

Fair-weather friends: Group size boosts reproduction in wet, cool years in a cooperative breeder

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Abstract

Climate change is altering global temperature and rainfall patterns, with measurable impacts on reproduction and population persistence. These effects are pronounced in dryland ecosystems that are characterized by high temperatures, and low, but highly variable rainfall. Cooperatively breeding species (where helpers provide parental care to other group members' offspring) are common in drylands, but it remains unclear whether cooperative breeding buffers against reproductive failure under unfavourable conditions (social buffering hypothesis) or enhances reproductive success under favourable conditions (social capitalisation hypothesis). Distinguishing between these hypotheses requires comparing the effects of helpers on breeding success under varying conditions, but such interaction analyses are rarely performed. Using data collected from 2006 to 2010 on apostlebirds *Struthidea cinerea*, a cooperative breeder inhabiting the climatically variable Australian drylands, we show that wet years were favourable and all groups produced more fledglings. However, compared to smaller groups, larger groups with more helpers had more successful breeding attempts and produced more fledglings particularly during cooler breeding seasons, supporting the social capitalisation hypothesis. This benefit likely reflects increased nestling provisioning in larger groups. Still, larger groups could not offset negative impacts during the hottest, driest breeding season when no groups successfully reproduced. Our findings highlight the importance of interactions between helper number and environmental conditions in shaping offspring production and thus, potentially population persistence under adverse climatic conditions. Further research could determine whether increased breeding success in favourable years maintains population viability despite adverse years.

Keywords: alloparents, altruistic bet-hedging, buffering, hard-life, helpers, variable environments

Introduction

Climate change is leading to higher mean temperatures, increased variability in precipitation patterns, and an increased frequency and intensity of extreme weather events (Zhang et al. 2024; Chen et al. 2025). These climatic changes are impacting animals in multiple ways, such as by changing the timing

of key life history events (Parmesan 2006; Thackeray et al. 2016) with impacts on breeding success and population persistence (Visser and Gienapp 2019; Halupka et al. 2023). In support, many temperate zone birds have advanced their lay dates to better coincide with advancing spring temperatures and prey peaks (Visser and Both 2005). For example, in the southern UK, great tits *Parus major* have advanced their lay dates by approximately 14 days over the past 47 years, largely reflecting individual plasticity rather than genetic evolution (Charmantier et al. 2008). In other cases, however, phenological responses seem to be inadequate (Radchuck et al. 2019) or are at odds with the direction of selection required to mitigate climate change effects (Visser et al. 2015; Cones et al. 2023).

Behavioural responses to climate change have received less attention than phenological responses, despite their potential importance (Komdeur and Ma 2021). Behavioural flexibility can enable individuals to respond rapidly to changing climatic conditions, making it a key mechanism for coping with climate change (Parmesan 2006; Van Buskirk 2012; Komdeur and Ma 2021; Blumstein et al. 2023). For example, peccaries *Tayassu peccari* are forest-living and predominantly diurnal mammals, but have increased nocturnal activity in response to raising temperatures to reduce the risk of overheating (Peterson et al. 2024). Changes in resource distribution can also modify behaviour, as shown by altered foraging patterns in seabirds following shifts in food availability (Grémillet and Boulinier 2009). Moreover, individuals can also adjust social behaviours in response to changes in climatic conditions (Komdeur & Ma, 2021; Blumstein et al. 2023). In species that live in stable social groups, individuals can be buffered against negative environmental impacts through social behaviours, or changes in group size and composition (Komdeur and Ma, 2021; Moss and Wile, 2021). Because sociality can influence reproductive behaviour and performance, understanding the role of sociality is important for predicting species' responses to climate change.

An outstanding question is whether behavioural responses to current climatic changes will safeguard animal populations against declines, especially in understudied biomes such as drylands (i.e., savannah grasslands, semi-deserts, deserts) that are severely affected by climate change. In the global

drylands, temperatures tend to be predictable, but rainfall is low and often variable within and across years. For this biome, most climate projections forecast increased temperatures and more frequent droughts (Smith et al. 2024; Chen et al. 2025). Animals have evolved multiple adaptations to cope with these conditions, including cooperative breeding where group members (i.e., helpers) provide parental care for other group members' offspring (Rubenstein and Lovette 2007; Griesser et al. 2017; Ben Mocha et al. 2023). Recent theory and comparative work propose that cooperative breeding can buffer against reproductive failure under unfavourable conditions (Kennedy et al. 2018; Bliard et al. 2026), which would be particularly beneficial in drylands. In support of this idea (hereafter termed social buffering), field studies in a dryland bird (white-browed sparrow weaver *Plocepasser mahali* (Capilla-Lasheras et al. 2021)), showed that broods wherein helpers provide additional food to nestlings had a lower probability of reproductive failure in unfavourable, drier years compared to broods without helpers. However, in other bird species, helpers have beneficial effects in favourable years (hereafter termed social capitalisation). For example, in superb starlings *Lamprotornis superbus*, male survival increased with group size in favourable, wetter years (Guindre-Parker and Rubenstein 2020). However, too few studies have investigated the interactive effects between the number of helpers and weather conditions on breeding success to make generalisations. Furthermore, in variable environments, climatic conditions can exert multi-seasonal impacts across life-history stages. A long-term study on cooperatively breeding superb fairy-wrens *Malurus cyaneus* found that spring rainfall affected recruitment, while summer heatwaves and winter thermal spikes reduced survival (Lv et al. 2023; Lv et al. 2026). Thus, understanding how sociality interacts with seasonal climate drivers is essential for predicting species' persistence under climate change.

The aim of our study was to test the predictions of the social buffering and social capitalisation hypotheses using data from a population of cooperatively breeding apostlebirds (*Struthidea cinerea*) living in the arid zone of New South Wales, Australia. This 100-150 g omnivorous bird (Higgins et al. 2006) is highly social and lives year-round in groups that vary size within and among seasons (Griesser et al. 2009; Warrington et al. 2013). Previous research on this species comes from both a mesic

population in northern Victoria (Woxvold and Magrath 2005) and an arid population (Warrington et al. 2013). In the mesic population, apostlebirds live in stable groups of 3-17 individuals (mean = 7.6) in year-round territories, with helpers having a positive effect on the numbers of fledglings produced. In contrast, in the arid population, apostlebirds are non-territorial throughout the year and live outside of breeding periods in large social groups of 6-24 individuals (mean $\pm$ SE = 15.4 ± 2.2) (Griesser et al. 2009). Before the onset of the breeding season, groups partially disband into a variable number of smaller units of 2-22 individuals (mean $\pm$ SE = 8.7 ± 0.5) that typically include a single monogamous breeding pair and non-breeding helpers that aid primarily with feeding nestlings and fledglings, with additional individuals sometimes obtaining a reproductive share (Warrington et al., 2013).

Our study site in the arid zone is characterised by predictable seasonal variation in temperature, but low and highly variable annual rainfall (Acworth et al. 2016). During our study period, 2006-2010, annual rainfall varied from 103 to 523 mm (mean = 224 mm). Thus, variation in both weather patterns and breeding unit sizes make this apostlebird population an ideal model to test whether breeding in larger groups buffers breeders against reproductive failure in unfavourable years (as predicted by social buffering) or allows breeders to elevate breeding success in favourable years (as predicted by social capitalisation). To this end, we first assessed if weather conditions prior to the breeding season (temperature, rainfall) influence breeding group sizes. Second, we assessed if the interaction between group size and weather conditions during our three climatic windows (pre-breeding, breeding, and the combined pre-breeding + breeding window) influenced: (i) the number of breeding attempts; (ii) the number of successful breeding attempts; and (iii) the number of fledglings produced within a breeding season.

Methods

Field data collection

Apostlebirds were studied in a colour-ringed population from 2006 to 2010, at Fowlers Gap Arid Zone Research Station (31°05'S, 141°43'E, New South Wales, Australia). Here, the ecology is typical of the

Australian arid zone (Morton et al. 2011). The landscape is characterized by low open chenopod shrubland with small stands of the dominant trees (mulga, *Acacia aneura*; belah, *Casuarina pauper*) and large expanses of bare ground, bedrock and loose sandy clay (Russell et al. 2010). It also includes a few large desert creeks that typically run for only a few days per year, and two semi-permanent artificial water bodies, each lined with river red gums (*Eucalyptus camaldulensis*). Apostlebirds typically nest alongside these creeks and artificial water bodies, as they rely on patches of soft mud to construct nests in nearby gum trees (Baldwin 1975).

Group membership was assessed 2-3 times a week during each breeding season via standardized social observations at and away from the nest (Warrington et al. 2014). These observations showed that once groups started to incubate, their size and composition remained largely stable. Adults and subadults were caught using walk-in traps, and young were either caught as nestlings (ca. day 15 at accessible nests) or caught by hand as fledglings (ca. 1-3 days post fledgling when they are still poor flyers). Un-ringed individuals were colour-ringed with a unique combination of three plastic colour rings and a numbered metal ring to aid individual identification in the field. We took a small blood sample from all individuals for genetic analyses (see Warrington et al. 2013 for further details).

At the study site, apostlebirds breed exclusively in the Austral spring and early summer (August to December), before temperatures become prohibitively hot for breeding during the summer months. Groups often start building several nests at once and do not complete all nests (Warrington, Russell & Griffith, *personal observation*). We hypothesise that nest building serves as a group-cohesion activity that helps consolidate breeding group membership, and thus, does not reflect a genuine breeding attempt (Warrington & Russell, *personal observation*). Accordingly, we categorised the initiation of a breeding attempt as the completion of a fully formed nest containing at least one egg. Nests were checked at least once a week using a mirror on the end of a telescopic pole and a pair of binoculars. Fledglings were counted within 1-3 days after fledging, as apostlebirds leave the nest area once all young have fledged around 15 days post-hatching (Warrington et al. 2014).

Breeding group features and reproduction

The sex and parentage of all individuals in the population were determined using the molecular methods described in Warrington et al. (2013). For each breeding group, we defined the following features: group size (i.e., the number of all adults observed at a nest and foraging sites); number of breeders (i.e., all individuals in a group that sired offspring, determined via genetics); and the number of non-breeding group members (i.e., all other adult group members > 9 months old, excluding juveniles born in the same year). Reproductive parameters per group were assessed as: the number of breeding attempts (i.e., nests including at least one egg); the number of successful breeding attempts (i.e., those producing at least 1 fledgling); and the total number of fledglings, for all nests produced by a group that year. Note that we did not consider clutch size in our analyses; about a third of nests were difficult to access or found after incubation, and thus clutch size data were not available.

Of the 15 to 19 groups (120 group-seasons) observed from 2006 to 2010, we recorded in 108 group-seasons a nest with at least 1 egg. However, in 45 group-seasons, groups included ≥ 2 un-ringed individuals (estimated mean un-ringed individuals = 4.1), making precise counts of breeding group sizes unreliable (Warrington et al. 2026). We note that a high number of un-ringed individuals mostly occurred in new groups that were included in the study population via expansion of the study site. Thus, we excluded groups with ≥ 2 un-ringed individuals from the analyses. Their exclusion is unlikely to introduce a bias as they were similar in their estimated size (estimated mean $\pm$ SE = 8.3 ± 0.82) to groups included in the analyses (mean $\pm$ SE = 8.7 ± 0.5 , Table 1). We note that we did not include groups that did not initiate breeding. Given the fission-fusion social system of apostlebirds across seasons (Griesser et al. 2009), non-breeding groups do not split into smaller breeding preventing us from including these data.

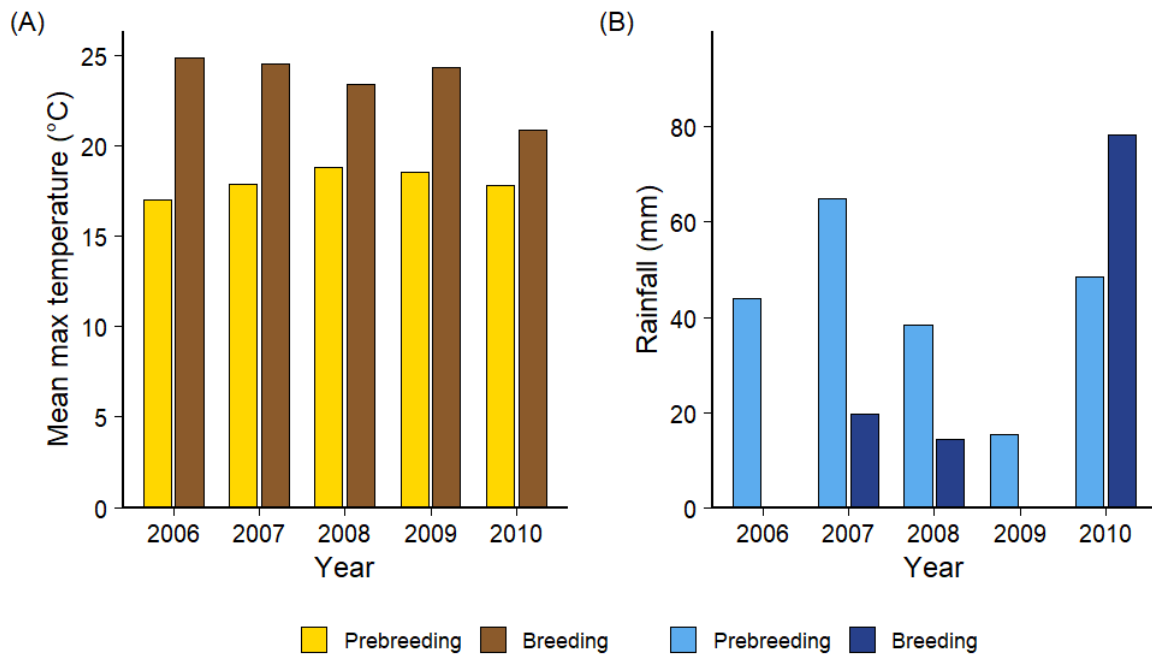
Identifying salient climate windows and climatic parameters for analyses

Data were obtained from the weather station at the study site (Fowlers Gap station, Australian Bureau of Meteorology), with temperature measured hourly and rainfall measured daily. Temperature varied

substantially across the year, with cool winters giving way to hot summers (Fig. 1A). By contrast, rainfall is highly stochastic in timing and magnitude throughout the year (Fig. 1B). This stochasticity leads to an aliasing of year and rainfall, and thus an inability to perform formal climate window analyses (e.g., using ‘climwin’; Bailey and van de Pol 2016). Instead, we grouped rainfall and temperature measures into two biologically meaningful climatic windows based on lay-dates and the effect of rainfall and temperature on reproduction (Fig. 1A, B). In our study population, lay-dates for first attempts varied between mid-August to the end of September (mean date of first attempts varied from 20 Aug to 5 Sept across years), with laying for any subsequent attempts occurring between early September (i.e., replacements for failed first attempts) and late November. The initiation of first attempts peaked at the end of August, while most subsequent attempts peaked around mid-October. Thus, we defined two climate windows: the pre-season that precedes first attempts (i.e., May to July, see below for justification), and the breeding season that encompasses the main laying and rearing period (August-October), and when occurring, second or third attempts (mean fledging date mid-November). We note that extending the breeding season window to include November does not change any results (see Supplemental Materials Table S1).

We also note that while relative climate windows have frequently been adopted in the literature to link environmental conditions with specific stages of the breeding cycle, we considered absolute-date windows to be more appropriate in our study system. Absolute dates provide a common temporal reference across years, capture seasonal cues experienced simultaneously by all individuals, and avoid circularity in which breeding date determines the climatic period under investigation. By standardising climate windows using absolute dates, we sought to reduce the risk of comparing biologically non-equivalent periods and improve our ability to distinguish climatic effects from differences in territory quality.

Figure 1. Annual climatic conditions at Fowlers Gap from 2006-2010 during the prebreeding season (May-July) and the main breeding season (August-October). A) Average mean maximum temperature ($^{\circ}\text{C}$), B) total rainfall (mm) (only including rainfalls $> 10\text{mm}$ per 24hrs, see methods for rationale). Note that there was no rainfall (0 mm) during the breeding season in 2006 and 2009.



The pre-breeding season window (May to July) was defined based on the onset of the breeding season (i.e., August) and the effect of preceding rainfall on vegetation growth and breeding. Observations at the study site over the past 20 years showed that rainfall of $< 10\text{ mm}$ per 24 hrs failed to result in water flow within the creeks or induce any obvious plant growth or development (e.g., flowering or germination of ephemeral plants) (Russell pers. obs.). Thus, to calculate the amount of daily rainfall, we only considered rainfall exceeding 10 mm per 24 hrs. Moreover, rain fall prior to May appears to have no impact on the subsequent breeding season. In support, only five breeding attempts were initiated in 2009, despite good amounts of rainfall preceding the pre-breeding season (i.e., 57 mm in December 2008, 18 mm in March 2009). Similarly, the timing of breeding was unaffected in 2010 despite $> 100\text{ mm}$ of rain falling in January 2010. We further note that no rainfall events occurred in April in all years (2006-2010) of this study.

To capture the total thermal exposure, we used the mean daily maximum temperatures during each climatic window and calculated the area under the curve. We elected to use this approach because our time windows preceded the summer months when short heatwaves can have marked reductions in offspring survival (e.g. McCowan & Griffith 2021). We note that the biological effect of temperature depends on the climatic window (i.e., season). Temperatures outside the thermoneutral zones (i.e., too cold, too hot) impose physiological constraints (Mitchell et al. 2018), and can limit plant growth. During the pre-breeding season, warmer temperatures are likely beneficial as they facilitate plant growth and thus are associated with higher insect abundances. During the breeding season, however, cooler temperatures are likely beneficial as they are associated with lower evaporation rates and thus higher insect abundances (Harvey et al. 2020), and a lower risk of heat stress.

Statistical analysis

All statistical analyses were performed in the statistical environment R version 4.3.1 (R Core Team 2024). We used the core package for non-parametric tests, glmmTMB (Brooks et al. 2017) for mixed models, and MuMIn (Barton 2015) as well as DHARMA (Hartig 2017) for model diagnostics. We visually inspected the qqplots and histograms of residuals via the package DHARMA to confirm appropriate model fits and evaluated the significance of all fixed variables using the Wald Z statistics and p-values calculated from the conditional model. We used a model selection and model averaging approach to include all models with a $\Delta AICc < 2$ for each response variable in each climatic window model series. We note that using a $\Delta AICc < 5$ results in qualitatively the same results (see Supplemental Materials Table S2). All models included group identity as a random factor to control for repeated measurements in the same group across years.

We first used generalised linear mixed effect models to assess if weather conditions during the pre-breeding season when breeding groups are formed (Griesser et al. 2009) were associated with breeding group sizes. Then, we used generalised linear mixed effect models to assess how weather parameters (rainfall, temperature), group features and their interaction were associated with the

number of breeding attempts, the number of successful breeding attempts, and the number of fledglings. We initially also considered group composition (number of males, number of females, sex-ratio, number of non-breeders, number of breeders) as fixed covariates. However, all these composition features were highly correlated to group size ($r = 0.89-0.99$), and thus, for subsequent analyses, we only included group size as a fixed covariate. We note that group size included all individuals older than one year. Individuals born in the previous year were classified as adults following established ageing criteria. However, reaching adulthood does not necessarily imply reproductive status. Individuals typically do not begin breeding until approximately 3-5 years of age (Warrington et al. 2015), consistent with the delayed onset of reproduction characteristic of many cooperative breeders (Mourocq et al. 2016). Consequently, many adult individuals remain non-breeding helpers despite having attained adult age.

To consider the effect of climatic variables on reproductive parameters, we ran three series of models: one for each of the two climatic windows defined above, and a third model series that combined parameters from both windows. For the two climatic windows, we ran 12 separate models for each response variable (number of breeding attempts, number of successful breeding attempts, number of fledglings), examining the effect of both rainfall and temperature, rainfall only, and temperature only (with and without their interaction with group size). Group size was included in all these models. We also ran models only including a single explanatory variable of either rainfall, temperature, or group size. Finally, we ran a null model, only including group identity. All models included group identity as random parameter to control for repeated sampling across years. For the models combining parameters from both seasons, we used the same approach as above running 23 separate models, only including the parameters that were associated with reproductive parameters in the pre-breeding and breeding windows. All these models included at least one parameter from the pre-breeding and the breeding season. See Supplementary Material Table S2 for all models.

Ethical note

All bird handling (capture, ringing, observing, accessing nests) was done under the licence of the Australian Bird and Bat Banding Scheme, the University of New South Wales Animal Care and Ethics Committee (authority no. 06/40A), the Macquarie University Animal Ethics Committee (authority no. 2010/032), and NSW National Parks and Wildlife Service (Scientific License SL100378).

Results

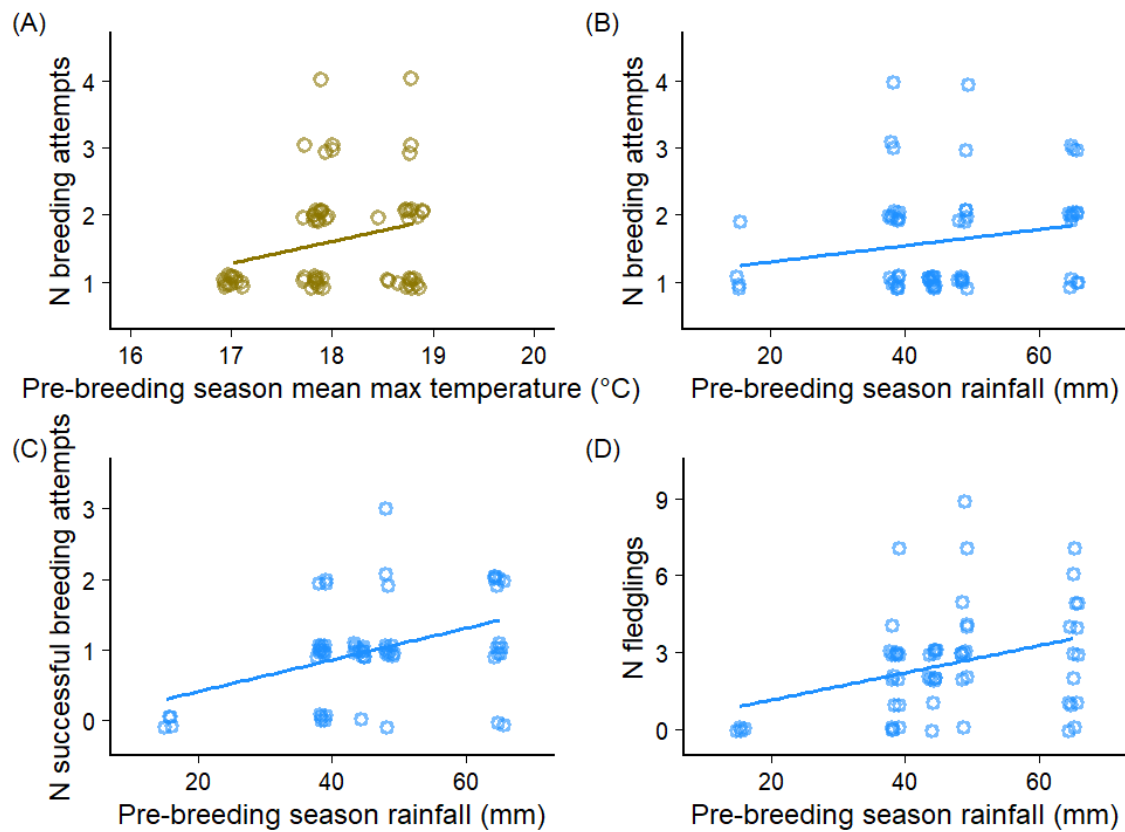
Overall, the mean number of breeding attempts, successful breeding attempts and the number of fledglings varied across years (Table 1). One group that only consisted of a breeding pair failed to raise young.

Effects of preseason weather conditions

The preseason weather conditions influenced group sizes during the subsequent breeding season. Wetter preseasons were associated with smaller breeding group sizes (GLMM: rainfall: estimate $\pm$ SE: -0.88 ± 0.410 , $p = 0.032$), while preseason temperatures were not associated with breeding group sizes.

Warmer and wetter preseason weather had a positive effect on reproduction. Warmer temperatures and wetter conditions were associated with more breeding attempts (Fig. 2, Table 2). Wetter conditions also had a positive effect on the number of successful breeding attempts and the number of fledglings (Fig. 2, Table 2). Notably, these effects were independent of group size.

Figure 2. Effects of weather variables during the preseason (May-July) on reproductive parameters during the subsequent breeding season. A) Effect of temperature on the number of breeding attempts during the subsequent breeding season. Effect of preseason rainfall on B) the number of breeding attempts, C) the number of successful broods, and D) the number of fledglings. Points are jittered to reduce overplotting. Solid lines show least square regression fits.

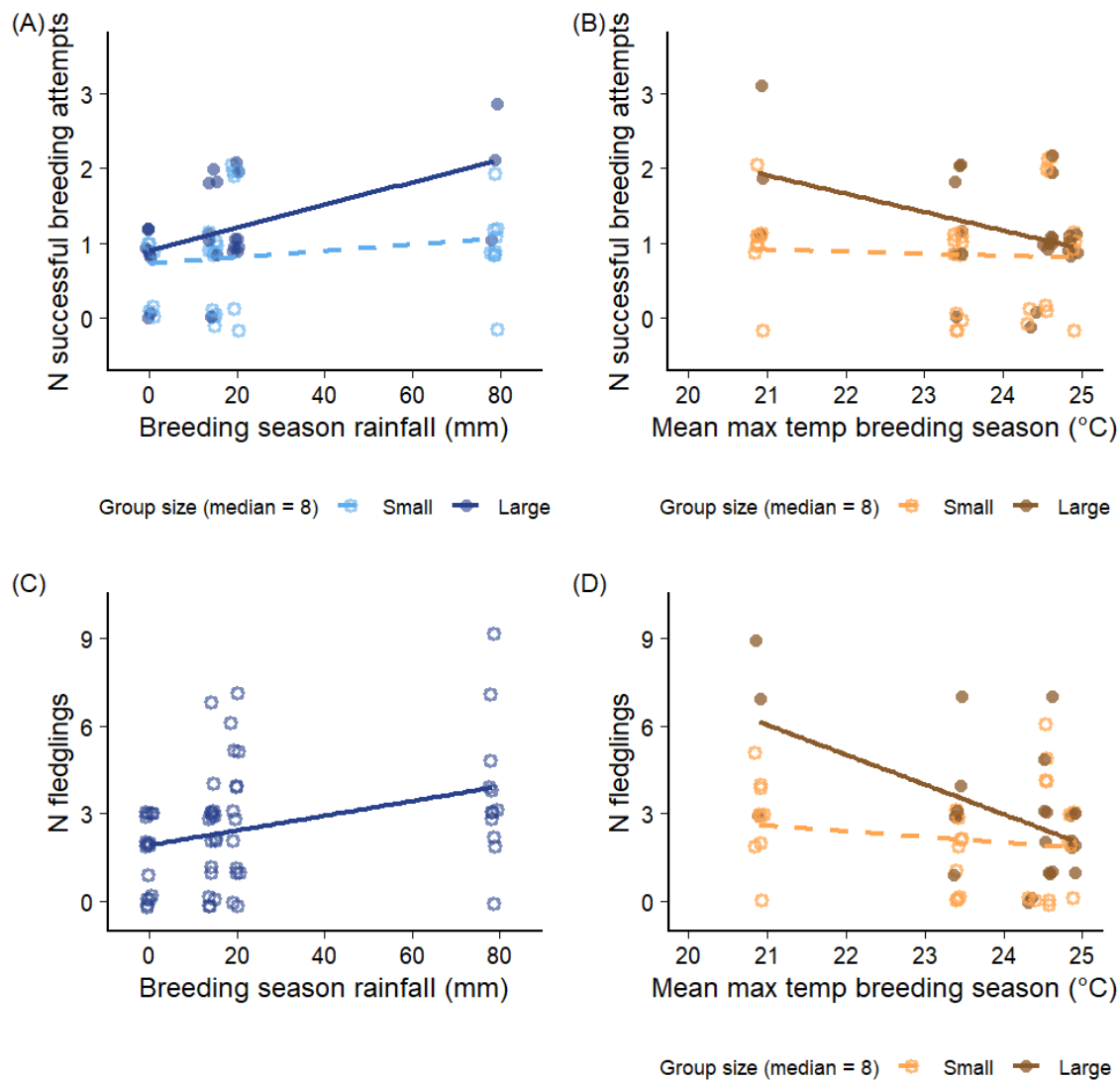


Effects of breeding season weather conditions

Wetter conditions during the breeding season were associated with an increased number of successful breeding attempts, and number of fledglings, but they were not associated with the number of breeding attempts (Fig. 3, Table 2). Notably, larger groups had more successful breeding attempts during wetter conditions compared to smaller groups, but all groups produced more fledglings during wetter conditions, independent of group size. In contrast, during cooler breeding seasons, larger groups had more successful breeding attempts and an increased number of fledglings compared to smaller groups. During warmer breeding seasons, however, all groups had a reduced number of successful breeding attempts and fledglings, independent of their size.

Figure 3. Effects of weather variables during the breeding season (August - October) on reproductive parameters in apostlebirds. A-B) Effect of the interaction between breeding season rainfall and group size (A) and mean maximum temperature and group size (B) on the number of successful breeding attempts. C) Effect of breeding season rainfall on the number of fledglings, irrespective of group size.

D) Effect of the interaction between mean maximum temperature and group size on the number of fledglings. Plot shows small groups (≤ 8 individuals) and large groups (> 8 individuals), group sizes were separated using median split method. Points are jittered to reduce overplotting. Solid and dashed lines show least square regression fits.

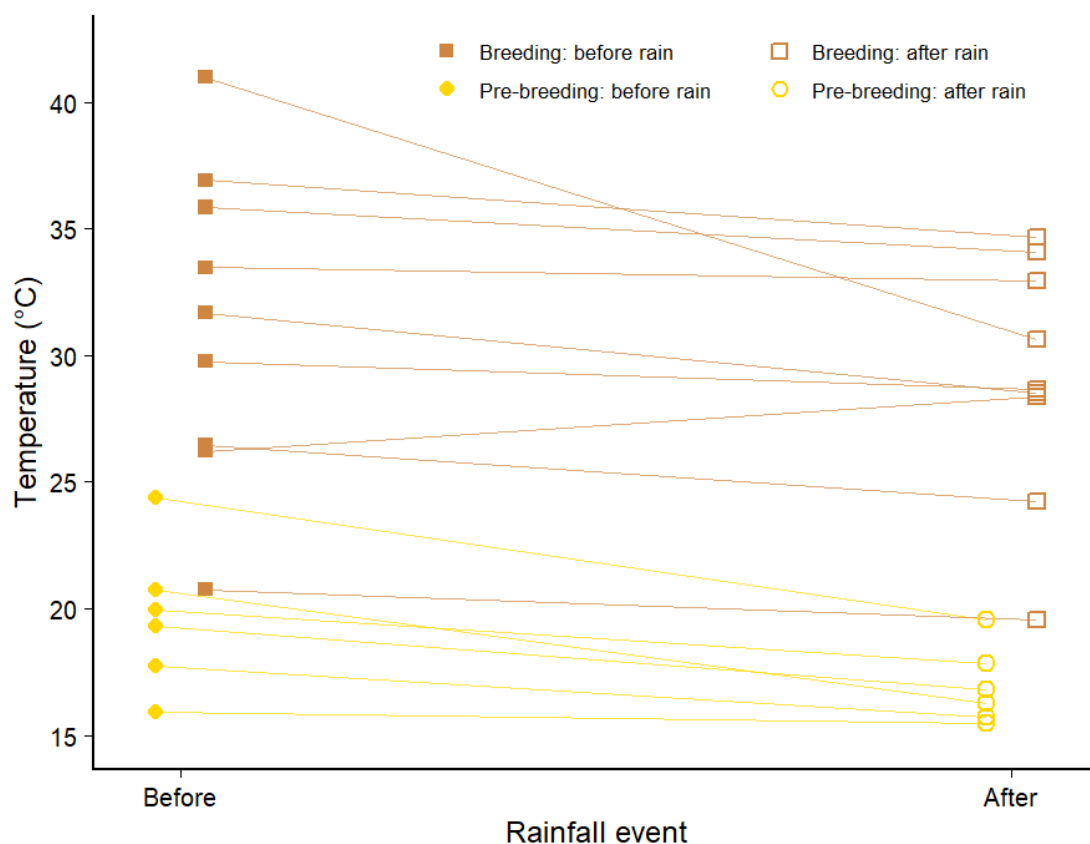


Combined effects of prebreeding and breeding season weather conditions

Models that combined climatic parameters from both windows were consistent with single window models (Table 2), supporting the positive effect of warm and wet preseasons, and cooler breeding seasons on reproductive parameters, particularly in larger groups with more helpers. Notably, the AICc of the combined model was lower than the AICc of the models assessing the effect of the climatic

conditions separately (Table 2), indicating that the weather conditions during both the pre-season and breeding season influence reproductive success. However, the combined models did not include a significant effect of rainfall during the breeding season on reproductive parameters, potentially reflecting an association between rainfall and temperature. To explore this association, we performed a post-hoc analysis comparing the average maximum temperatures 10 days before a rainfall event with the maximum temperature 10 days thereafter. We found that rainfall events were followed by a subsequent drop of 2.5 °C (paired T-test: $p = 0.003$, Fig. 4).

Figure 4. The effect of a rainfall event (> 10 mm per 24 hrs) during the prebreeding (circles) and breeding season (squares) on maximum temperatures 10 days before rainfall events, and 10 days thereafter, in cases with a singular rainfall event, excluding cases where windows were shorter than 10 days due to multiple rainfall events within these 10 days. On average, maximum temperatures dropped 2.5 °C after a rainfall event.



Discussion

Our study examined whether group characteristics in a cooperative breeder buffer reproductive failure during unfavourable conditions (social buffering) or enhance reproductive success during favourable conditions (social capitalisation). Using five years of data from an apostlebird population in a variable dryland environment, our results partially support the social capitalisation hypothesis. Rainfall during the prebreeding season increased the number of fledglings produced, independent of group size, showing that wet conditions are generally favourable for reproduction in this dryland population of apostlebirds. However, larger groups had more fledglings during cooler breeding seasons compared to smaller groups, supporting the social capitalisation hypothesis. This benefit most likely reflects increased food availability during cooler breeding seasons, allowing larger groups with more helpers to raise more offspring. Our findings add to the growing body of studies showing that the mechanisms underlying the reproductive benefits of cooperative breeding are nuanced and measuring effects depend on the type of climatic variable examined.

Prebreeding season weather effects on breeding group size

Our results showed that pre-breeding climatic conditions affected breeding group size. Apostlebird groups at our study site have a fission-fusion system where several breeding groups form larger non-breeding groups that separate into smaller groups before the next breeding season (Griesser et al. 2009). This social flexibility is likely adaptive, influencing group size and composition, which can have fitness consequences (Blumstein et al. 2023; Alamán et al. 2024). Interestingly, apostlebird group sizes during the breeding season were smaller in wetter, cooler years, even though larger groups produced more young. This apparent contradiction likely reflects that during favourable (wet, cooler) conditions small groups can breed successfully, whereas under unfavourable conditions these groups would fail to reproduce. Although breeding in larger groups is overall beneficial, individual fitness could be higher when breeding in smaller groups in favourable years, but we lack the data to test this hypothesis.

Climate-dependent variation in group size and its fitness consequences has also been documented in other cooperative breeders. In greater anis *Crotophaga major*, smaller groups perform better under dry conditions with limited food whereas larger groups have a reproductive advantage in wetter conditions with more food (Riehl & Smart, 2022). In Arabian babblers *Argya squamiceps*, group sizes vary depending on habitat type where groups living in resource-rich agricultural landscapes were smaller and had a higher breeding success than groups inhabiting resource-poor natural habitats (Alamán et al. 2024), indicating that resource availability can influence group formation processes. Similar to apostlebirds, other cooperative breeders exhibit flexibility in group sizes either within or between breeding seasons. Within seasons, breeders that fail to reproduce join neighbouring groups to help raising offspring (e.g., azure-winged magpie, *Cyanopica cyanus* (Canário et al. 2004); long-tailed tit, *Aegithalos caudatus* (Green and Hatchwell 2018)). In other species, breeding groups re-organise group membership across seasons, as seen in apostlebirds. For example, in the closely related white-winged chough *Corcorax melanorhamphos*, groups reorganised following an intense drought and a particularly harsh, cold winter, resulting in changes group size and composition, with increased rates of reproductive sharing following the drought (Heinsohn et al. 2000). Such changes also occur in other dryland cooperative breeders that can include multiple same-sex breeders (e.g., chestnut crowed babbler, *Pomatostomus ruficeps* (Russell 2016), superb starling (Rubenstein 2016)). Together, these studies suggest that cooperatively breeding species can respond to environmental variability through flexible social organisation. Thus, our findings highlight the need to examine the mechanisms underlying reproductive and helping decisions, to understand how group-living species can respond to rapidly changing environmental conditions.

Mechanisms underlying helper benefits

Previous work in a mesic population of apostlebirds did not assess the influence of weather parameters on breeding success, but showed that the number of group members which fed nestlings, but not group size *per se*, increase annual fledging success (Woxvold and Magrath 2005). While we did not measure the feeding effort of individual group members in our study, larger groups produced

more fledglings under favourable (cooler) breeding conditions. These conditions are associated with a higher food abundance, likely allowing larger groups to deliver an increased amount of food to the nest, highlighting the importance of assessing how helpers influence breeding success in cooperatively breeding species. Breeding in a larger group, however, is not associated with an increased number of breeding attempts. This pattern supports the idea that helpers are particularly beneficial during the nestling phase via an increased amount of food. Notably, this benefit may also allow breeders to increase their reproductive allocation in subsequent broods, but we lack the data to test this idea.

Helpers can contribute not only to feeding nestlings and fledglings, but also to constructing nests, incubating eggs, and protecting nestlings and fledglings (Ben Mocha et al. 2023). The actual benefits that helpers provide, however, are often unknown, and as the case in our study, many studies use group size as a proxy to assess the benefits of cooperative breeding. Fewer studies assess the actual parental care effort of helpers. For example, in white-browed sparrow weavers, female helpers, in particular, fed nestlings and increased fledgling success, and consequently, their experimental removal led to a drop in the total delivery rate (Capilla-Lasheras et al. 2021). Clearly, more detailed measures of helper contributions and reproductive share among group members (Ben Mocha et al. 2026) are critical to understand how climate change will affect cooperatively breeding species.

Interplay between the presence of helpers and climatic conditions

Across cooperatively breeding birds and mammals, helpers can provide benefits irrespective of climatic conditions. Despite this broad pattern, most studies linking helper presence (or number) to breeding success do not account for climatic variation, in part because they are typically conducted in populations with limited interannual climatic variability (Woolfenden and Fitzpatrick 1990; Morinay et al. 2025). Notably, of those studies that do assess the interactions between climatic conditions and group size, some find that helpers provide advantages independent of conditions (Riehl and Smart 2022; Borger et al. 2023). For example, in Seychelles warblers *Acrocephalus sechellensis*, helpers increase both reproductive output and breeder survival independent of climatic conditions (Borger et

al. 2023). However, it is unclear whether this reflects insufficient inter-annual variation or selection on helpers to benefit breeders across the range of conditions experienced.

In cooperative breeders studied in variable environments (e.g., drylands), large groups can increase reproductive success under favourable (social capitalisation), unfavourable conditions (social buffering), or independent of the conditions. Similar to apostlebirds, social capitalisation has been reported in other cooperatively breeding species (Guindre-Parker and Rubenstein 2020; Diehl et al. 2025). For example, in fairy-wrens, helpers increase the amount of food that is delivered to nestlings especially during favourable conditions (Diehl et al. 2025). In other dryland cooperative breeders, helpers mitigate the effects of unfavourable conditions, supporting the social buffering hypothesis (Ebensperger et al. 2014; Capilla-Lasheras et al. 2021). For example, white-browed sparrow weaver helpers reduce the risk of failure in dry years, but reduce breeding success in wet years (Capilla-Lasheras et al. 2021). In sociable weavers *Philetairus socius*, larger groups have higher reproductive success than smaller groups, but all groups perform best at intermediate temperatures. Consequently, larger group do not buffer breeders against the negative effects of extreme weather (D'Amelio et al. 2022), similar to what we observed in our study, where at the height of a drought period (2009), no group bred successfully. Thus, while social buffering can immediately alleviate unfavourable conditions, social capitalisation can at least partly compensate for low breeding success in bad seasons, by increased reproductive output in favourable conditions, as for example observed in southern pied babblers *Turdoides bicolor* (Bourne et al. 2020a).

Ecological effects of climatic conditions

The differences in species' responses to climatic conditions could arise from how their primary food resources respond to rainfall and temperature. At our study site, rainfall leads to increases in insect presence. Over the course of dry years (2006-2009), moth and locust presence, as well as average insect abundances dropped, but they all rebounded in 2010 following significant rainfall (Warrington et al. 2013) indicating that insects are more abundant in wetter years. However, insects are sensitive

to high temperatures because of desiccation (Hoffmann et al. 2013), such that hotter temperatures (which increase throughout the breeding season) can compromise this food source. In contrast, seeds (i.e., the primary food source of white-browed sparrow weavers) develop more slowly after rainfall but are relatively insensitive to temperature once they have developed. Given that apostlebirds are generalist feeders (Baldwin 1974), further work is needed to examine variation in the food sources fed to nestlings. Thus, differences in diets within and between species highlight the need for further work to explore how species' ecological traits shape whether cooperative breeding leads to social buffering or social capitalisation under highly variable climatic conditions.

Our findings show that temperature affects reproductive success in different ways depending on the stage of the breeding cycle. In our study population, warm pre-breeding seasons but cool breeding seasons are associated with higher reproductive output. This pattern may reflect the contrasting effects of temperature on food availability. Warm pre-breeding periods promote plant growth and insect emergence, whereas hot conditions during the breeding season suppress both, reducing the resources available to breeding birds. Moreover, post-hoc analyses showed that rainfall had a cooling effect (Fig. 4), reflecting that rainfall is also associated with increased cloud cover, evaporative cooling, and the higher heat capacity of moist soils (Pan et al. 2021). These effects likely explain why breeding season rainfall is not in the top models that combine climatic parameters of both seasons (Table 2). Together, these patterns highlight the importance of considering climatic parameters separately across temporal windows that differ in thermal limitations (here, cold pre-breeding periods versus hot breeding seasons).

Given the rapidly increasing temperatures in global drylands, many studies emphasize physiological limitations associated with high temperatures. In pied babblers, a dryland cooperative breeder, temperatures above 38 °C are lethal to nestlings (Bourne et al. 2020b), reflecting reduced nestling feeding rates (Wiley and Ridley 2016). However, physiological impacts are not restricted to extreme threshold spikes; heat stress in both adults and nestlings typically begins at lower temperatures (ca.

35-37 °C) and escalates progressively as temperatures rise. Furthermore, even infrequent spikes above 38 °C, such as a single day of acute heat at a critical developmental stage, can have catastrophic effects on nest survival (McCowan and Griffith 2021). While daily maximum temperatures rarely exceeded 38 °C during our 2006-2010 study period, the negative impacts of warmer breeding seasons likely reflect a combination of reduced food availability and direct sublethal or acute thermal stress. We note that thermal responses vary by species and developmental stage. Thermal responses also vary across species, traits, and developmental stages; for instance, in dryland common fiscals *Lanius collaris*, nestling trait thresholds ranged between 33 °C and 37 °C, with heatwaves having accelerating negative effects on fledgling success (Cunningham et al. 2013). Since the end of this apostlebird study in 2010, breeding season temperatures at the study site have regularly exceeded 38 °C, and rainfall events and storms have become more intense (with the latter contributing to nesting failure in 2009 and 2010; Warrington, pers. obs.) However, population declines can also reflect the accumulation of multiple small, sub-lethal climate impacts across the annual cycle (Lv et al. 2026). In apostlebirds, increasingly frequent heatwaves and drier breeding seasons may similarly exert cumulative impacts across both reproductive and non-reproductive periods, leading to broader population vulnerability. Thus, further studies examining temperature thresholds at different developmental stages would further elucidate how raising temperatures at the study site have impacted reproductive success and the subsequent population decline at the study site observed between 2010 and 2024 (Warrington, Griesser, Russell pers. obs.).

Study limitations

Our study only spanned five breeding seasons, limiting our ability to identify the effects of fine-scale climatic windows on social behaviour and reproduction. Studies with longer-term data can use more comprehensive climatic analyses, such as a sliding window analysis (Bailey and van de Pol 2016) that can identify the most influential time period for the response variables (e.g., D'Amelio et al., 2022). Furthermore, the availability of mud to build nests varied across territories and could have influenced the onset of reproduction but, unfortunately, we did not collect these data or other proxies of territory

quality. Evidently, breeding on a high-quality territory favours successful reproduction but it remains unknown whether changing climatic conditions will particularly affect groups on low-quality territories or reduce breeding success across all territories. We could not examine the effects of group size on other fitness proxies, including the survival of juveniles, breeders and helpers, due to frequent changes in group membership and extensive movement of individuals and groups outside the study area between seasons. Thus, we encourage researchers with access to long-term population datasets to examine whether social parameters and dynamics could protect groups from the impact of increasingly challenging eco-climatic conditions.

Conclusion

Our study showed that in a dryland cooperative breeder, larger group sizes enhanced reproductive success particularly under favourable climatic conditions whereby helpers can increase nestling provisioning rates, consistent with the social capitalisation hypothesis. This finding adds to the growing literature showing how helpers can offset the negative impacts of unfavourable weather conditions that are brought upon by climate change, highlighting the differing ways that cooperatively breeding is beneficial. However, the proximate mechanisms mitigating the negative impacts of climate change remains unclear in many species. Our study emphasises the need for further research examining the mechanisms behind the benefits of cooperative breeding, particularly in the face of rapid environmental and climatic change. Understanding these dynamics is crucial, especially as climate change continues to alter environmental conditions, potentially impacting the reproductive success and survival of many species.

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Table 1: Overview of social group features and reproductive parameters from 2006 to 2010 at Fowlers

Gap, for groups with ≤ 1 un-ringed individual (N = 63 groups).

Social group features			Reproductive parameters (per group)			
Year	Number of groups	Group size range	Mean $\pm$ SE group size	Mean $\pm$ SE number of breeding attempts	Mean $\pm$ SE number of successful breeding attempts	Mean $\pm$ SE number of fledglings
2006	12	3 - 22	9.8 $\pm$ 1.7	1.0 $\pm$ 0	0.92 $\pm$ 0.08	2.2 $\pm$ 0.3
2007	14	4 - 22	9.5 $\pm$ 1.2	1.9 $\pm$ 0.2	1.29 $\pm$ 0.19	3.0 $\pm$ 0.6
2008	19	2 - 13	8.2 $\pm$ 0.7	1.8 $\pm$ 0.2	0.89 $\pm$ 0.16	2.2 $\pm$ 0.4
2009	4	8 - 16	10.8 $\pm$ 1.9	1.3 $\pm$ 0.3	0	0
2010	14	3 - 15	6.9 $\pm$ 0.9	1.7 $\pm$ 0.2	1.25 $\pm$ 0.20	3.6 $\pm$ 0.7

Table 2: Generalized linear mixed models to examine the effect of group size and climatic variables on reproductive parameters. Significant variables are bolded. gs = group size, AICc = Akaike Information Criterion, av = averaged weighed values, cR² = conditional r-squared, temp = temperature. * = only one model with a Δ AICc < 2. Empty cells reflect parameters that were not included in the models with a Δ AICc < 2 (see Supplemental Material table 2). ^Note that significant interaction effects indicate that the relationship between the fixed variable (i.e., temperature or rainfall) and the response variable varies with group size; therefore, the main effect reflects the effect at the reference group size only.

	Response variable	N breeding attempts				N successful breeding attempts				N fledglings			
Window	Parameter	Effect size	SE	z-value	P-value	Effect size	SE	z-value	P-value	Effect size	SE	z-value	P-value
Pre breeding season	intercept	0.40	0.068	5.98	<0.00001	1.00	0.080	12.40	<0.00001	0.89	0.105	8.49	<0.00001
	rainfall pre	0.22	0.058	3.69	0.0002	0.32	0.080	4.01	0.00006	0.28	0.098	2.88	0.004
	temperature pre	0.24	0.064	3.71	0.0002								
	group size	0.08	0.057	1.31	0.19	0.11	0.080	1.36	0.18				
	rainfall pre x gs	-0.06	0.055	1.15	0.25	-0.11	0.084	-1.36	0.17				
	temp pre x gs	0.06	0.068	0.81	0.42								
		av AICc: 132.94		av cR ² : 0.41		av AICc: 123.53		av cR ² : 0.25		* AICc: 239.12		cR ² : 0.15	
		Effect size	SE	z-value	P-value	Effect size	SE	z-value	P-value	Effect size	SE	z-value	P-value
Breeding season	intercept	0.46	0.069	6.64	<0.00001	1.29	0.068	19.05	<0.00001	0.96	0.087	11.03	<0.00001
	rainfall breed	0.10	0.130	0.73	0.46	0.76^	0.184	4.13	0.00004	0.75	0.248	3.03	0.002
	temperature breed	0.02	0.105	0.22	0.83	0.49^	0.175	2.82	0.005	0.39^	0.243	1.62	0.10
	group size	0.06	0.068	0.87	0.39	0.35	0.070	4.96	<0.00001	0.24	0.091	2.61	0.009
	rainfall breed x gs	-0.09	0.169	0.56	0.58	-0.62	0.192	-3.23	0.001				
	temp breed x gs	-0.15	0.210	0.69	0.49	-0.95	0.185	-5.14	<0.00001	-0.26	0.091	-2.89	0.004
		av AICc: 147.93		av cR ² : 0.18		* AICc: 112.30		cR ² : 0.54		* AICc: 234.61		cR ² : 0.27	
		Effect size	SE	z-value	P-value	Effect size	SE	z-value	P-value	Effect size	SE	z-value	P-value
Both seasons combined	intercept	0.37	0.074	5.08	<0.00001	1.22	0.069	17.60	<0.00001	0.99	0.099	10.04	<0.00001
	rainfall pre	0.20	0.058	3.51	0.0005	0.37	0.061	6.11	<0.00001	0.36	0.100	3.60	0.0003
	rainfall breed	0.09	0.051	1.85	0.063								
	temperature pre	0.26	0.062	4.09	0.00004								
	temperature breed	-0.14	0.051	2.79	0.005	-0.29^	0.072	-4.04	0.00005	-0.32^	0.084	-3.83	0.0001
	group size	0.11	0.056	2.02	0.044	0.29	0.073	4.03	0.00006	0.21	0.098	2.09	0.037
		av AICc: 129.64		av cR ² : 0.50		* AICc: 106.47		cR ² : 0.54		* AICc: 229.29		cR ² : 0.40	
		Effect size	SE	z-value	P-value	Effect size	SE	z-value	P-value	Effect size	SE	z-value	P-value
Both seasons combined	intercept	0.37	0.074	5.08	<0.00001	1.22	0.069	17.60	<0.00001	0.99	0.099	10.04	<0.00001
	rainfall pre	0.20	0.058	3.51	0.0005	0.37	0.061	6.11	<0.00001	0.36	0.100	3.60	0.0003
	rainfall breed	0.09	0.051	1.85	0.063								
	temperature pre	0.26	0.062	4.09	0.00004								
	temperature breed	-0.14	0.051	2.79	0.005	-0.29^	0.072	-4.04	0.00005	-0.32^	0.084	-3.83	0.0001
	group size	0.11	0.056	2.02	0.044	0.29	0.073	4.03	0.00006	0.21	0.098	2.09	0.037
		av AICc: 129.64		av cR ² : 0.50		* AICc: 106.47		cR ² : 0.54		* AICc: 229.29		cR ² : 0.40	
		Effect size	SE	z-value	P-value	Effect size	SE	z-value	P-value	Effect size	SE	z-value	P-value
Both seasons combined	intercept	0.37	0.074	5.08	<0.00001	1.22	0.069	17.60	<0.00001	0.99	0.099	10.04	<0.00001
	rainfall pre	0.20	0.058	3.51	0.0005	0.37	0.061	6.11	<0.00001	0.36	0.100	3.60	0.0003
	rainfall breed	0.09	0.051	1.85	0.063								
	temperature pre	0.26	0.062	4.09	0.00004								

Supplemental Materials Table S1. Results for generalized linear mixed models to examine the effect of group size and climatic variables during the extended breeding season (BE: August-November) on reproductive parameters. Significant variables are bolded, gs = group size, AICc = Akaike Information Criterion, av = averaged weighed values, cR² = conditional r-squared, temp = temperature, * = only one model with a Δ AICc < 2. ^Note that significant interaction effects indicate that the relationship between the fixed variable (i.e., temperature or rainfall) and the response variable varies with group size; therefore, the main effect reflects the effect at the reference group size only.

Window	Response variable	N breeding attempts				N successful breeding attempts				N fledglings			
	Parameter	Effect size	SE	z-value	P-value	Effect size	SE	z-value	P-value	Effect size	SE	z-value	P-value
breeding season extended	intercept	0.42	0.069	6.11	<0.00001	1.11	0.083	13.33	<0.00001	1.01	0.151	6.74	<0.00001
	rainfall BE	-0.39	0.220	1.79	0.073					0.21	0.551	0.38	0.70
	temperature BE	-0.55	0.226	2.41	0.016	-0.30	0.089	-3.40	0.0007	0.14	0.104	1.34	0.18
	group size	0.10	0.060	1.70	0.090	0.29	0.092	3.13	0.002	-0.08	0.798	0.10	0.92
	rainfall BE x gs	-0.18	0.283	0.64	0.52					0.18^	0.089	2.04	0.041
	temp BE x gs	-0.29	0.287	1.00	0.32	-0.29^	0.090	-3.24	0.001				
		av AICc: 139.50		av cR ² : 0.34		* AICc: 122.55		cR ² : 0.23		av AICc: 239.8		cR ² : 0.05	

Supplementary Material Table S2-1: All models run for the pre-breeding season (P); gs = group size. '1' in columns rain P, temp P, rain P X gs, temp P X gs, and gs indicate that these independent variables were included in the models. Green highlights: models < $\Delta 2$ AICc, blue highlights: models < $\Delta 5$ AICc. The top model is bolded.

response variable	model nr	rain P	temp P	rain P X gs	temp P X gs	gs	convergence	AICc	df	R ²	Δ AICc
attempts	1	1	1	1	1	1	ok	134.03	55	0.406	1.85
	2	1	1	1		1	ok	132.18	56	0.412	0.00
	3	1	1		1	1	ok	145.76	56	0.396	13.58
	4	1	1			1	ok	133.70	57	0.419	1.52
	5		1			1	ok	142.21	58	0.212	10.03
	6		1		1	1	ok	146.18	57	0.199	14.00
	7	1				1	ok	144.37	58	0.220	12.20
	8	1		1		1	ok	157.41	56	0.097	25.23
	9					1	convergence issues	148.37	58	0.136	NA
	10						ok	146.38	59	0.129	14.21
	11	1					convergence issues	142.69	59	0.195	NA
	12		1				ok	140.30	59	0.213	8.12
successful attempts	1	1	1	1	1	1	ok	127.38	52	0.308	4.37
	2	1	1	1		1	ok	125.90	53	0.316	2.90
	3	1	1		1	1	convergence issues	126.55	53	0.263	NA
	4	1	1			1	convergence issues	125.48	54	0.273	NA
	5	1				1	ok	124.96	54	0.260	1.95
	6	1		1		1	ok	123.01	54	0.253	0.00
	7		1			1	convergence issues	149.01	55	0.021	NA
	8		1		1	1	convergence issues	150.65	54	0.045	NA
	9					1	convergence issues	133.29	55	0.019	NA
	10						convergence issues	129.51	57	0.000	NA
	11	1					convergence issues	121.44	56	0.198	NA
	12		1				convergence issues	130.65	56	0.026	NA
fledglings	1	1	1	1	1	1	ok	250.29	49	0.481	11.17
	2	1	1	1		1	ok	253.05	51	0.173	13.93
	3	1	1		1	1	ok	254.03	51	0.155	14.91
	4	1	1			1	convergence issues	246.34	51	0.457	NA
	5	1				1	convergence issues	249.43	53	0.139	NA
	6	1		1		1	ok	250.61	53	0.171	11.49
	7		1			1	ok	251.41	52	0.008	12.29
	8		1		1	1	ok	246.78	53	0.036	7.66
	9					1	ok	244.81	54	0.000	5.69
	10						ok	256.81	56	0.000	17.69
	11	1					ok	239.12	55	0.152	0.00
	12		1			1	convergence issues	252.12	55	0.264	NA

Supplementary Material Table S2-2: All models run for the breeding season (B); gs = group size. '1' in columns rain B, temp B, rain B X gs, temp B X gs, and gs indicate that these independent variables were included in the models. Green highlights: models < $\Delta 2$ AICc, blue highlights: models < $\Delta 5$ AICc. The top model is bolded.

response variable	model nr	rain B	temp B	rain B x gs	temp B x gs	gs	convergence	AICc	df	R ²	Δ AICc
attempts	1	1	1	1	1	1	ok	146.04	55	0.221	0.00
	2	1	1		1	1	ok	153.62	55	0.153	7.58
	3	1	1	1		1	convergence issues	156.98	55	0.104	NA
	4	1	1			1	convergence issues	147.56	57	0.189	NA
	5	1				1	ok	147.60	57	0.188	1.56
	6	1		1		1	convergence issues	154.54	56	0.101	NA
	7		1			1	convergence issues	158.06	57	0.161	NA
	8		1		1	1	convergence issues	155.20	56	0.208	NA
	9					1	convergence issues	155.41	59	0.120	NA
	10						ok	146.38	59	0.129	0.35
	11	1					convergence issues	146.34	58	0.164	NA
	12		1				convergence issues	146.86	58	0.156	NA
successful attempts	1	1	1	1	1	1	ok	112.30	51	0.539	0.00
	2	1	1	1		1	convergence issues	122.96	53	0.253	NA
	3	1	1		1	1	random not estimable	118.09	53	0.311	5.79
	4	1	1			1	ok	127.68	54	0.162	15.37
	5	1				1	random not estimable	130.58	55	0.089	18.28
	6	1		1		1	ok	125.86	54	0.188	13.55
	7		1			1	ok	128.86	55	0.109	16.55
	8		1		1	1	ok	125.25	53	0.230	12.94
	9					1	convergence issues	133.29	53	0.019	NA
	10						ok	130.97	57	0.000	18.67
	11	1					convergence issues	129.42	56	0.063	NA
	12		1				convergence issues	147.02	56	0.014	NA
fledglings	1	1	1	1	1	1	ok	244.96	51	0.341	10.35
	2	1	1		1	1	ok	234.61	52	0.089	0.00
	3	1	1	1		1	ok	239.62	51	0.077	5.01
	4	1	1			1	ok	247.86	52	0.182	13.25
	5	1				1	ok	239.84	53	0.050	5.23
	6	1		1		1	ok	238.41	52	0.058	3.80
	7		1			1	convergence issues	249.54	53	0.088	NA
	8		1		1	1	ok	246.18	52	0.180	11.57
	9					1	convergence issues	258.59	55	0.009	NA
	10						ok	256.81	56	<0.001	22.20
	11	1					ok	251.39	56	0.125	16.78
	12		1				convergence issues	254.85	56	0.071	NA

Supplementary Material Table S2-3: All models run for the combined prebreeding (P) and breeding season (B); gs = group size. '1' in columns rain P, temp P, rain B, temp B, temp B x gs, and gs indicate that these independent variables were included in the models. Green highlights: models < $\Delta 2$ AICc, blue highlights: models < $\Delta 5$ AICc. The top model is bolded.

response variable	model nr	rain P	temp P	rain B	temp B	temp B x gs	gs	status	AICc	df	R ²	Δ AICc
attempts	1	1		1	1	1	1	convergence issues	137.59	55	0.42	NA
	2	1		1	1			ok	141.82	56	0.37	12.69
	3	1		1				convergence issues	146.13	57	0.21	NA
	4	1			1	1	1	convergence issues	142.91	55	0.30	NA
	5	1			1			convergence issues	142.60	58	0.23	NA
	6	1		1	1		1	ok	155.49	55	0.34	26.36
	7	1		1			1	ok	157.89	56	0.23	28.77
	8	1			1		1	convergence issues	143.21	57	0.28	NA
	9	1	1		1	1	1	ok	130.89	54	0.52	1.76
	10	1	1	1	1	1	1	ok	133.66	53	0.52	4.53
	11	1	1	1	1		1	convergence issues	131.17	55	0.54	NA
	12		1	1	1	1	1	ok	134.11	55	0.48	4.98
	13		1	1	1		1	convergence issues	148.07	56	0.37	NA
	14	1	1		1	1	1	ok	146.00	54	0.45	16.88
	15	1	1		1		1	convergence issues	128.54	56	0.54	NA
	16		1		1	1	1	convergence issues	154.43	55	0.26	NA
	17		1		1		1	convergence issues	145.02	56	0.25	NA
	18	1	1	1				ok	129.13	57	0.49	0.00
	19		1		1			ok	141.15	58	0.24	12.02
	20		1	1				ok	140.81	57	0.29	11.68
	21	1	1	1			1	convergence issues	131.29	55	0.54	NA
	22		1	1	1			ok	132.20	57	0.46	3.07
	23		1	1			1	ok	141.59	56	0.31	12.46
successful attempts	1	1		1	1	1	1	ok	113.47	52	0.60	7.00
	2	1		1	1			ok	122.11	54	0.48	15.63
	3	1		1				ok	121.83	55	0.26	15.35
	4	1			1	1	1	ok	106.47	52	0.54	0.00
	5	1			1			ok	121.32	55	0.28	14.85
	6	1		1	1		1	ok	120.88	53	0.62	14.41
	7	1		1			1	convergence issues	122.14	54	0.32	NA
	8	1			1		1	ok	123.61	53	0.31	17.14
	9	1	1		1	1	1	convergence issues	108.82	51	0.55	NA
	10	1	1	1	1	1	1	ok	110.60	50	0.56	4.13
	11	1	1	1	1		1	ok	126.08	51	0.49	19.60
	12		1	1	1	1	1	ok	119.38	51	0.42	12.90
	13		1	1	1		1	convergence issues	132.83	52	0.17	NA
	14	1	1		1	1	1	convergence issues	108.82	51	0.55	NA
	15	1	1		1		1	ok	125.42	52	0.32	18.94
	16		1		1	1	1	ok	125.54	52	0.26	19.07

	17		1		1		1	convergence issues	132.98	54	0.08	NA
	18	1	1	1				ok	124.29	54	0.26	17.82
	19		1		1			convergence issues	132.62	55	0.05	NA
	20		1	1				does not converge	NA	NA	NA	NA
	21	1	1	1			1	convergence issues	127.12	52	0.32	NA
	22		1	1	1		1	convergence issues	131.92	52	0.20	NA
	23		1	1			1	convergence issues	129.44	54	0.14	NA
fledglings	1	1		1	1	1	1	ok	240.80	50	0.39	11.51
	2	1		1	1			ok	235.29	53	0.15	6.01
	3	1		1				ok	235.69	54	0.09	6.41
	4	1			1	1	1	ok	229.29	51	0.40	0.00
	5	1			1			ok	235.26	55	0.34	5.98
	6	1		1	1		1	ok	234.75	52	0.17	5.46
	7	1		1			1	ok	245.43	52	0.25	16.15
	8	1			1		1	ok	245.43	52	0.25	16.15
	9	1	1		1	1	1	convergence issues	239.88	50	0.40	NA
	10	1	1	1	1	1	1	ok	242.46	49	0.41	13.17
	11	1	1	1	1		1	ok	249.43	50	0.29	20.14
	12		1	1	1	1	1	ok	243.60	50	0.33	14.32
	13		1	1	1		1	ok	250.41	51	0.18	21.12
	14	1	1		1	1	1	convergence issues	239.88	50	0.40	NA
	15	1	1		1		1	ok	247.29	51	0.27	18.01
	16		1		1	1	1	ok	246.41	51	0.23	17.12
	17		1		1		1	convergence issues	255.36	53	0.14	NA
	18	1	1	1				ok	238.15	53	0.09	8.87
	19		1		1			convergence issues	255.17	54	0.10	NA
	20		1	1				convergence issues	240.97	53	0.04	NA
	21	1	1	1			1	convergence issues	239.84	51	0.12	NA
	22		1	1	1		1	convergence issues	243.27	51	0.07	NA
	23		1	1			1	convergence issues	252.66	53	0.18	NA

Supplementary Material Table S2-4: All models run for the extended breeding season (BE). '1' in columns rain P, temp P, rain B, temp B, temp B x gs, and gs indicate that these independent variables were included in the models. Green highlights: models < $\Delta 2$ AICc, blue highlights: models < $\Delta 5$ AICc. The top model is bolded.

response variable	model nr	rain BE	temp BE	rain BE x gs	temp BE x gs	gs	convergence	AICc	df	R ²	Δ AICc
attempts	1	1	1	1	1	1	ok	140.09	55	0.34	0.95
	2	1	1		1	1	random not estimable	151.12	55	0.16	11.97
	3	1	1	1		1	ok	149.96	56	0.32	10.81
	4	1	1			1	ok	139.15	57	0.31	0.00
	5	1				1	convergence issues	144.24	58	0.20	NA
	6	1		1		1	convergence issues	144.93	56	0.22	NA
	7		1			1	ok	141.28	58	0.25	2.13
	8		1		1	1	convergence issues	148.36	57	0.30	NA
	9					1	convergence issues	146.01	59	0.14	NA
	10						ok	146.38	59	0.13	7.24
	11	1					convergence issues	174.59	60	0.02	NA
	12		1				convergence issues	151.20	59	0.20	NA
successful attempts	1	1	1	1	1	1	ok	125.04	52	0.27	2.49
	2	1	1	1		1	ok	127.77	53	0.20	5.22
	3	1	1		1	1	ok	127.55	52	0.25	5.00
	4	1	1			1	ok	130.97	54	0.11	8.42
	5	1				1	ok	129.74	55	0.10	7.19
	6	1		1		1	ok	122.55	54	0.23	0.00
	7		1			1	ok	131.33	55	0.07	8.78
	8		1		1	1	ok	129.19	53	0.19	6.64
	9					1	convergence issues	144.81	57	0.01	NA
	10						random not estimable	131.80	56	0.00	9.25
	11	1					does not converge	NA	NA	NA	NA
	12		1				convergence issues	131.31	56	0.03	NA
fledglings	1	1	1	1	1	1	ok	251.24	51	0.27	9.60
	2	1	1		1	1	ok	250.15	52	0.25	8.51
	3	1	1	1		1	ok	242.42	51	0.05	0.78
	4	1	1			1	ok	243.12	52	0.06	1.48
	5	1				1	ok	241.64	53	0.04	0.00
	6	1		1		1	ok	245.86	52	0.18	4.21
	7		1			1	convergence issues	247.88	53	0.12	NA
	8		1		1	1	ok	245.80	52	0.20	4.16
	9					1	convergence issues	258.59	55	0.01	NA
	10						ok	256.81	56	0.00	15.17
	11	1					convergence issues	253.82	55	0.09	NA
	12		1				convergence issues	252.85	55	0.10	NA

Supplementary Material Table S3: Generalized linear mixed models to examine the effect of group size and climatic variables on reproductive parameters during the prebreeding (P), breeding (B) and extended breeding (BE) season, showing conditional models $\Delta AICc < 5$. Significant variables are bolded. gs = group size, AICc = Akaike Information Criterion, av = averaged weighed values, cR² = conditional r-squared, temp = temperature, zi = zero inflation intercept. ^Note that significant interaction effects indicate that the relationship between the fixed variable (i.e., temperature or rainfall) and the response variable varies with group size; therefore, the main effect reflects the effect at the reference group size only.

Climate window	Response variable	Parameter	Effect size	SE	z-value	P-value
prebreeding	breeding group sizes av AICc: 367.16 av cR ² : 0.70	intercept	8.46	0.733	11.3	<0.00001
		zi	-21.87	7105.761	0.00	1.00
		rainfall P	-0.87	0.414	2.06	0.04
		temp max P	0.25	0.496	0.49	0.62
prebreeding	number of attempts, same as $\Delta AICc < 2$ av AICc: 132.95 av cR ² : 0.41	intercept	0.40	0.066	5.98	<0.00001
		zi	-22.94	12080	0.00	1.00
		rainfall P	0.22	0.057	3.69	0.0002
		temp max P	0.24	0.062	3.71	0.0002
		gs	0.08	0.056	1.31	0.19
		gs x rainfall P	-0.06^	0.054	1.15	0.25
		gs x temp max P	0.06^	0.066	0.81	0.42
prebreeding	number of successful attempts av AICc: 125.37 av cR ² : 0.27	intercept	0.58	0.50	1.16	0.25
		zi	-2.69	1.162	2.27	0.024
		rainfall P	0.30	0.083	3.58	0.0004
		gs	0.10	0.083	1.14	0.26
		gs x rainfall P	-0.11^	0.081	1.34	0.18
		temp max P	0.02	0.096	0.16	0.87
		gs x temp max P	0.09^	0.088	1.03	0.30
prebreeding	number of fledglings					
breeding	number of attempts, same as $\Delta AICc < 2$ av AICc: 147.39 av cR ² : 0.18	intercept	0.46	0.067	6.64	<0.00001
		zi	-23.06	12840	0	1.00
		rainfall B	0.15	0.133	1.11	0.27
		gs	0.09	0.063	1.44	0.15
		temp max B	0.05	0.151	0.35	0.73
		gs x rainfall B	-0.22^	0.194	1.10	0.27

		gs x temp max B	-0.33^	0.192	1.71	0.088
breeding	number of successful attempts					
breeding	number of fledglings	intercept	0.98	0.103	9.35	<0.00001
	av AICc: 235.10	zi	-1.77	0.599	2.88	0.004
	av cR ² : 0.25	rainfall B	0.69	0.282	2.40	0.016
		temp max B	0.39	0.243	1.59	0.11
		gs	0.22	0.10	2.19	0.028
		gs x temp max B	-0.26^	0.091	2.83	0.005
		gs x rainfall B	0.20^	0.095	2.01	0.045
combined pre- and breeding	number of attempts	intercept	0.37	0.072	5.08	<0.00001
		zi	-23.31	14500	0.00	1.00
	av AICc: 130.19	rainfall P	0.20	0.057	3.51	0.0005
	av cR ² : 0.50	temp max P	0.26	0.061	4.09	<0.00001
		rainfall B	0.09	0.05	1.85	0.064
		temp max B	-0.14	0.049	2.79	0.005
		gs	0.11	0.055	2.02	0.044
		gs x temp max B	-0.10^	0.052	1.83	0.068
combined pre- and breeding	number of successful attempts	intercept	1.22	0.069	17.22	<0.00001
	av AICc: 106.92	zi	-2.45	0.651	3.68	0.0002
	av cR ² : 0.55	rainfall P	0.39	0.077	4.87	<0.00001
		temp max B	-0.34	0.211	1.60	0.11
		gs	0.30	0.073	3.94	<0.00001
		gs x temp max B	-0.38^	0.076	4.91	<0.00001
		temp max P	-0.09	0.081	1.10	0.27
		rainfall B	-0.46	0.428	1.04	0.30
combined pre- and breeding	number of fledglings					
breeding extended	number of attempts	intercept	0.42	0.067	6.15	<0.00001
	av AICc: 141.32	rainfall BE	-0.39	0.216	1.79	0.073
	av cR ² : 0.32	temp max BE	-0.48	0.253	1.86	0.063
		gs	0.10	0.059	1.64	0.10
		gs x rainfall BE	-0.18^	0.277	0.64	0.52

		gs x temp max BE	-0.29^	0.281	1.00	0.32
breeding extended	number of successful attempts av AICc: 123.10 av cR ² : 0.24	intercept	1.11	0.083	13.06	<0.00001
		temp max BE	-0.31	0.166	1.80	0.073
		gs	0.29	0.092	3.06	0.002
		gs x temp max BE	-0.42^	0.307	1.36	0.17
		rainfall BE	-0.06	0.315	0.18	0.86
		gs x rainfall BE	-0.62^	0.377	1.61	0.11
breeding extended	number of fledglings av AICc: 242.57 av cR ² : 0.06	intercept	1.23	0.665	1.85	0.064
		zi	-1.80	0.683	2.58	0.01
		rainfall BE	0.25	0.552	0.44	0.66
		gs	0.19	0.193	0.95	0.34
		temp max BE	-0.16	0.787	0.20	0.84
		gs x rainfall BE	0.25^	0.217	1.15	0.25
		gs x temp max BE	-0.63^	0.282	2.17	0.03