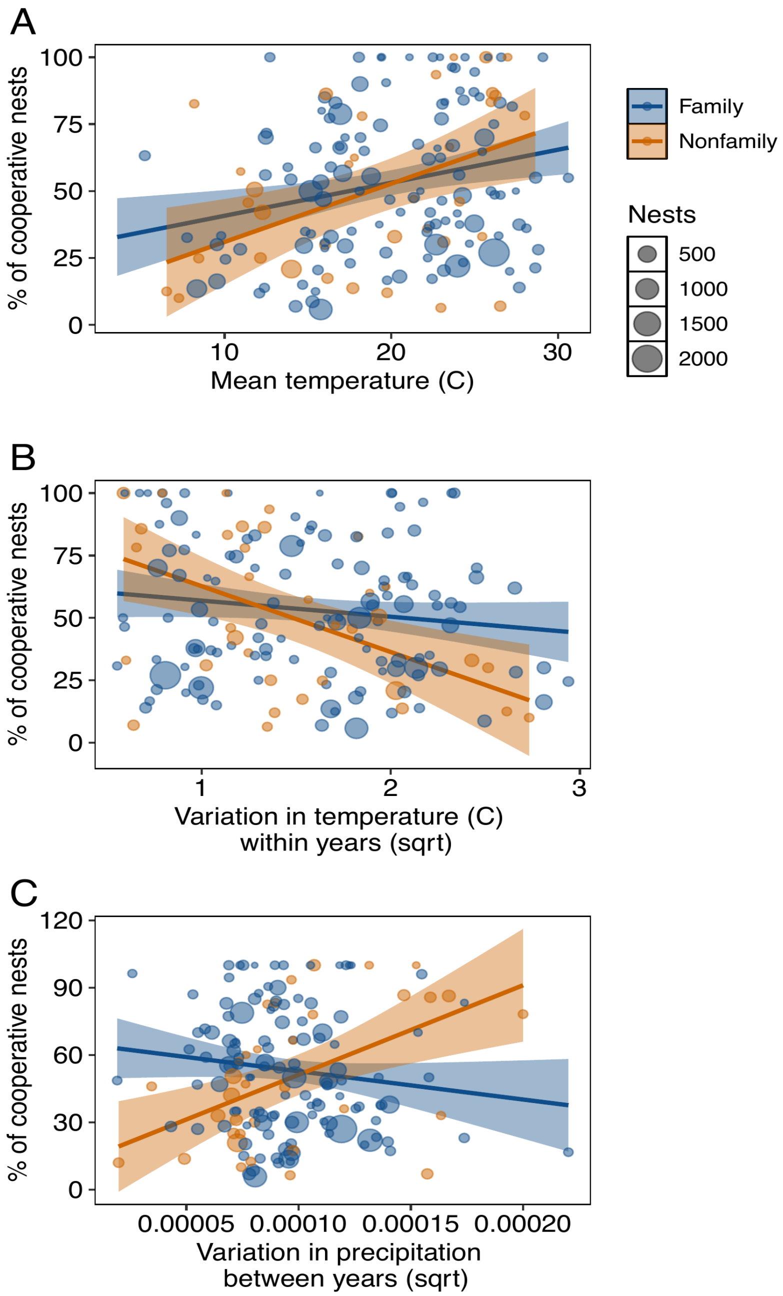

Figure 3: The frequency of cooperative breeding (% nests with >2 adults) increases with fluctuations in precipitation in nonfamily cooperative breeders, but stable, high temperatures in family cooperative breeders. Points represent species with the size of circles proportional to the number of nests studied to ascertain % of cooperative

nests. Regression lines with 95% confidence intervals are plotted. For relationships between % of cooperative nests and all climatic variables see Supplementary figure 5.

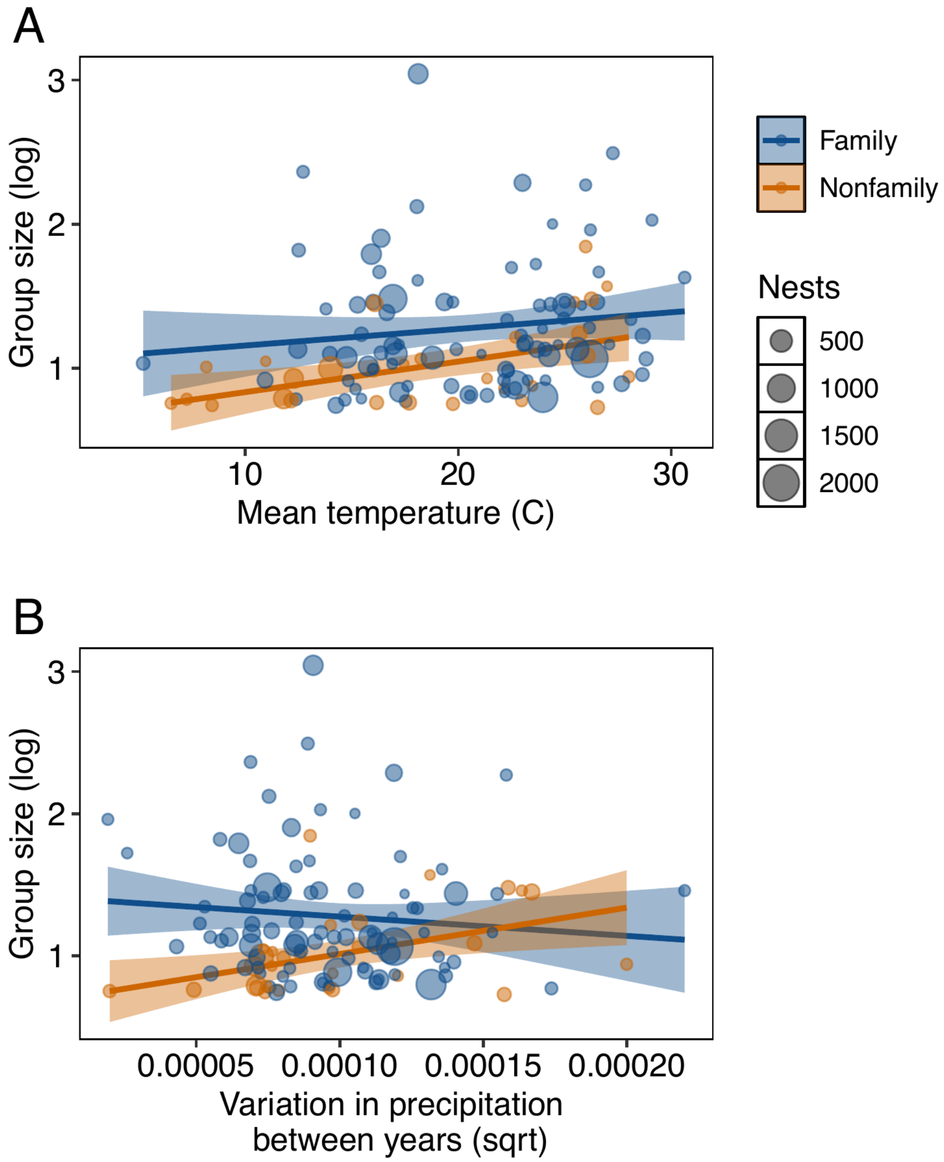

Figure 4: Group size (mean, log transformed) increases with fluctuations in precipitation and temperature in nonfamily cooperative breeders, but not family cooperative breeders. Points represent species with the size of circles proportional to the number of nests studied to ascertain % of cooperative nests. Regression lines with 95% confidence intervals are plotted. For relationships between % of cooperative nests and all climatic variables see Supplementary figure 6.

Methods

To quantify variation across cooperative breeding systems, we used published papers to collect data on the how groups form, relatedness among group members, the presence of cobreeders, the presence of non-reproductive adults that assisted with offspring care, the frequency of nests in the population where group breeding was observed and the size of cooperative groups. To compare cooperative breeders to pair breeders, we selected the five most closely related pair breeding species to each cooperative species using phylogenetic information from Jetz *et. al* 2012[53] and breeding system information from Cockburn 2006[54]. To quantify the environments where species live we extracted climate data for breeding and nonbreeding seasons from study sites and breeding ranges (i.e. temperature and precipitation) from 1979 to 2018 using the ERA5 global bioclimatic indicators dataset derived from reanalysis[55]. We analyzed our data using Bayesian phylogenetic mixed models.

Data collection

We used the species list of cooperative breeders and corresponding literature from Downing et al. 2020[19], supplemented with additional literature (full list of references in Supplementary table 1). To find additional species the following search terms were used: “cooperative breeding” OR “helper” OR “related” OR ”unrelated” OR “kin” OR “nonkin” OR “nonfamily” OR “family” AND “bird” OR “avian”. Where required data were missing for specific species, we also searched for references using only the common and Latin names of the species as given by BirdLife and Handbook of Birds of World. For our searches we used Google Scholar, Pub Med and the library database at Lund University.

Data on breeding systems, helpers and helper relatedness

Classification of breeding systems

Species were classified according to the presence of cobreeders in groups (pair or multiple breeders) and the presence of related and/or unrelated individuals that helped raise offspring (Table 1). Pairs within cooperative species were socially monogamous pairs with one or more helpers. Multiple breeders were any species where more than two adults contribute offspring to the brood, ascertained using information on joint nesting females and rates of within-group multiple paternity. Classifications were based on species-specific articles and available information in review articles on avian breeding systems (Supplementary tables S1 & S2)[13,19,26,54]. Data were only included if exact percentages of nests with cobreeders (pair versus multiple) and the presence of nonfamily and family helpers (yes versus no) were recorded (but see section 'Sensitivity to breeding system classficiations' for relaxation of this criteria). This reduced the number of species from 39 to 32 for nonfamily cooperative breeders and 128 to 58 for family cooperative breeders. Classifications of breeders and helpers were made at a threshold of >10% of nests, for example, species were recorded as having multiple breeders if there were more than two breeding adults at more than 10% of nests.

Table 1. Classification of different cooperative breeding systems.

Breeders	Family Helpers	Nonfamily Helpers	Group size	Detailed Classification	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

Breeders = reproducing individuals, Helpers = adult individuals foregoing reproduction, Group size >2 = cooperative species. Note there were no species with clear evidence of a pair of breeders with nonfamily helpers.

Classification of helpers and helper behaviour

Helpers were defined as adult non-reproducing individuals that assisted with offspring care. Immature individuals were disregarded in this study and not included in any data or analyses. For example, if a species had helpers at 100% of nests but 50% of the helpers were juveniles, species were recorded as having helpers at 50% of nests. If it was clear that both juvenile and adult helpers were present at nests, but it was not possible to disentangle the exact percentage of helper presence for each age group from any references, we assummed an estimate of 50% for each helper age group. While helping traditionally includes a wide range of behaviours (e.g., nest construction, incubation, provisioning of the incubation female, nest and chick defence and provisioning of chicks), our data collection only included verified accounts of incubation and/or feeding of chicks or fledglings. Studies including other accounts of helping behaviour were excluded. Studies in which observations of incubation or feeding were rare (i.e. only for one nest or only observed on one occasion) were also excluded.

Relatedness of helpers to breeders

The relatedness of helpers to the breeding pair and chicks they helped raise was assessed as high, medium or low using information on genetic markers and pedigrees constructed from ringing data. In cases of multiple studies on the same species using different methods, we first used information from genetic markers to assess relatedness, followed by pedigree data (Supplementary table 3). For species with polygamous, polyandrous or polygynandrous mating systems, we assume that breeding/adult individuals are unrelated unless genetic analyses of the population specifically state otherwise. If data on relatedness was too sparse to assess if groups members were nonfamily or family, species were excluded from analyses.

Sensitivity to different breeding system classifications

The quality of data we were able to extract from the available literature varied across species. For the analyses presented in the manuscript we used a threshold of >10% nests where citeria were met. However, to assess the sensitivity of our results to excluding species without data on the exact percentages of nests with cobreeders and the presence of nonfamily and family helpers, we classified as many species as possible using a summary of available information from all references for a given species (Supplementary table 1). In cases of discrepancies between references, we implemented a hierarchical decision-making process with advantage given to information based genetic data, then ringing data, then observational data and lastly anecdotal or referred to information (i.e. information based on other studies, unpublished data, personal communication or references of unclear origin).

We also examined the sensitivity of our results to classifying species at a 10% threshold by reclassifying breeding systems at a threshold of >30% of nests (Supplementary table 1). For example, if a species had multiple breeders at 15% of nests, nonfamily helpers at 20% of nests and family helpers at 40% of nests it would be classified at the 10% threshold as “multiple mixed” (main analyses) whereas it would be reclassfied at a >30% threshold as “pair family”.

Breeding seasons

As some cooperative species have widespread distributions, breeding seasons can vary widely between study sites. We therefore applied a two-step approach in assessing breeding seasons. First, we assessed breeding seasons for the specific study site for each species given in references (Supplementary table 1). In the few cases where a breeding season was not stated in the reference, we used breeding seasons given for the same species at identical study sites, or sites within reasonable proximity in different references, or lastly from Handbook of Birds of the World[56]. In cases where breeding seasons given for species at the same location did not match across references, we recorded all months where breeding was reported to occur across references. For the breeding seasons of pair breeding species we used Handbook of Birds of the World[56] (Supplementary table S2).

Climate data

Information on temperature and precipitation was extracted from the ERA5 global bioclimatic indicators dataset[55]. This dataset combines multiple sources of observational data with forecast models to accurately reconstruct the global weather conditions between 1979 to 2018 at a resolution of 0.5° x 0.5°. We extracted data on monthly mean air temperature at 2m above the surface in units of Kelvin and monthly mean precipitation as accumulated liquid and frozen water, comprising rain and snow, falling onto the Earth's surface in meters per second.

The primary benefit of using the ERA5 reanalysis data over observational data is gap-free coverage in both space and time. This approach also assimilates a vast array of observational weather data from different sources into a model that accounts for how different climatic variables interact, resulting in highly reliable estimates of past climatic conditions[57]. Precipitation datasets based purely on in-situ direct observations, such as the CRU dataset (one of the longest running observational climate datasets that has previously been used in studies of cooperative breeding e.g.[11,13,58], are more influenced by individual rain-gauge estimates, which are sensitive to factors such as local topological features[59]. Reanalysis data, in contrast, assimilates multiple sources of observational data e.g. from satellites and weather stations, into a forecast model to generate estimates. Consequently, reanalysis data may be less impacted by anomalies in single sources of observational data[57,59,60].

For all species we extracted information on temperature and precipitation for study sites for cooperative breeding species and centroid coordinates for pair breeding species. We also examined temperature and precipitation values across entire distributions by intersecting climate data with range maps from BirdLife International[61] and Handbook of Birds of the World[56]. The map shapefiles contain information on the seasonal distribution of each species, allowing us to separate breeding and wintering ranges. To extract the climatic data for the relevant coordinates for each species from the gridded ERA5 dataset the R package 'Raster' was used[62]. This resulted in datasets containing monthly mean estimates of temperature and precipitation for each species between 1979-2018. For the data extracted using species ranges (ii) we then calculated a median value across the range for each time point. From each of these datasets, we selected only the breeding season months for each species (see 'Breeding seasons'). Three summary values were then calculated for each dataset for each species: (i) the median breeding season temperature and precipitation across the full 40 year period (calculated from yearly medians); (ii) the within breeding season variation in temperature or precipitation as the median of the standard deviation within years of each of these variables; and (iii), the between breeding season variation in temperature or precipitation as the standard deviation of the yearly medians of each of these variables.

There was strong correspondence between measurements at study sites/centroid values and measurements across whole ranges (correlation coefficients across datasets (r): temperature median and variation r >0.79; precipitation median and variation r >0.73. See R script "data_nonfam.R"). Therefore we only analysed climate data from study sites/centroid values.

Data compilation

Raw data on cooperative breeding species is presented in Supplementary table 1 with references. Data on breeding seasons and climate data for all species, together with summarised information on cooperative breeders, is presented in Supplementary table 2. Datasets were compiled using the R script 'data_nonfam.R'.

Statistical analyses

General Overview

Three sets of analyses were conducted using multi-response Bayesian Phylogenetic mixed models (MR-BPMM) with Markov chain Monte Carlo (MCMC) estimation implemented in the R package MCMCglmm[63]. First, we tested if there were mean differences in the climates occupied by different types of cooperative breeders and pair breeders. Second, we examined if the relationships between climate variables differed between cooperative and pair breeders. Third, we analysed if the percentage of nests with cooperative breeding and the number of individuals in groups were related to climate across nonfamily and family cooperative breeders.

Model settings

For MR-BPMMs default priors were used for fixed effects (independent normal priors with zero mean and large variance (10^10)) and for random effects inverse-gamma priors were used (V = diag(n), nu = n − 1 + 0.002, where nu is the degree of belief and n was equivalent to the number of response traits). Phylogenetic relationships were modelled by fitting a variance-covariance matrix constructed from the phylogeny as a random effect. To account for uncertainty in phylogenetic relationships, we ran models across a sample of 1500 trees. Estimates from the last iteration from tree i were used as starting values for tree i+1. Estimates from the last iteration of each tree were saved, with samples from the first 500 trees being discarded as a burn-in. Each tree was sampled for 2000 iterations with a burn-in of 1999 and a thinning interval of 1. Model convergence was examined by repeating each analysis three times and examining the correspondence between chains using the R package 'coda'[64] in the following ways: (i) visually inspecting the traces of the MCMC posterior estimates and their overlap; (ii) calculating the autocorrelation and effective sample size of the posterior distribution of each chain; and (iii) using Gelman and Rubin's convergence diagnostic test that compares within- and between- chain variance using a potential scale reduction factor (PSR). PSR values substantially higher than 1.1 indicate chains with poor convergence properties.

Parameter estimation

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

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

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

where V_i is the focal random effect, V_{RE} is the sum of all random effects and V_e is the residual variance on the latent scale[65,66].

Specific analyses

Median climatic differences across cooperative breeders and pair breeders

To test for climatic differences across breeding systems a MR-BPMM was used with the responses of median, variation within years and variation between years for temperature and precipitation (six responses) and breeding system (nonfamily cooperative breeders, family cooperative and pair breeders) as a fixed effect. The "at.level" notation in MCMCglmm was used to estimate each response variable at the level of each breeding system. For details see model m3 in R code.

To verify that our results were not dependent on how breeding systems were classifications we re-ran model m3 with the breeding system defined as: i) 'pair breeders', 'pair with family helpers', 'pair with family and nonfamily helpers', 'multiple breeders with family helpers' and 'nonfamily' (Table 1. Rcode model m4. Supplmentary table 4); ii) 'pair breeders', 'pair with helpers', 'multiple breeders' (Rcode model m5. Supplmentary table 5); and iii) 'pair breeders', 'family helpers', 'family and nonfamily helpers' and 'nonfamily' (Rcode model m6. Supplmentary table 6). We also tested whether classifying species as having multiple breeders, family helpers and nonfamily helpers using all information and a 30% threshold influenced our results by re-running model m3 including all species (Rcode models m7.Supplmentary table 7) and 30% classifications (Rcode models m8. Supplmentary table 8). Across all these analyses we found qualitatively and quantitatively similar results (Supplementary tables 3 to 9. Model numbers correspond to table numbers).

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

To examine if the correlations between climatic variables differed across breeding systems we re-ran model m3 including separate phylogenetic variance-covariance matrices for each breeding system (nonfamily cooperative breeders, family cooperative and pair breeders). This was done using the “at.level” notation in MCMCglmm and variance-covariance estimates were used to calculated phylogenetic correlations between all climate variables for each breeding system (Rcode model m9).

It is possible that including more pair breeding species (460 versus 39 nonfamily and 128 family) may bias variance and covariance estimates across climate variables. We therefore verified that our phylogenetic variance-covariance estimates for pair breeders were not different from cooperative breeders by down-sampling our data to the same number of species as family cooperative breeders and re-running analyses (Rcode model m10). The results were qualitatively and quantitatively similar (Supplementary table S10).

To analyse the structure of the phylogenetic covariance matrices across breeding systems we calculated the eigenvectors and their eigenvalues for each posterior sample from model m9 for each breeding system using the R function ‘eigen’. To test if the structure of the covariances between climate variables was different across breeding systems, we calculated the posterior mode and 95% CIs of the pairwise differences between pair, family cooperative and nonfamily cooperative breeders in the proportion of variance in eigenvalues explained by each eigenvector (Fig. 2). Differences where the 95% CIs did not span 0 and less than 5% of iterations was greater or less than 0 were considered statistically significant.

Differences in the % of nests with cooperative breeder and number of individuals in groups in relation to climate

To test if the proportion of nests where there was cooperative breeding was related to the climate, we re-ran model m3 including the proportion of nests with more than two individuals (logit transformed) as a covariate interacted with each climate variable separately for nonfamily and family cooperative breeders using the ‘at.level’ notation in MCMCglmm (Rcode model m11). Finally, the relationship between the number of individuals in groups and climate across family and nonfamily cooperative breeders was estimated using the same setup as model m11, but including the number of individuals in groups instead of the proportion of cooperative nests (Rcode model m12).

Data and code availability

All code, data and analysis results are available at the open science framework (osf.io project number qhvs5) and can be located at doi.org using the doi number (https://doi.org/10.17605/OSF.IO/QHVS5). Full citations of references in supplementary tables are given in the method references[65-498].

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Ethics declarations

Competing interests

The authors have no competing interests.

Supplementary Information

Supplementary tables 1 to 12 are provided in xlsx and html format in the files “SupplementaryTables.html” and “SupplementaryTables.xlsx”. Full citations of references in supplementary tables are given in the method references 65-498