Research

Author for correspondence:
Allison E. Johnson
e-mail: ajohnson165@unl.edu

†Present address: Department of Biology, University of Nevada Reno, Reno, NV 89557, USA.
‡Present address: School of Biological Sciences, Monash University, Clayton, VIC 3800, Australia.

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

Allison E. Johnson[1], Joseph F. Welklin[2,3,†], Ian R. Hoppe[4,‡] and Daizaburo Shizuka[5]

[1]School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE 68588, USA
[2]Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14850, USA
[3]Cornell Laboratory of Ornithology, Ithaca, NY 14850, USA
[4]School of Natural Resources, University of Nebraska-Lincoln, Lincoln, NE 68583, USA
[4]School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE 68588, USA

(iD) AEJ, 0000-0002-6447-3179; JFW, 0000-0002-7534-8795; IRH, 0000-0001-6482-2386; DS, 0000-0002-0478-6309

Cooperatively breeding species exhibit a range of social behaviours associated with different costs and benefits to group living, often in association with different environmental conditions. For example, recent phylogenetic studies have collectively shown that the evolution and distribution of cooperative breeding behaviour is related to the environment. However, little is known about how environmental variation may drive differences in social systems across populations within species, and how the relationship between environmental conditions and sociality may differ across species. Here, we examine variation in social group size along a steep environmental gradient for two congeneric cooperatively breeding species of fairywrens (Maluridae) and show that they exhibit opposing ecogeographic patterns. Purple-backed fairywrens, a species in which helpers increase group productivity, have larger groups in hot, dry environments and smaller groups in cool, wet environments. By contrast, superb fairywrens, a species with helpers that do not increase group productivity despite the presence of alloparental care, exhibit the opposite trend. We suggest differences in the costs and benefits of sociality contribute to these opposing ecogeographical patterns and demonstrate that comparisons of intraspecific patterns of social variation across species can provide insight into how ecology shapes social systems.

1. Introduction

The evolution of cooperative breeding social systems, in which individuals beyond a single breeding pair (such as non-breeding helpers) contribute to rearing of young, is thought to be driven by a combination of kin-selection benefits, social benefits of group living and constraints on breeding opportunities [1–5]. Each of these benefits and constraints associated with cooperative breeding interacts with environmental variation in different ways [6–8]. For example, social benefits of group living may buffer the negative effects of harsh and unpredictable environments on individuals when helpers contribute to breeder reproduction, offspring care and increased survival of group members (social benefits hypothesis; [9–12]). Conversely, environmental factors also influence the availability of opportunities for independent breeding and, when such opportunities are limited, can promote the formation of extended family groups through delayed dispersal of young (ecological constraints hypothesis; [2,13–16]).

Accumulating evidence suggests that the interplay between environmental variation and contributions of helpers to breeding output has in fact shaped the evolution and occurrence of cooperative breeding species. For example, species in which helpers provide alloparental care (care directed towards non-descendant
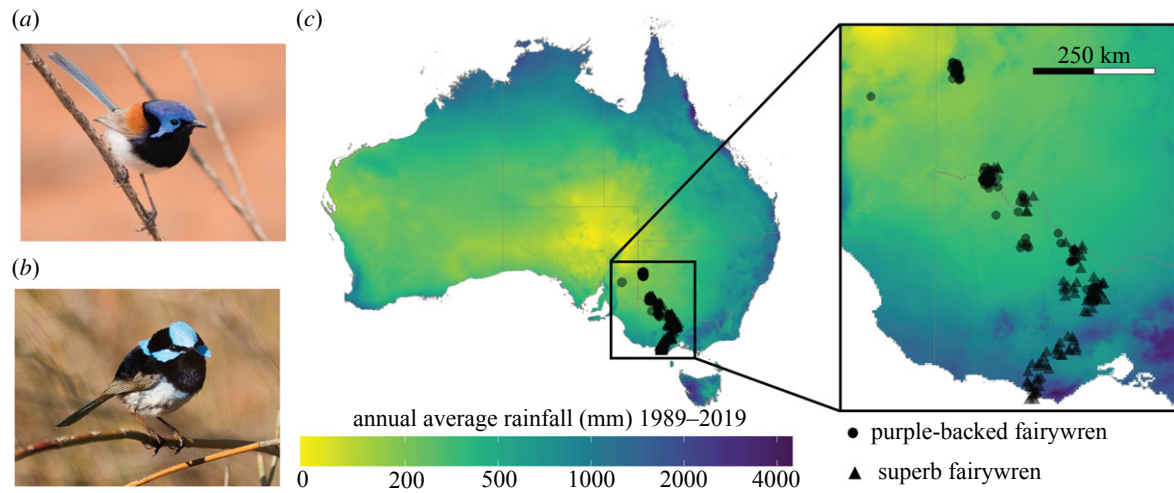
Figure 1. Study system and study locations. Fairywren group size was observed across a climate gradient in southeastern Australia for (a) purple-backed and (b) superb fairywrens (illustrations depict males of each species). (c) Map shows average annual rainfall, one aspect of climate variation, in Australia from 1989 to 2019 (the timespan covered by the axis of long-term climate represented in the analyses), and points represent locations where each social group was observed. Inset is an enlargement of the region where groups were observed. Circles are purple-backed fairywren populations and triangles are superb fairywren populations. Most sites had several groups observed, and many had observations for both species, thus we jittered points for visual clarity.

young) are more prevalent in habitats with high environmental variability, whereas species without alloparental care are more prevalent in less variable environments [11,17,18]. Further, clade-specific analyses within birds reveal that the relationships between environmental conditions and the distribution of cooperative breeding species differ between clades with different types of within-group dynamics. In starlings (Sturnidae), a clade in which subordinates can increase the reproductive output of breeders, cooperatively breeding species are associated with harsh and unpredictable environments [9], whereas in hornbills (Bucerotidae), a clade in which helpers primarily contribute to resource defence, cooperatively breeding species are more likely to occur in benign and stable environments [19]. One explanation proposed for such opposing relationships between environmental conditions and cooperative breeding in different clades is that environmental conditions affect within-group conflict differently based on different helper contributions [8,20]. Thus, multiple lines of evidence suggest that variation in the contributions of helpers appears to affect how environmental variability relates to the evolution and distribution of cooperative breeding species, and emphasize that cooperative breeding behaviour encompasses a spectrum of social behaviours that can vary in their relationship with the environment [21].

In contrast with the existing work on the evolutionary origins and distributions of cooperative breeding species, relatively few studies have asked how environmental variation regulates variation of attributes, such as group size, in cooperative breeding groups between populations within species. There are at least two hypotheses to explain how environmental variation can regulate variation in group size across populations within species which parallel the two main hypotheses for the evolution of cooperative breeding. First, harsher environmental conditions may favour larger group size in species where helpers provide alloparental care that buffers the effects of lower or less predictable resource availability. This extends the 'social benefits' hypothesis for the evolution of cooperative breeding to intraspecific variation in sociality. Alternatively, group sizes could be larger in environments

associated with higher reproductive output, leading to few breeding vacancies at higher population density, forcing queuing [22]. This extends the 'ecological constraints' hypothesis to intraspecific variation in sociality.

Fairywrens present an ideal system for examining intraspecific variation in group size because (i) all species exhibit some degree of cooperative breeding, (ii) they are well studied and thus we have a good understanding of the benefits of cooperation across various species, and (iii) many species range over a variety of climates. Further, climate has been tied to reproductive success in this family, with rainfall positively predicting nest initiation, clutch size, and reproductive success [23–30], probably because of the positive correlation between precipitation and resource availability (e.g. insect availability; [28,31,32]). Importantly, there are steep gradients in rainfall and temperature across many species' ranges, providing an opportunity to test how climate variation relates to social variation within species. Here, we examine social variation in the purple-backed and superb fairywrens (*Malurus assimilis* and *Malurus cyaneus*), a pair of congeneric species that coexist along the same rainfall and temperature gradient in Australia (figure 1), with the two species overlapping in southeastern Australia. Both species are considered cooperative breeders, but they exhibit a stark contrast in the benefits that alloparental care confers to their groups. In the purple-backed fairywren, breeders with helpers have higher reproductive output than those in pairs, suggesting that they gain direct reproductive benefits from the presence of helpers at the nest [33,34]. By contrast, the presence of helpers in superb fairywren groups provides primarily indirect fitness benefits such as load-lightening (reduced provisioning effort when helpers provide compensatory allocare; [35]) and increased female survival, but does not directly increase reproductive success [26,36]. Instead, evidence suggests that group living in superb fairywrens is driven primarily by juvenile males that stay in their natal territory when breeding vacancies are lacking, thus benefiting from queuing or survival opportunities [14,37]. As such, purple-backed fairywrens fit the expectations of the 'social benefits' hypothesis for cooperative

breeding, while superb fairywrens better fit the expectations of the 'ecological constraints' hypothesis for cooperative breeding.

The overlapping ranges of these two species in a region with a steep environmental gradient and the stark contrast in the role of helpers within their social groups provides an ideal opportunity to test hypotheses about the effects of environmental conditions on intraspecific variation in cooperative social systems. Because there are little data on intraspecific variation in group size in any cooperative breeding bird species, we first test whether clinal variation in group size exists along the same environmental gradient in both species. We then examine whether the pattern of clinal variation in each species conforms to expectations under the social benefits or ecological constraints hypotheses, which predict opposite patterns. We expect that purple-backed fairywrens—the species with greater reproductive benefit from helpers—should exhibit patterns predicted by the social benefits hypothesis. That is, they should have larger groups in arid, harsh environments where group living could buffer groups against the uncertainty of resources, and smaller groups in benign habitats where helpers might become unnecessary for successful reproduction and where helpers would gain greater reproductive fitness from breeding on their own. By contrast, we expect that superb fairywrens should exhibit patterns predicted by the ecological benefits hypothesis: larger group sizes in benign environments where the habitat is more saturated and more juveniles delay dispersal owing to lack of breeding opportunities.

We tested these predictions by performing two observational transects along the region of co-occurrence between the two species (figure 1). We show that these species do indeed exhibit opposing patterns of social group size variation in the directions predicted by the social benefits and ecological constraints hypotheses, providing further evidence that responses of social systems to environmental variation can be dependent on the types of benefits and costs that group members can experience.

2. Material and methods

(a) Study system

Purple-backed (figure 1a) and superb fairywrens (figure 1b) are small, cooperatively breeding passerines native to Australia [25]. The purple-backed fairywren (previously *Malurus lamberti assimilis*, a subspecies of the variegated fairywren, and recently elevated to species status; [38–40]) can be found throughout much of Australia west of the Great Dividing Range, while the superb fairywren is primarily found in southeastern to central-eastern Australia, with the two species co-occurring over much of southeastern Australia.

While both species can breed in pairs, they often form cooperative breeding groups that are most frequently composed of one breeding pair and one or more typically non-breeding helpers. The social behaviour of these species differs in several ways. In purple-backed fairywrens, allocare by helpers increases breeder productivity by enhancing offspring survival [33,34]. While most purple-backed fairywren helpers are young males who are related to the breeding pair, 43% of helpers are females who are typically unrelated [33]. Of offspring with known age and origin ($n = 65$ males and 17 females), 88.89% of males remain in their natal territory their first year and sometimes stay their whole lives, while only 11.76% of females remain in

their natal territory their first year (unpublished data collected by A. E. Johnson 2019). Helpers of both sexes provision young, and extra-pair paternity rates decrease in groups with helpers [34], suggesting that male helpers gain inclusive fitness benefits through kin selection by remaining in their natal territory and rearing related young. While male helpers are reluctant to disperse into experimentally made breeding vacancies, female helpers readily disperse, suggesting that females may join unrelated groups in order to queue for breeding vacancies and may 'pay-to-stay' through provisioning young (A. E. Johnson and S. Pruett-Jones 2018, unpublished data; [36,41]).

Superb fairywren helpers are almost exclusively male offspring of one or both members of the breeding pair from a previous breeding attempt. In some populations, nearly all first-year males (87%; [42]) remain in their natal territory, and many stay in their natal territories their whole lives. All superb fairywren helpers provision young [43], and while the presence of helpers is correlated with increased breeding female survival, they do not increase reproductive output of the group [26]. Extra-pair paternity is extremely high in superb fairywrens (95% of all broods and 76% of offspring in one population), and rates of extra-pair paternity are higher in groups with helpers [44]. As a result, helpers probably gain little inclusive fitness through kin selection while remaining in their natal territory [26,36]. Instead, superb fairywren helper males probably stay owing to a lack of available territories to disperse into; when dispersal does occur, it is typically short in distance and in response to breeding vacancies [14,37,42]. Thus, despite exhibiting allocare, superb fairywrens largely fit the criteria for 'family-living' social systems (*sensu* Griesser *et al*. [18]) in which breeders tolerate the presence of helpers provided there are enough resources, and helpers stay because they can gain survival and other benefits [18,37,45].

(b) Population observation and group size estimation

We performed two observational sampling transects, one over 10 days in December 2018 (late breeding season) and the second over 7 days in August 2019 (early breeding season). We visited local parks, conservation areas and national parks, starting in coastal Victoria and extending north to inland New South Wales, passively observing fairywren social groups and recording their composition (group size and sex of individuals) at populations along the transect (figure 1c). Fairywren social groups are gregarious, and group size can be easily and accurately identified in a short period of time (A. E. Johnson (12 years) and J. F. Welklin (10 years), personal experience). Males of both species are distinguished from females during the breeding season by bright blue and black plumage, while females are generally brown. While some first-year males exhibit delayed plumage maturation, they can be distinguished from females by black rather than brown bills. We distinguished fledglings from females by behaviour, presence of yellow gapes and shorter tails. Fledglings, when present, were excluded from group size calculations. We observed each group until we were confident all adult group members had been seen. Incomplete groups, or observations that were obviously of multiple groups disputing a territory boundary where we could not confidently assign group composition to the participating groups, were not included in subsequent analyses. We observed 87 complete superb fairywren social groups and 92 purple-backed fairywren social groups. Each social group is considered one data point. Complete data (including incomplete groups) are available by request via eBird [46], where data are submitted as checklists with comments describing the social groups at each site.

(c) Climate variables

To understand the relationship between sociality and environmental conditions in these two species, we examined climate

metrics at two different scales: a long-term scale (30 years) and a short-term scale (1 year). These scales represent two ways climate may impact social group size. If social group size is shaped by environmental effects on social evolution, then variation across populations should relate to a metric which encompasses variation in climate over a long timescale [17]. However, social group size may also be the product of year-to-year variation in reproductive success, thus the climate in the year preceding the observation may have a strong effect on group size.

We downloaded two gridded datasets, monthly rainfall and monthly maximum temperature, from the Australian Bureau of Meteorology. Rainfall grids have a resolution of 0.05 degrees (approx. 5 km; [47]) and maximum temperature grids have a resolution of 0.025 degrees (approx. 2.5 km; [48]). For the long-term climate metrics, we used a window of grids from March 1988 to February 2019, spanning 30 years of data. Within this time window, a single year's annual data was considered to span March–February, such that each year begins in the austral fall and ends with the austral summer. For each checklist location, we generated one average annual value and two measures of variation in both rainfall and temperature from the long-term climate grids (*sensu* Jetz & Rubenstein [17]). *Average annual rainfall* was calculated by summing rainfall totals for each month in a year, then averaging rainfall across years and log transforming the result. *Rainfall variation within years* was calculated by summing non-transformed seasonal rainfall totals (autumn: March–May, winter: June–August, spring: September–November, summer: December–February) and calculating s.d. across seasons within each year. We then averaged s.d. across all years, providing an estimate of the seasonality of rainfall. *Rainfall variation across years* was determined by calculating seasonal s.d. of the non-transformed average seasonal rainfall across all years, then averaging across all seasons. Temperature metrics were determined similarly. *Average monthly maximum temperature* was calculated by averaging the maximum monthly temperatures within a year, then averaging across years. *Temperature variation within years* was determined by calculating the s.d. of average seasonal maximum temperatures within each year, then averaging the s.d. across all years. *Temperature variation across years* was determined by calculating the seasonal s.d. of average seasonal maximum temperatures across all years, then averaging across all seasons.

For the short-term climate metrics we used gridded data from the calendar year preceding the date each social group was observed during, spanning September of the prior year to August of the same year (i.e. September 2017–August 2018 for points collected in 2018 and September 2018–August 2019 for points collected in 2019). From these data, we generated two rainfall values, *total annual rainfall* (the sum of monthly rainfall log-transformed) and *monthly variation in rainfall* (the s.d. of non-transformed monthly rainfall), and two temperature values, *average monthly maximum temperature* and *monthly variation in maximum temperature* (the s.d. of maximum monthly temperature).

Both long- and short-term climate variables were extracted from each raster for the corresponding latitude and longitude where each social group was observed. The calculated climate variables are closely related. Thus, we performed principal components (PC) analyses on the 30-year time window and on the 1-year time window separately to reduce the dimensionality of climate variables used in subsequent analyses.

For the long-term window, climate variables loaded heavily onto PC1 and to a lesser extent onto PC2 (PC1$_{long}$ and PC2$_{long}$ throughout). PC1$_{long}$ explains 80.87% of the variance in long-term climate and describes an inverse relationship between temperature and rainfall. Sites with high PC1$_{long}$ have relatively higher, more variable rainfall and lower, less variable temperatures and represent more benign environments for fairywren reproduction, while sites with low PC1$_{long}$ are more arid and hotter, representing harsher environments. PC2$_{long}$ explains 13.40% of the total variance and is best described as an axis of across-year stability in climate (electronic supplementary material, table S1 and figure S1). As PC1$_{long}$ explains the large majority of the variance in long-term climate, we excluded PC2$_{long}$ from subsequent analyses.

For the short-time window, climate variables similarly loaded heavily onto PC1 and not to PC2 (PC1$_{short}$ and PC2$_{short}$ throughout). PC1$_{short}$ explains 86.7% of the variance and describes an inverse relationship between temperature and rainfall, similar to PC1$_{long}$. PC2$_{short}$ explains 10.1% of the total variance and is also best described as an axis of monthly temperature stability (electronic supplementary material, table S2 and figure S2). As PC1$_{short}$ explains the large majority of the variance in short-term climate, we excluded PC2$_{short}$ from subsequent analyses.

Gridded climate data manipulation and PC analyses were conducted in R 4.1.0 [49].

(d) Analysis of the ecogeographic correlates of social group size

To identify predictors of social group size, we fitted generalized linear mixed-effects models (GLMMs) in R using the package *lme4* [50]. We used the number of helper individuals (group size − 2) as the response to improve the fit of a Poisson model, as group size will never be less than two (a single breeding pair). We tested five models, each with a Poisson error distribution and log link function: (i) null (intercept only), (ii) species only, (iii) species, PC1$_{long}$, and species x PC1$_{long}$ interaction, (iv) species, PC1$_{short}$, and species x PC1$_{short}$ interaction, and (v) a global model which included main effects of species, PC1$_{long}$, and PC1$_{short}$ as well as species x PC1$_{long}$ interaction and species x PC1$_{short}$ interaction. To account for non-independence of groups seen at the same location, we included a random intercept of checklist identity (ID) in all models. Year (2018 or 2019) was also included as a random effect to account for non-independence of observations within each season [51]. The best-performing model was selected based on lowest Akaike information criterion for small sample size (AIC$_c$), calculated using the package *MuMIn* (electronic supplementary material, table S2; [52]). We performed residual diagnostics to test residual fit and to test for overdispersion on the best-fitting model using the package *DHARMa* [53] and detected no significant issues. We calculated *p*-values from type 3 Wald chi-squared tests for fixed effects in models with interaction terms. While analyses were conducted on the number of helpers, the plotting of the results, predictions and discussion of such are framed in terms of groups, with all values predicted from the model being back transformed, then adding two to account for the presence of the breeding pair and to make estimates easier to interpret.

3. Results

(a) Climate variables

The long-term climate variable PC1$_{long}$ strongly correlates with latitude (Spearman rank correlation: $r_s = -0.88$, $p \leq 0.001$), with northern sites becoming increasingly arid and hot. The short-term climate variable PC1$_{short}$ similarly strongly correlates with latitude (Spearman rank correlation: $r_s = -0.97$, $p \leq 0.001$) and again indicates northern sites becoming increasingly arid and hot.
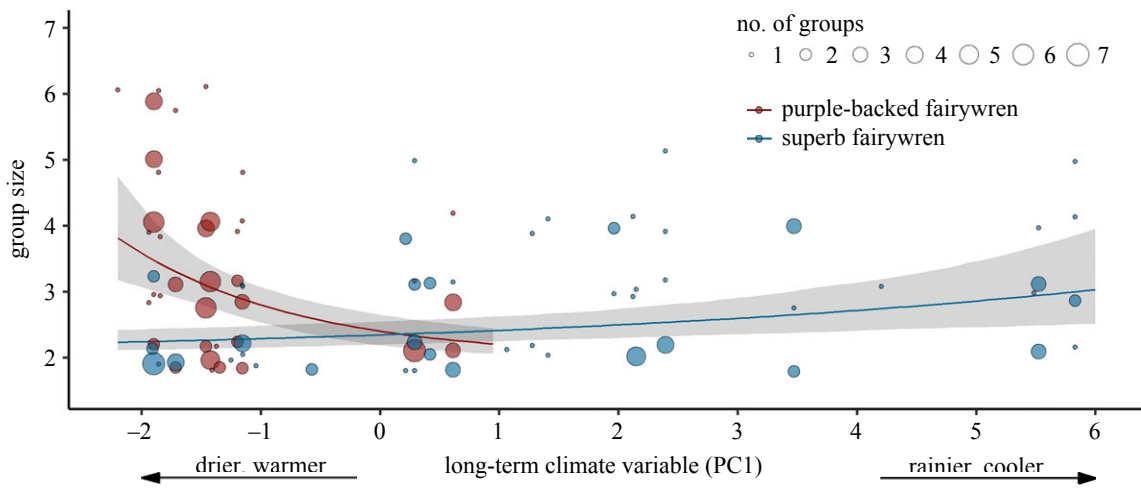
Figure 2. Group size in relation to an axis of long-term climate ($PC1_{long}$). Purple-backed fairywrens (red) and superb fairywrens (blue) show opposing patterns of intraspecific variation in group size along an axis of long-term climate (GLMM; species $\times$ $PC1_{long}$ interaction: $p < 0.001$). Points are groups, scaled by the number of groups within the same PC1 value (population) with the same group size. Points are jittered vertically and are transparent for visualization of overlapping points. Lines and bootstrapped 95% confidence intervals are predicted from the model and back transformed for ease of interpretation. See table 1 for full model description.

Table 1. Full description of Poisson-distributed GLMM describing the relationship between the number of helpers and the fixed effects of *species* and an axis of long-term climate, $PC1_{long}$, with random effects of checklist ID and year. (*p*-values were obtained from a type 3 Wald chi-squared test; italicized *p*-values indicate significant differences ($\alpha = 0.05$).)

	estimate	s.e.	χ^2	*p*-value
intercept	−0.844	0.313	7.268	*0.007*
species(superb)	0.0518	0.372	0.019	0.889
$PC1_{long}$	−0.769	0.205	14.145	*<0.001*
species(superb) * $PC1_{long}$	0.957	0.208	21.13	*<0.001*

(b) Ecogeographical correlates of group size

The best-fitting model had species, $PC1_{long}$, and species by $PC1_{long}$ interaction as fixed effects (table 1 for top model estimates; see the electronic supplementary material, table S3 for model comparisons). The AIC_c of this model was 3.62 lower than the second best-performing model (the global model) and has 6.12 times the empirical support (evidence ratio of 0.16; [54]). The rest of the models (1, 2 and 4 as listed above) had ΔAIC_c values of greater than or equal to 9.83 relative to the best-fit model (evidence ratio of less than 0.007). Below, we only discuss the best-fitting model, however, the full description of the second best-fitting model can be found in the electronic supplementary material, table S4.

Purple-backed and superb fairywrens showed opposing patterns of group size variation along the same environmental gradient in long-term climate (GLMM, fixed effect species by $PC1_{long}$: $p < 0.001$; table 1, figure 2). Purple-backed fairywrens exhibited larger group sizes in drier, hotter climates and smaller groups sizes in wetter, cooler climates (purple-backed fairywren slope estimate $\pm$ s.e.: −0.78 $\pm$ 0.20). Superb fairywrens exhibited the opposite trend with larger group sizes in wetter, cooler climates and smaller group sizes in drier, hotter climates (superb fairywren slope estimate $\pm$ s.e.: 0.19 $\pm$ 0.05). There was a twofold decrease in the predicted group size of purple-backed fairywrens from the hottest, driest end to the wettest, coolest end of their distribution along the gradient (calculated from $PC1_{long} = -2.2$ to $PC1_{long} = 0.95$, approximate extremes of the range observed). For superb fairywrens, we saw a 1.5-fold increase in the predicted group size from the hottest, driest end to the wettest, coolest end of their distribution along the gradient (calculated from $PC1_{long} = -2.2$ to $PC1_{long} = 6.00$, approximate extremes of the range observed). Running the top model separately for each species confirmed the results from species by $PC1_{long}$ interaction: purple-backed fairywren group size exhibited a negative relationship with $PC1_{long}$ (GLMM, fixed effect $PC1_{long}$: $p < 0.001$; slope $\pm$ s.e.: −0.78 $\pm$ 0.19; model summary can be found in the electronic supplementary material, table S5), and superb fairywren group size exhibited a positive relationship with $PC1_{long}$ (GLMM, fixed effect $PC1_{long}$: $p < 0.001$; slope $\pm$ s.e.: 0.20 $\pm$ 0.01; model summary can be found in the electronic supplementary material, table S6).

4. Discussion

Our results confirm that social group size shows clinal variation along an environmental gradient in two related cooperative breeding species. However, the two focal species exhibited opposing patterns of clinal variation along the same transect. Specifically, purple-backed fairywrens exhibited increasing group size in inland populations with harsher conditions (relatively lower rainfall and higher temperatures), while superb fairywrens exhibited increasing group size in coastal populations with more benign conditions (relatively higher rainfall, cooler weather). Our study shows that the interplay between environmental conditions and sociality, and the clinal variation they produce across populations, can differ substantially between species.

The deep knowledge of the differences in the cooperative breeding systems of our two focal species stemming from long-term studies allows us to make some inferences about

the causes of these opposing patterns of clinal variation in group size. A long-term study of purple-backed fairywrens at an inland, arid site (Brookfield Conservation Park, South Australia) previously showed that helpers contribute to increased reproductive output of breeders [33]. Experiments show that male helpers are reluctant to disperse from their natal territory even when breeding vacancies are nearby, suggesting that male helpers are not simply queuing to gain access to breeding vacancies (A. E. Johnson and S. Pruett-Jones 2018, unpublished data). Thus, cooperative breeding groups in purple-backed fairywrens are probably driven by social benefits of groups rather than ecological constraints on breeding opportunities. Given this, we suggest that the formation of large social groups in hot, dry climates may be related to greater effect of helper contributions to nest success, while the formation of small groups or pairs in cool, wet climates is possible when the addition of helpers is unnecessary for high reproductive output. This hypothesis could be tested by examining whether group size is correlated with reproductive success in harsher habitats but not in benign habitats.

By contrast, prior long-term studies show that superb fairywren reproductive output is related to rainfall and likely territory quality, but not the number of helpers [26]. Superb fairywren helpers are primarily young males that delay dispersal to remain in their natal territory, and these helpers quickly occupy breeding vacancies at nearby territories when they arise [14,37]. Thus, cooperative breeding in superb fairywrens is thought to be driven primarily by ecological constraints. Given this prior evidence, we suggest that superb fairywrens may be more likely to form social groups in wet, cool climates when the habitat is saturated owing to high reproductive output and survival, but breed in pairs in hot, dry climates where reproductive output and survival may be lower. Helpers may be tolerated by breeders in mild conditions because helpers in resource-dense environments may inflict little cost to breeders. Previous field experiments have shown there is substantial potential for conflict between dominant and subordinate males in this species [55]. This hypothesis could be tested by examining whether conflict is alleviated in benign environments compared to harsh environments.

The patterns we document here are consistent with recent theoretical studies demonstrating that environmental variation can have different effects on cooperatively breeding social groups, depending on the different forms and intensities of helping behaviour [20,56,57]. Shen et al. [20] used insider-outsider conflict theory to show that cooperatively breeding groups which gain collective social benefits may perform better in harsh environments, while conflict will be exacerbated in groups with helpers which do not increase group productivity. Similarly, García-Ruiz et al. [57] modelled coevolution of dispersal and helping behaviour under different ecological scenarios to show that group benefits drive evolution of cooperative breeding in harsh environments but not benign environments. Finally, Kao et al. [56] used simulation models to show that groups in which additional members increase the per capita resources available to the group through their contributions to resource acquisition will increase in size under resource scarcity. Collectively, these theoretical studies pose the hypothesis that the specific forms of benefits accrued by cooperative breeding group members influence how those groups respond to differences in environmental conditions owing to their effects on within-group social dynamics. We suggest that broader examination
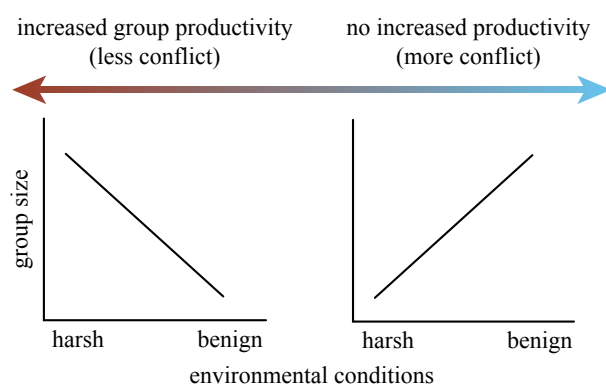
Figure 3. Conceptual illustration of the proposed relationship between group size and environmental conditions in cooperatively breeding species with different sources of benefit gained from sociality. Globally, species in which helpers contribute more reproductive benefits to the group are primarily found in harsh environments, whereas species in which helpers contribute less to the group or provide only resource defense benefits are primarily found in benign environments. In line with this, and with work suggesting intra-group conflict and benefit will shift with environmental conditions, we propose that these expectations can extend to social group size variation within species, generating opposing ecogeographic patterns in different species. Here we show expectations for the extreme ends of this social spectrum; species in which helpers contribute more reproductive benefits should form larger groups in harsh environments (left graph), where the potential productivity increase from help at the nest is highest, and should have smaller groups in benign environments, where pairs might be expected to successfully raise young on their own. However, we expect that species in which helpers contribute less should only form groups in benign environments where young individuals lack dispersal opportunities (right graph).

of intraspecific variation in social groups across environmental gradients in different species could generate empirical data to test this hypothesis (figure 3). Under this hypothesis, species with greater contribution by helpers will have the largest social groups in harsh environments but the smallest group sizes in benign environments (figure 3, left side), whereas species with helpers that provide little benefit to the group should have the smallest groups in harsh environments but the largest group sizes in benign environments (figure 3, right side). Ideally, such empirical tests will also involve field experiments to demonstrate the social mechanisms regulating group size in these systems—e.g. do conflicts between breeders and potential helpers change across environmental conditions, or does helping behaviour and its impact on reproductive output change across environmental conditions?

Clear evidence for intraspecific ecogeographical patterns in cooperative social groups has remained rare, but anecdotal evidence suggests that such intraspecific variation in sociality may be common. For example, acorn woodpeckers (Melanerpes formicivorous) in central California, USA form large cooperatively breeding social groups that defend acorn granaries which support their year-round territories [58], while populations in southeastern Arizona, USA where acorns are insufficiently plentiful to support year-round residency, primarily breed in pairs and migrate [59]. Cooperative breeding is recovered in the Columbian Andes, where aseasonal food sources can again support year-round residency [60]. This pattern suggests territory quality and the ability to defend a joint territory might be beneficial in environments with stable or defensible resources in the acorn woodpecker system. In grey-crowned babblers (Pomatostomus temporalis),

a species in which helpers increase group reproduction [61], group size was shown to increase along a latitudinal gradient from north to south in northern Australia, a relationship that could relate to increasing harshness experienced by southern populations within this gradient [62] and the social benefits of being in a group. Similarly, group size in Australian magpies (*Gymnohrina tibicen*) in which helper provisioning is additive to breeder provisioning [63] appears to be larger in more arid, southern populations across Australia [64–67]. Taken together, these observations suggest that the types of benefits received by cooperative breeders could indeed generate different relationships between group size and environmental quality in other systems.

Prior studies of the relationship between environmental conditions and social behaviour have tended to take one of two alternative approaches. The long-term population study approach has used temporal variation in environmental conditions and examines how such conditions intersect with life history and social dynamics to generate variation in group productivity, size and membership [26,68–72]. Meanwhile, phylogeographical studies identifying evolutionary patterns between species [8,18] have been used to address why species with different degrees of 'helping' by helpers are more prevalent in different environments. Both approaches have yielded important insights into the evolution of cooperative breeding, but the former typically involves focusing on single populations, overlooking variation in social behaviour between populations, while the latter overlooks both temporal and geographical variation within species by regarding sociality as a species-specific trait. However, it has long been recognized that social systems can vary widely between populations within species (e.g. carrion crow: [73], common mole rat: [74], prairie voles: [75]).

We argue that close examination of interspecific and intraspecific variation in social systems provides important additional information about the ecological correlates of the evolution of social behaviour. Those few studies that have examined both levels of variation have provided insight into ecological and evolutionary processes that differ between species (e.g. *Polistes* wasps; [76,77]). The *Malurus* fairywren systems are ideal for asking how benefits of sociality might alter the relationship between ecogeography and sociality, as the species in this clade are well known and their social behaviour is relatively easy to quantify. We show here that related species with similar social systems can exhibit opposite patterns of social group size variation across the same environmental gradient. Such variation in ecogeographical patterns may suggest generalizable biological principles that underlie adaptations to environmental conditions. Our finding motivates further behavioural experiments along such social and ecological gradients to test hypotheses regarding the mechanisms underlying ecogeographic patterns in social systems. More generally, we suggest that replicated studies along ecological gradients can enrich our understanding of the environmental contexts underlying the evolution of cooperative behaviour.

References

1. Hamilton WD. 1964 The genetical evolution of social behaviour. I and II. *J. Theor. Biol.* **7**, 1–52. (doi:10.1016/0022-5193(64)90039-6)

2. Emlen ST. 1982 The evolution of helping. I. An ecological constraints model. *Am. Nat.* **119**, 29–39.

3. Brown JL. 1987 *Helping and communal breeding in birds: ecology and evolution.* Princeton, NJ: Princeton University Press.

4. Wong M, Balshine S. 2011 The evolution of cooperative breeding in the African cichlid fish, *Neolamprologus pulcher. Biol. Rev.* **86**, 511–530. (doi:10.1111/j.1469-185X.2010.00158.x)

5. Riehl C. 2013 Evolutionary routes to non-kin cooperative breeding in birds. *Proc. R. Soc. B* **280**, 20132245. (doi:10.1098/rspb.2013.2245)

6. Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT. 1992 The evolution of delayed dispersal in cooperative breeders. *Q. Rev. Biol.* **67**, 111–150. (doi:10.1086/417552)

7. Covas R, Griesser M. 2007 Life history and the evolution of family living in birds. *Proc. R. Soc. B* **274**, 1349–1357. (doi:10.1098/rspb.2007.0117)

8. Lin YH, Chan SF, Rubenstein DR, Liu M, Shen SF. 2019 Resolving the paradox of environmental quality and sociality: the ecological causes and consequences of cooperative breeding in two lineages of birds. *Am. Nat.* **194**, 207–216. (doi:10.1086/704090)

9. Rubenstein DR, Lovette IJ. 2007 Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.* **17**, 1414–1419. (doi:10.1016/j.cub.2007.07.032)

10. Covas R, du Plessis MA, Doutrelant C. 2008 Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. *Behav. Ecol. Sociobiol.* **63**, 103–112. (doi:10.1007/s00265-008-0640-2)

11. Lukas D, Clutton-Brock T. 2017 Climate and the distribution of cooperative breeding in mammals. *R. Soc. Open Sci.* **4**, 160897. (doi:10.1098/rsos.160897)

12. Komdeur J, Ma L. 2021 Keeping up with environmental change: the importance of sociality. *Ethology* **127**, 790–807. (doi:10.1111/eth.13200)

13. Stacey PB. 1979 Habitat saturation and communal breeding in the acorn woodpecker. *Anim. Behav.* **27**, 1153–1166. (doi:10.1016/0003-3472(79)90063-0)

14. Pruett-Jones SG, Lewis MJ. 1990 Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature* **348**, 541–542. (doi:10.1038/348541a0)

15. Arnold KE. 1999 Cooperative breeding in birds: the role of ecology. *Behav. Ecol.* **10**, 465–471. (doi:10.1093/beheco/10.5.465)

16. Borger MJ, Richardson DS, Dugdale H, Burke T, Komdeur J. 2023 Testing the environmental buffering hypothesis of cooperative breeding in the Seychelles warbler. *Acta Ethol.* (doi:10.1007/s10211-022-00408-y)

17. Jetz W, Rubenstein DR. 2011 Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.* **21**, 72–78. (doi:10.1016/j.cub.2010.11.075)

18. Griesser M, Drobniak SM, Nakagawa S, Botero CA. 2017 Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLoS Biol.* **15**, e2000483. (doi:10.1371/journal.pbio.2000483)

19. Gonzalez JCT, Sheldon BC, Tobias JA. 2013 Environmental stability and the evolution of cooperative breeding in hornbills. *Proc. R. Soc. B* **280**, 20131297. (doi:10.1098/rspb.2013.1297)

20. Shen SF, Emlen ST, Koenig WD, Rubenstein DR. 2017 The ecology of cooperative breeding behaviour. *Ecol. Lett.* **20**, 708–720. (doi:10.1111/ele.12774)

21. Koenig WD. 2017 What drives cooperative breeding? *PLoS Biol.* **15**, e2002965. (doi:10.1371/journal.pbio.2002965)

22. Hatchwell BJ, Komdeur J. 2000 Ecological constraints, life history traits and the evolution of cooperative breeding. *Anim. Behav.* **59**, 1079–1086. (doi:10.1006/anbe.2000.1394)

23. Tidemann SC, Marples TG. 1987 Periodicity of breeding behaviour of three species of fairy-wrens (*Malurus* spp.). *Emu – Austral. Ornithol.* **87**, 73–77. (doi:10.1071/MU9870073)

24. Nias RC, Ford HA. 1992 The influence of group size and habitat on reproductive success in the superb fairy-wren *Malurus cyaneus*. *Emu – Austral. Ornithol.* **92**, 238–243. (doi:10.1071/MU9920238)

25. Rowley I, Russell EM. 1997 *Fairy-wrens and grasswrens: Maluridae*. Oxford, UK: Oxford University Press.

26. Cockburn A, Sims RA, Osmond HL, Green DJ, Double MC, Mulder RA. 2008 Can we measure the benefits of help in cooperatively breeding birds: the case of superb fairy-wrens *Malurus cyaneus*? *J. Anim. Ecol.* **77**, 430–438. (doi:10.1111/j.1365-2656.2007.01351.x)

27. van de Pol M *et al*. 2013 Problems with using large-scale oceanic climate indices to compare climatic sensitivities across populations and species. *Ecography* **36**, 249–255. (doi:10.1111/j.1600-0587.2012.00143.x)

28. Hidalgo Aranzamendi N, Hall ML, Kingma SA, van de Pol M, Peters A. 2019 Rapid plastic breeding response to rain matches peak prey abundance in a tropical savanna bird. *J. Anim. Ecol.* **88**, 1799–1811. (doi:10.1111/1365-2656.13068)

29. Lv L, Liu Y, Osmond HL, Cockburn A, Kruuk LEB. 2020 When to start and when to stop: effects of climate on breeding in a multi-brooded songbird. *Glob. Change Biol.* **26**, 443–457. (doi:10.1111/gcb.14831)

30. Welklin JF, Lantz SM, Khalil S, Moody NM, Karubian J, Webster MS. 2022 Photoperiod and rainfall are associated with seasonal shifts in social structure in a songbird. *Behav. Ecol.* **34**, 136–149. (doi:10.1093/beheco/arac110)

31. Recher HF, Majer JD, Ganesh S. 1996 Seasonality of canopy invertebrate communities in eucalypt forests of eastern and western Australia. *Austral. Ecol.* **21**, 64–80. (doi:10.1111/j.1442-9993.1996.tb00586.x)

32. Woinarski JCZ, Cullen JM. 1984 Distribution of invertebrates on foliage in forests of south-eastern Australia. *Austral. Ecol.* **9**, 207–232. (doi:10.1111/j.1442-9993.1984.tb01359.x)

33. Johnson AE. 2016 *Evolution and sociality in fairy-wrens (Aves: Maluridae)*. Chicago, IL: University of Chicago.

34. Johnson AE, Pruett-Jones S. 2018 Reproductive promiscuity in the variegated fairy-wren: an alternative reproductive strategy in the absence of helpers? *Anim. Behav.* **139**, 171–180. (doi:10.1016/j.anbehav.2018.03.015)

35. Hatchwell BJ, Russell AF. 1996 Provisioning rules in cooperatively breeding long-tailed tits *Aegithalos caudatus* : an experimental study. *Proc. R. Soc. Lond. B* **263**, 83–88. (doi:10.1098/rspb.1996.0014)

36. Dunn PO, Cockburn A, Mulder RA. 1995 Fairy-wren helpers often care for young to which they are unrelated. *Proc. R. Soc. Lond. B* **259**, 339–343. (doi:10.1098/rspb.1995.0050)

37. Cockburn A, Osmond HL, Mulder RA, Double MC, Green DJ. 2008 Demography of male reproductive queues in cooperatively breeding superb fairy-wrens *Malurus cyaneus*. *J. Anim. Ecol.* **77**, 297–304.

38. McLean AJ, Toon A, Schmidt DJ, Joseph L, Hughes JM. 2012 Speciation in chestnut-shouldered fairy-wrens (*Malurus* spp.) and rapid phenotypic divergence in variegated fairy-wrens (*Malurus lamberti*): a multilocus approach. *Mol. Phylogenet. Evol.* **63**, 668–678. (doi:10.1016/j.ympev.2012.02.016)

39. McLean AJ, Toon A, Schmidt DJ, Hughes JM, Joseph L. 2017 Phylogeography and geno-phenotypic discordance in a widespread Australian bird, the variegated fairy-wren, *Malurus lamberti* (Aves: Maluridae). *Biol. J. Linn. Soc.* **121**, 655–669. (doi:10.1093/biolinnean/blx004)

40. Gill F, Donsker D (eds). 2023 IOC World Bird List (v13.1). (doi:10.14344/IOC.ML.13.1)

41. Gaston AJ. 1978 The evolution of group territorial behavior and cooperative breeding. *Am. Nat.* **112**, 1091–1100.

42. Mulder RA. 1995 Natal and breeding dispersal in a co-operative, extra-group-mating bird. *J. Avian Biol.* **26**, 234–240. (doi:10.2307/3677324)

43. Dunn PO, Cockburn A. 1996 Evolution of male parental care in a bird with almost complete cuckoldry. *Evolution* **50**, 2542–2548. (doi:10.1111/j.1558-5646.1996.tb03643.x)

44. Mulder RA, Dunn PO, Cockburn A, Lazenby-Cohen KA, Howell MJ. 1994 Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. *Proc. R. Soc. Lond. B* **255**, 223–229. (doi:10.1098/rspb.1994.0032)

45. Drobniak SM, Wagner G, Mourocq E, Griesser M. 2015 Family living: an overlooked but pivotal social system to understand the evolution of cooperative breeding. *Behav. Ecol.* **26**, 805–811. (doi:10.1093/beheco/arv015)

46. Sullivan BL, Wood CL, Iliff MJ, Bonney RE, Fink D, Kelling S. 2009 eBird: a citizen-based bird observation network in the biological sciences. *Biol. Conserv.* **142**, 2282–2292. (doi:10.1016/j.biocon.2009.05.006)

47. Evans A, Jones D, Smalley R. 2020 An enhanced gridded rainfall analysis scheme for Australia. *Bureau of Meteorology Research Report*. No. 41.

48. Australian Bureau of Meteorology. 2021 *Maps of recent, past and average conditions*. Available at: http://www.bom.gov.au/climate/maps/ (accessed on 26 August 2021).

49. R Development Core Team. 2021 *R: a language and environment for statistical computing V 4.1.0*. Vienna, Austria: R Foundation for Statistical Computing.

50. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)

51. Gomes DGE. 2022 Should I use fixed effects or random effects when I have fewer than five levels of a grouping factor in a mixed-effects model? *PeerJ* **10**, e12794. (doi:10.7717/peerj.12794)

52. Bartoń K. 2020 MuMIn: Multi-Model Inference. R package version 1.43.17. See https://cran.r-project.org/web/packages/MuMIn/index.html. (Last accessed 23 Dec 2021).

53. Hartig F. 2021 DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.3. See https://CRAN.R-project.org/package=DHARMa. (Last accessed 23 Dec 2021).

54. Burnham KP, Anderson DR, Huyvaert KP. 2011 AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* **65**, 23–35. (doi:10.1007/s00265-010-1029-6)

55. Mulder R, Langmore N. 1993 Dominant males punish helpers for temporary defection in superb fairy-wrens. *Anim. Behav.* **45**, 830–833. (doi:10.1006/anbe.1993.1100)

56. Kao AB, Hund AK, Santos FP, Young JG, Bhat D, Garland J, Oomen RA, McCreery HF. 2020 Changes in group size during resource shifts reveal drivers of sociality across the tree of life. *bioRxiv* 2020.03.17.994343 (doi:10.1101/2020.03.17.994343)

57. García-Ruiz I, Quiñones A, Taborsky M. 2022 The evolution of cooperative breeding by direct and indirect fitness effects. *Sci. Adv.* **8**, eabl7853. (doi:10.1126/sciadv.abl7853)

58. Koenig WD. 1981 Reproductive success, group size, and the evolution of cooperative breeding in the acorn woodpecker. *Am. Nat.* **117**, 421–443.

59. Stacey PB, Bock CE. 1978 Social plasticity in the acorn woodpecker. *Science* **202**, 1298–1300. (doi:10.1126/science.202.4374.1298)

60. Kattan G. 1988 Food habits and social organization of acorn woodpeckers in Colombia. *The Condor* **90**, 100–106. (doi:10.2307/1368438)

61. Blackmore CJ, Heinsohn R. 2007 Reproductive success and helper effects in the cooperatively breeding grey-crowned babbler. *J. Zool.* **273**, 326–332. (doi:10.1111/j.1469-7998.2007.00332.x)

62. Edwards SV, Kot M. 1995 Comparative methods at the species level: geographic variation in morphology and group size in grey-crowned babblers (*Pomatostomus temporalis*). *Evolution* **49**, 1134. (doi:10.2307/2410438)

63. Pike KN, Ashton BJ, Morgan KV, Ridley AR. 2019 Social and individual factors influence variation in offspring care in the cooperatively breeding Western Australian magpie. *Front. Ecol. Evol.* **7**, 92. (doi:10.3389/fevo.2019.00092)

64. Hughes JM, Mather PB. 1991 Variation in the size of territorial groups in the Australian magpie *Gymnorhina tibicen*. *Proc. R. Soc. Qld.* **101**, 13–19.

65. Hughes JM, Hesp JDE, Kallioinen R, Kempster M, Lange CL, Hedstrom KE, Mather PB, Robinson A, Wellbourn MJ. 1996 Differences in social behaviour between populations of the Australian Magpie *Gymnorhina tibicen*. *Emu – Austral. Ornithol.* **96**, 65–70. (doi:10.1071/MU9960065)

66. Shurcliffe A, Shurcliffe K. 1974 Territory in the Australian magpie (*Gymnorhina tibicen*), an analysis of its size and change. *South Aust. Ornithol.* **26**, 127–132.

67. Carrick R. 1972 Population ecology of the Australian black-backed magpie, the royal penguin and silver gull. *U. S. Dep. Inter. Wildl. Res. Rep.* **2**, 41–99.

68. Stacey PB, Ligon JD. 1991 The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. *Am. Nat.* **137**, 831–846. (doi:10.1086/285196)

69. Nelson-Flower MJ, Wiley EM, Flower TP, Ridley AR. 2018 Individual dispersal delays in a cooperative breeder: ecological constraints, the benefits of philopatry and the social queue for dominance. *J. Anim. Ecol.* **87**, 1227–1238. (doi:10.1111/1365-2656.12814)

70. Groenewoud F, Clutton-Brock T. 2021 Meerkat helpers buffer the detrimental effects of adverse environmental conditions on fecundity, growth and survival. *J. Anim. Ecol.* **90**, 641–652. (doi:10.1111/1365-2656.13396)

71. Guindre-Parker S, Rubenstein DR. 2020 Survival benefits of group living in a fluctuating environment. *Am. Nat.* **195**, 1027–1036. (doi:10.1086/708496)

72. Riehl C, Smart ZF. 2022 Climate fluctuations influence variation in group size in a cooperative bird. *Curr. Biol.* **32**, 4264–4269.e3. (doi:10.1016/j.cub.2022.07.057)

73. Baglione V, Marcos JM, Canestrari D. 2002 Cooperatively breeding groups of carrion crow (*Corvus corone corone*) in northern Spain. *The Auk* **119**, 790–799. (doi:10.1093/auk/119.3.790)

74. Bishop JM, Jarvis JUM, Spinks AC, Bennett NC, O'Ryan C. 2004 Molecular insight into patterns of colony composition and paternity in the common mole-rat *Cryptomys hottentotus hottentotus*. *Mol. Ecol.* **13**, 1217–1229. (doi:10.1111/j.1365-294X.2004.02131.x)

75. Streatfeild CA, Mabry KE, Keane B, Crist TO, Solomon NG. 2011 Intraspecific variability in the social and genetic mating systems of prairie voles, *Microtus ochrogaster*. *Anim. Behav.* **82**, 1387–1398. (doi:10.1016/j.anbehav.2011.09.023)

76. Sheehan MJ, Botero CA, Hendry TA, Sedio BE, Jandt JM, Weiner S, Toth AL, Tibbetts EA. 2015 Different axes of environmental variation explain the presence vs. extent of cooperative nest founding associations in *Polistes* paper wasps. *Ecol. Lett.* **18**, 1057–1067. (doi:10.1111/ele.12488)

77. Tumulty JP *et al.* 2021 Evidence for a selective link between cooperation and individual recognition. *bioRxiv*, 2021.09.07.459327. (doi:10.1101/2021.09.07.459327)

78. Johnson AE, Welklin JF, Hoppe I, Shizuka D. 2023 Data from: Ecogeography of group size suggests differences in drivers of sociality among cooperatively breeding fairywrens. *Dryad Digital Repository*. (doi:10.5061/dryad.1c59zw40g)

79. Johnson AE, Welklin JF, Hoppe IR, Shizuka D. 2023 Ecogeography of group size suggests differences in drivers of sociality among cooperatively breeding fairywrens. Figshare. (doi:10.6084/m9.figshare.c.6444353)

80. Johnson A, Welklin J, Hoppe IR, Shizuka D. 2022 Ecogeography of group size suggests differences in drivers of sociality among cooperatively breeding fairywrens. *EcoEvoRxiv* (doi:10.32942/OSF.IO/729BE)