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Hot-Dry Weather Is Associated with Worse Reproductive Outcomes Regardless of Group Composition in a Long-Lived Cooperatively Breeding Bird

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ABSTRACT: Anthropogenic climate change is driving increases in temperature and droughts. Cooperative breeding, common in regions with greater environmental variation, has been proposed to buffer against such conditions, but findings across taxa are mixed. Life history strategies may partly explain these discrepancies, as long-lived species should invest less in reproduction. We examined how climatic, social, and life history factors affect reproduction in the long-lived cooperative southern ground-hornbill (*Bucorvus leadbeateri*). Using 17 years of data from 23 groups within the Greater Kruger National Park, South Africa, we tested for associations between temperature, rainfall and group composition, and several reproductive parameters. Low winter rainfall decreased breeding probability, while higher temperatures delayed laying and reduced nestling mass, regardless of group composition. Nestlings had longer tarsi in groups with more adults, and groups with more juveniles bred earlier and were more likely to breed, likely reflecting territory quality rather than group composition. In conclusion, hot and dry conditions negatively impacted ground-hornbill breeding, and, as expected given their life history, group composition did not mitigate these effects. We suggest that life history strategies and nonreproductive benefits of collective behavior, such as resource defense and survival, should be considered when assessing cooperative breeders' responses to environmental fluctuations.

Keywords: climate mitigation, cooperative breeding, group composition, rainfall, reproduction, temperature.

Introduction

Anthropogenic climate change is leading to an increase in global temperatures and weather extremes (IPCC 2021), which are expected to be particularly important in arid and semiarid environments (van Wilgen et al. 2016; Mbokodo et al. 2020). Such climatic variation is known to influence breeding decisions and outcomes in a wide range of species through its influence on food availability and adult condition (e.g., Drent and Daan 1980; Cruz-McDonnell and Wolf 2016; Legagneux et al. 2016; Jean-Gagnon et al. 2018; Bourne et al. 2021). In cooperatively breeding species, parents are assisted by helpers in raising offspring, and some studies have suggested that the presence of helpers could provide additional food that would mitigate the negative effects of adverse environmental conditions on reproduction (Rubenstein and Lovette 2007; Covas et al. 2008; Jetz and Rubenstein 2011; Rubenstein 2011). This association is noteworthy because it could imply a greater resilience of cooperative species to increasing climatic extremes. However, while cooperative breeding appears to occur predominantly in regions with lower rainfall and greater environmental variability (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011), recent studies found that having more helpers was not associated with improved reproductive output under adverse conditions (Bourne et al. 2020*a*; D'Amelio et al. 2022; Borger et al. 2023). This raises fundamental questions about the conditions under which helpers contribute meaningfully to reproductive outputs.

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When assisted by helpers, parents can reduce their workload in order to invest in self-maintenance and survival ("load-lightening"; Hatchwell 1999) or maintain their feeding rates, leading to "additive" care, which can increase nestling condition and survival (Hatchwell 1999; Johnstone 2011; van Boheemen et al. 2019). Breeding groups may also have flexible strategies according to breeding conditions, such that the presence of helpers leads to improved breeding output under adverse conditions but go unnoticed under good conditions (Covas et al. 2008; Rubenstein 2011; Groenewoud and Clutton-Brock 2021).

Decisions on how much to invest in reproduction or helping should be strongly influenced by a species' life history strategy, as they are part of a trade-off between investment in self-maintenance versus reproduction, which is strongly influenced by adult survival prospects (Stearns 1992). Long-lived species typically maximize their lifetime reproductive success through maximizing the number of lifetime breeding events, instead of increasing reproductive effort on a given occasion (Clutton-Brock 1988). A similar reproduction versus survival trade-off should also apply to helpers, which balance their decisions of how much to help according to the cost of helping (Mendonça et al. 2020; Covas et al. 2022). As such, the benefits of having helpers in long-lived cooperatively breeding species may not be strongly associated with reproduction but instead be associated with other collective behaviors that enhance access to resources and increase survival (Shen et al. 2017; Lin et al. 2019; Liu et al. 2020). A schematic representation of this hypothesized interplay between different factors is shown in figure 1.

Indirect support for such a role of life history comes from the hornbill family (Bucerotidae), where, in contrast with other studies (Rubenstein and Lovette 2007; Jetz and Rubenstein 2011; Lukas and Clutton-Brock 2017), cooperative breeding was found to be positively associated with more humid environments and climatic stability (Gonzalez et al. 2013). The authors suggested that this family's life history, characterized by larger body sizes, high survival, low fecundity, and stable year-round food supply, made the presence of helpers less relevant for reproduction. Instead, the primary mechanism linking cooperative breeding to climate is likely a result of habitat saturation and ecological constraints, under which helper contributions to predator deterrence and to the defense of territories with nest cavities for reproduction might overshadow their role on reproductive output (see also Hinde 2008; Shen et al. 2017; Nelson-Flower et al. 2018; Humphries et al. 2021).

However, most studies of the effects of helpers on reproduction have focused on small, insectivorous passerines with relatively short lifespans, hampering our understanding of whether variation in life history influences the effect of helpers on reproductive outcomes. In this study, we focus instead on a large cooperative breeder with an exceptionally slow life history, the southern ground-hornbill *Bucorvus leadbeateri* (hereafter, "ground-hornbill"). We investigate how climatic and social factors are associated with reproductive outcomes in this species and specifically assess whether group members help to mitigate the effects of adverse weather in this life history context. Ground-hornbills are faunivorous birds with generalist diets that inhabit semiarid savannah habitats (Kemp 2017), despite being relatively heat intolerant (i.e., they begin heat dissipation behaviors at around 26°C; Janse van Vuuren et al. 2020) and having limited cavities for nesting (Carstens 2017). They are large (3–5 kg), are very long-lived (up to 60 years), and develop slowly, reaching adulthood from around 6–8 years old (Kemp and Kemp 1980; Kemp 2017). Groups consist of 2–11 individuals, comprising one breeding pair assisted usually by males from previous broods (and sometimes immigrant males), all of which contribute toward raising offspring. Their slow development results in a mosaic of individuals of distinct ages (readily identifiable; see "Methods") with differing experience, which could further influence group reproductive performance, as younger individuals may lack the skills to efficiently feed the offspring and may even still be dependent on older birds (Woxvold 2004; Woxvold et al. 2006). Furthermore, the age and experience of individuals may influence the costs and benefits of helping (Covas and Griesser 2007; Covas et al. 2022), leading to different investment strategies and potentially modulating the effect of group size on reproductive outcomes. Our specific objectives here were to use a long-term dataset (17 years) to investigate whether group composition, group size, temperature, and rainfall are associated with reproductive performance and output and whether helpers mitigate the adverse effects of poor breeding conditions.

Specifically, in long-lived species we expect that breeders and helpers will readily forego reproduction or reduce reproductive investment when conditions are poor because they have high residual reproductive value (Clutton-Brock 1988; Stearns 1992; Covas and Griesser 2007). Given the ground-hornbill's size, longevity, and heat sensitivity, we hypothesize that high temperatures and low rainfall will reduce breeding propensity and reproductive output (i.e., resulting in higher incidence of groups not attempting to breed, delayed laying dates, and nestlings in poor condition). We further expect that reproductive parameters should depend on group composition because adult, subadult, and juvenile birds differ in their contributions (Middleton 2022). We therefore distinguish between age classes in our analyses rather than pooling potentially relevant biological variation into a single measure of group size. Adult and subadult birds contribute to nest lining, provisioning, and defense (Middleton 2022), so they should have a positive effect on reproduction. By contrast, juveniles have extended dependence on older individuals and contribute less toward nestling care, so they

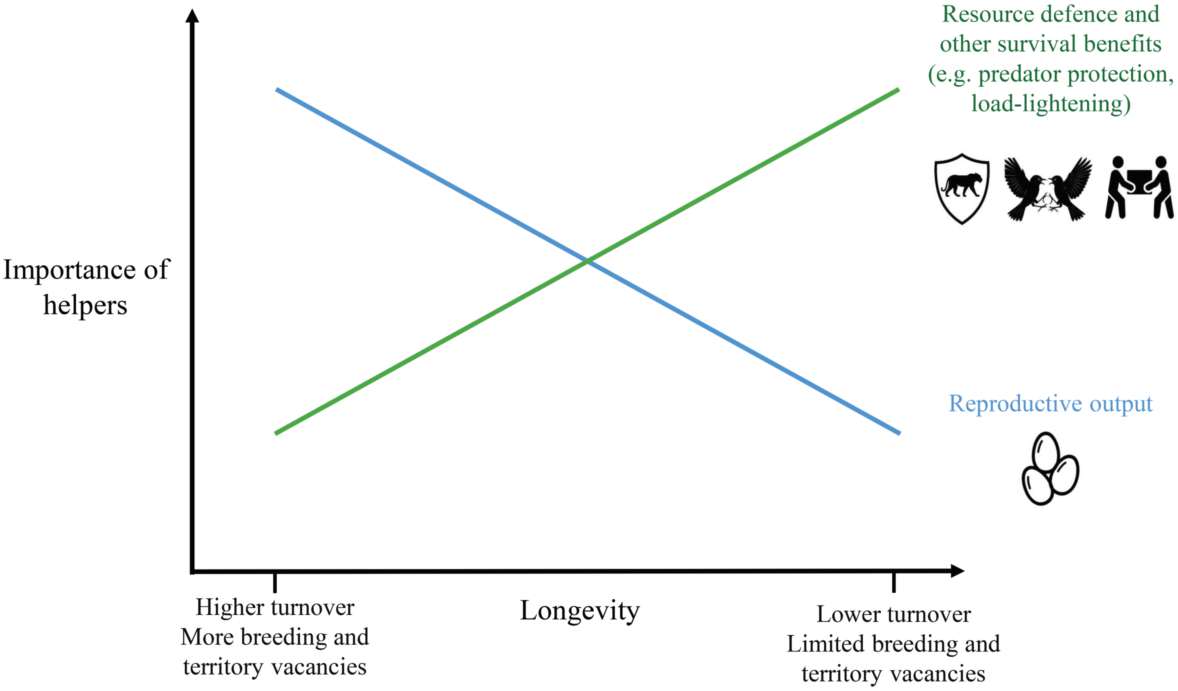

Figure 1: Visual representation of the importance of helpers for reproduction (blue line) and other collective behaviors (green line) in relation to species longevity. Long-lived species are expected to have very low turnover with limited breeding and territory vacancies; therefore, the benefits of having helpers are likely to be less associated with reproduction (and their potential to buffer against harsh environmental conditions). Instead, the benefits of helpers are more likely to derive from improved resource defense and survival.

should have a negative effect on reproduction. Finally, given that ground-hornbills inhabit a highly variable environment, the hypothesis that helpers could contribute to mitigate the effects of adverse breeding conditions on reproduction may be applicable (Jetz and Rubenstein 2011). However, given this species' slow life history, stable generalist diet (Gonzalez et al. 2013), and nesting site constraints, a more likely expectation is that any mitigating effects should be weak or absent (fig. 1).

Methods

Study Species

Southern ground-hornbills inhabit savannah habitats from Kenya to South Africa. They require large territories (up to 200 km^2), resulting in low population densities (Carstens 2017; Theron et al. 2013). They are classified as vulnerable throughout their range, and habitat loss drives population decline (Kemp 2017). Nests are often a scarce resource: they are located several meters off the ground, mostly within large tree cavities, and so ground-hornbills require landscapes with large, old trees in which to breed (Combrink 2016; Loftie-Eaton 2017). They feed on a wide variety of animals, from invertebrates to relatively large vertebrates such as hares and snakes (Combrink 2016).

Groups usually contain a single adult female and several males. Adult and subadult females have a blue skin patch on the throat. Individuals can be classified into three age categories according to the development of their plumage, bare facial skin, and beak color (Kemp and Kemp 1980; Carstens 2017): (1) juveniles (0–2 years old), (2) subadults (2–8 years old), and (3) adults (>8 years old).

Breeding occurs during summer (the rainy season) from September to March, and a breeding cycle usually lasts up to 130 days from egg laying to fledging (Kemp and Kemp 1980; Wilson and Hockey 2013). Clutches comprise one or two eggs laid asynchronously about 5 days apart. Hatching is also asynchronous, and second-hatched chicks are consequently smaller and always starve, resulting in a lone survivor (Kemp 2017). Incubation occurs solely by the female and takes ~40 days. The surviving nestling fledges after 80–90 days (Kemp 2017). During incubation, the group provides food and nest lining to the incubating female, and the whole group (including the female) provides food for the surviving nestling (Kemp 1988).

Study Site

We worked in a 2,000 km^2 area of the Greater Kruger National Park, on the Associated Private Nature Reserves

(APNR; centered on 24.16°S, 31.18°E), South Africa. The APNR comprises five private nature reserves: Klaserie, Timbavati, Umbabat, Balule, and Thornybush. The area has an annual rainfall range of 400–600 mm with distinct wet (October–March; average: 367 mm) and dry (April–September; average: 54 mm) seasons. Dry seasons coincide with winter, although maximum temperatures can be relatively hot during this period: mean minimum and maximum temperatures are 12°C/26°C for dry seasons and 20°C/33°C for wet seasons. The vegetation throughout the study area varies from open savannah to closed woodland (Carstens 2017).

Data Collection

Long-term survey and research on ground-hornbills commenced in 2000 at our study site. The rarity of natural breeding cavities within the study site led to artificial nests being used to increase breeding productivity and facilitate monitoring (Carstens et al. 2019). Each group typically has one nest within their home range (Carstens 2017).

Nests were visited once every 7–10 days from 2000 to 2021 to ascertain the breeding status of groups. After initial egg discovery, nests were visited 5 days later to check for second-laid eggs. Subsequent visits occurred 40 and 45 days later, to check for hatching of each egg. Accurate lay dates (to within a day or two) could then be determined by backdating based on the age of the first-hatched chick. Final visits, between days 53 and 81, involved ringing and measuring nestlings' mass and tarsus length using a hanging scale and Vernier callipers, respectively.

The study is largely based on noninvasive methods (apart from the handling of nestlings described above). Since 2017, adults were identified through unique facial features (e.g., sideburns, pouch shape) based on images from camera traps placed at nesting sites. Group sizes and compositions from 1998 to 2021 (except 2008–2010, which were subsequently excluded from all analyses) were documented through sightings and photographs by researchers, local wildlife guides and citizen scientists, camera traps, and aerial censuses. Birds were linked to specific group areas based on the proximity of the sighting to the nearest nesting sites and from prerecorded group home ranges (Wyness 2011). Since group size and composition may vary depending on the time of the year, only sighting data from within and just prior to the breeding season (July–April) were used. Data collection sought to balance effective monitoring with the impact of human presence and was approved by the University of Cape Town Science Faculty Animal Ethics Committee (approval 2020/2019/V5/RC/A1).

Temperature data were collected from weather stations in Hoedspruit and Phalaborwa towns, and rainfall estimates came from 16 gauges across the study site. We selected the stations and gauges closest to each nest (0.97–14.66 km).

Statistical Analyses

We aimed to investigate how climatic factors (rainfall and maximum temperatures), social factors, and age (number of group members of different ages) were associated with reproductive parameters. We also tested interactions between these factors to investigate whether the number of group members mitigated the effects of adverse conditions. Throughout, we accounted for other factors likely to influence reproduction (see below). We focused on four reproductive variables: (1) breeding probability (0/1), (2) laying date (number of days after September 1 when the first egg was laid), (3) fledging success (0/1), and (4) nestling condition—mass and tarsus length of nestlings prior to fledging (for variable descriptions, see table S1; tables S1–S19 are available online).

To investigate associations with climate, all analyses (except for fledging success; see below) included the mean maximum temperature and rainfall (continuous variables), although the period captured by these variables varied for each analysis depending on what was considered biologically meaningful (table S1). For breeding probability and lay date, we used winter and spring mean maximum temperatures and rainfall, as well as the previous year's rainfall. For nestling condition, we used mean maximum temperatures and rainfall for the period from hatching to measurement. Analyses of fledging success excluded climate variables, since the duration of the nestling period (and hence the amount of rainfall and average maximum temperature experienced) was very different between nests that succeeded and nests that failed at different stages. We never observed evidence of first-hatched nestlings dying of starvation (or even losing condition between visits), and camera trap footage strongly indicates that predation is the main cause of breeding failure (K.-M. Middleton and C. Hickman, unpublished data). Nest height and lay date were also included in the analyses of fledging success, following Carstens et al. (2019), who suggested that groups were more successful in higher nests and when laying earlier in the season (presumably due to reduced predation, better synchrony with food abundance, and reduced overlap of incubation with the hottest months). Temperature-rainfall interaction effects were also tested, since hot and humid conditions are expected to be more detrimental because of increased thermoregulatory constraints (Powers 1992; Gerson et al. 2014).

To investigate effects of social factors and helper age, in each model we considered the number of adult males, subadults, and juveniles in the group as explanatory variables. To investigate possible mitigating effects of helpers, we included interactions between the climatic and group composition variables.

All statistical analyses were conducted in R (ver. 4.0.1; R Core Team 2020) using packages lme4 (ver. 1.1.23) and MuMIn (ver. 1.43.17). Data exploration followed Zuur et al. (2010). Potential predictors of breeding probability, lay date, fledging success, and nestling condition were investigated by fitting general and generalized linear mixed models (GLMMs). Continuous variables were scaled by centering and standardizing by the mean (Schielzeth 2010). Strongly correlated variables ($r > 0.30$) were not included in the same models (see below for each analysis). Group identity was included as a random term in all analyses. Year was included as a random term only in analyses of fledging success and nestling condition and not in analyses of breeding probability and lay date because for the latter two, all observations within each year had climate values from the same temporal period. Groups with only one or two breeding records were excluded because of convergence issues. This resulted in 23 groups monitored over 17 years, although sample sizes varied between analyses. Residuals of final models were visually inspected to ensure that model assumptions were met. Models were compared using the Akaike information criterion corrected for small sample size (AICc) and chosen when AICc values reduced by >2. Model likelihoods relative to other models tested were also checked using Akaike's model weights. When models had similar weights and $\Delta\text{AICc} < 2$, the simpler model with fewer parameters was used for further inference (Richards 2008; Richards et al. 2011). Random effects were tested using likelihood ratio tests and considered significant when P values were <.05. Marginal and conditional R^2 values were also calculated to show variance explained by fixed effects and by both fixed and random effects, respectively.

Results

During 2000–2021, the mean ± SE group size was 3.98 ± 0.07 individuals (range: 2–7 individuals). These groups contained a mean ± SE of 1.84 ± 0.05 adult males (range: 1–4 individuals), 0.60 ± 0.05 subadults (range: 0–3 individuals), and 0.50 ± 0.04 juveniles (range: 0–2 individuals).

Probability of Breeding

We used a GLMM with binomial (binary) error structure and breeding data from 22 different groups from 2000 to 2007 and from 2011 to 2021 ($n = 244$ group-years; for yearly breeding probability details, see table S2). Mean maximum winter temperatures and previous year's rainfall were strongly correlated ($r > 0.45$) and so were included in different models.

There were two nested best-fit models for breeding probability ($\Delta\text{AICc} < 2$) and similar model weights (0.46 and 0.19), so the simpler model was chosen. This included group composition, winter mean maximum temperature, and winter rainfall (for top five models; see table S3). However, neither the number of adult males (estimate $= -0.12 \pm 0.18$, 95% confidence interval (CI) $= -0.47$ to 0.23; for full model outputs, see table S4) nor the mean maximum winter temperature (estimate $= -0.12 \pm 0.16$, 95% CI $= -0.21$ to 0.44; table S4) had any clear effects, with both having 95% CIs that broadly overlapped zero (table S4). There was clearer support for a positive association between breeding probability and increased number of subadults (estimate $= 0.38 \pm 0.19$, 95% CI = 0.02 to 0.78; table S4; fig. 2*A*) and juveniles (estimate $= 0.58 \pm 0.18$, 95% CI = 0.23 to 0.95; table S4; fig. 2*B*) as well as between breeding probability and amount of winter rainfall (estimate $= 0.47 \pm 0.18$, 95% CI = 0.14 to 0.84; table S4; fig. 2*C*). Breeding probability was also related to group identity (variance = 0.92, $P \leq .001$; for model output of the random variable, see table S5), and this random effect explained more variance (conditional $R^2 = 33.3\%$) than the fixed effects (marginal $R^2 = 14.6\%$), while 66.6% was unexplained (for a summary of heterogeneity in breeding parameters among groups, see also table S19).

Lay Date

We used a GLMM with Gaussian error structure and maximum likelihoods for 23 groups over 14 years ($n = 153$ group-years; for yearly lay date details, refer to table S6). Mean maximum winter temperatures and previous year's rainfall were strongly correlated ($r > 0.45$) and so were tested in different models.

There were two nested best-fit models for lay date, where $\Delta\text{AICc} < 2$ and the model weights were close (0.48 and 0.32), and so the simpler was used for further inference (for top five models, see table S7). This model included group composition, winter and spring rainfall, winter and spring mean maximum temperatures, and interactions between winter and spring mean maximum temperatures and rainfall (table S7). No clear effects were detected for the number of adult males, subadults, winter and spring rainfall, spring mean maximum temperatures, and the interaction between spring mean maximum temperatures and spring rainfall (for full model outputs, see table S8). Earlier laying was associated with the number of juveniles present in the group (estimate $= -3.89 \pm 1.69$, 95% CI $= -7.23$ to -0.52; table S8; fig. 3). Increases in the mean maximum winter temperature were associated with delayed laying (estimate $= 3.90 \pm 1.80$, 95% CI = 0.36 to 7.44; table S8), and there was an interaction between winter mean maximum temperature and winter rainfall (estimate $= 4.66 \pm 1.94$,

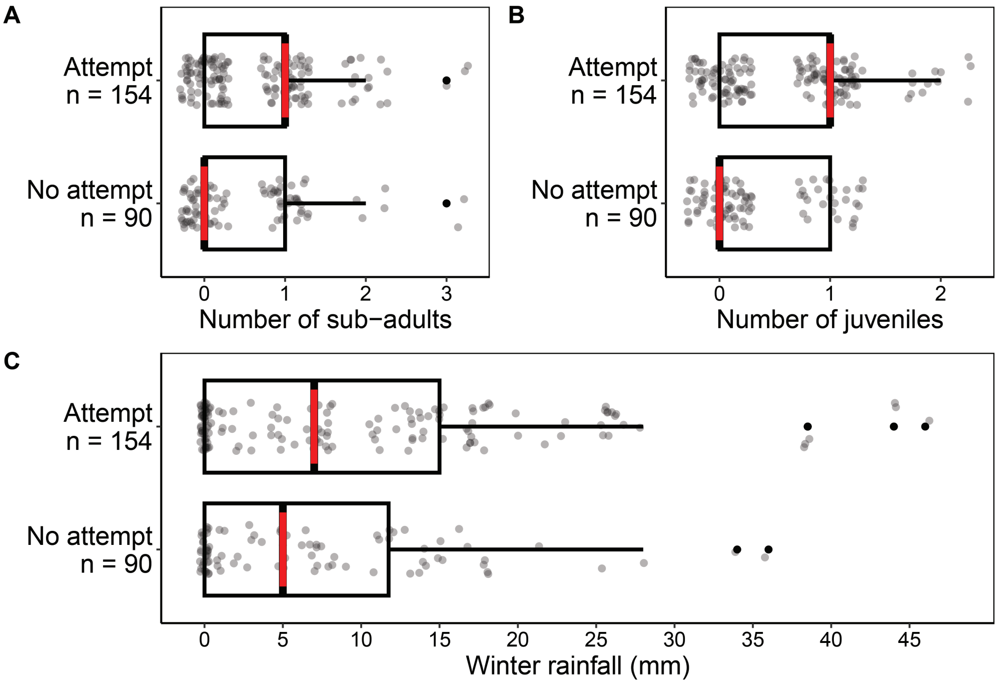

Figure 2: Breeding probability in relation to the number of subadults (*A*), the number of juveniles (*B*), and winter rainfall (*C*). Boxplots show median values (red lines), first and third quartiles (box), and the interquartile range (whiskers). Data points are jittered for improved visibility.

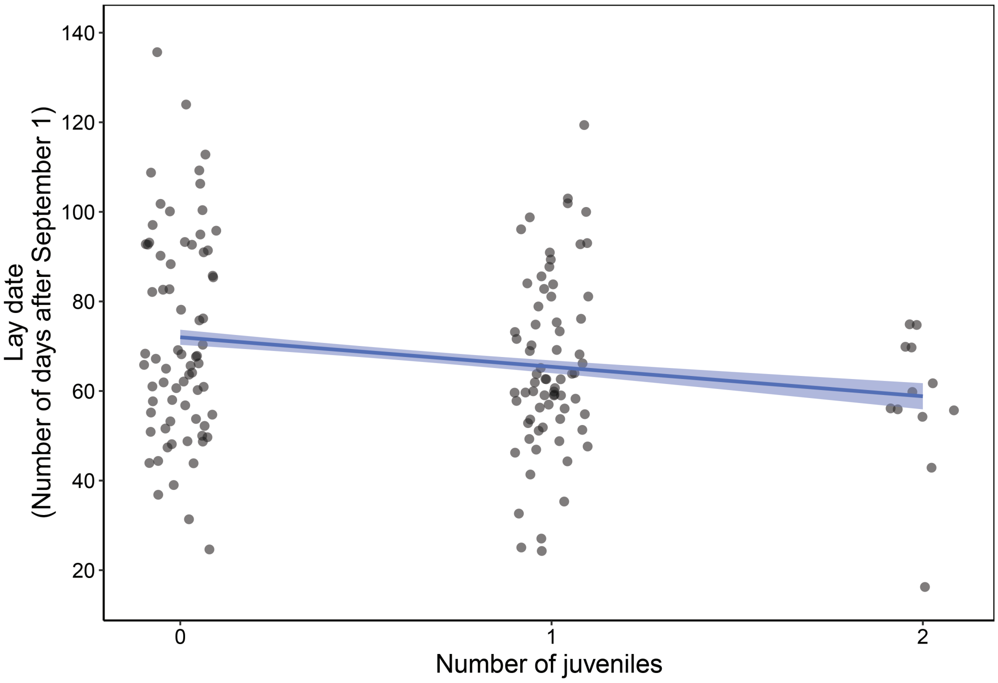

Figure 3: Lay date in relation to the number of juvenile group members. Jittered data points represent different nests, and the blue line and confidence intervals represent the model-predicted relationship.

95% CI = 0.82 to 8.49; table S8), suggesting that hot and wet winters were associated with later laying (fig. 4). Most of the model variation was unexplained (80.9%), and the random effect of group identity (for model output of the random variable, see table S9) explained very little of the model's variation (conditional $R^2 = 19.1\%$, marginal $R^2 = 15.1\%$).

Fledging Success

We used a GLMM with a binomial (binary) error structure for 18 groups from 2002 to 2007 and from 2011 to 2021 ($n = 142$ group-years; for yearly fledging success details, refer to table S10). The best-fit model was the null model with a model weight of 0.78, indicating that none of the variables clearly predicted fledging probability in our dataset (table 1). There was also no effect of the random factors of group identity and year (for model output of the random variables, see table S11).

Nestling Condition

We used GLMMs with Gaussian error structures and maximum likelihoods, and body mass and tarsus length as indicators of body condition (see Labocha and Hayes 2012), for a total of 18 groups from 2004 to 2008 and from 2011 to 2021 (nestling mass: $n = 79$; tarsus length: $n = 80$; for yearly nestling condition details, refer to table S12). The age at which nestlings were measured varied from 53 to 81 days (owing to field conditions determining access), and so nestling age was included in the models. Temperature and rainfall variables were highly correlated ($r > 0.30$) and so were included in separate models. Tarsus length was included as a covariate to nestling mass to account for nestlings' structural size.

Nestling mass. Mean nestling mass ± SD at ringing was 3,050 ± 374 g (range: 2,150–4,150 g). The best-fit model had a model weight of 0.76 (for top five models, see table S13) and included group composition, mean maximum temperature for the nestling growth period, and tarsus length, with no interactions. The model parameters, however, did not indicate a clear association between nestling mass and the number of adult males, subadults, or juveniles (for full model outputs, see table S14). Increasing mean maximum temperature was associated with lower nestling mass. For example, a 1°C increase in mean maximum temperature was estimated to be associated with an 88.5-g decrease in nestling mass: estimate = −107.50 ± 47.90, 95% CI = −213.18 to −11.89 (table S14; fig. 5). There was also a positive association

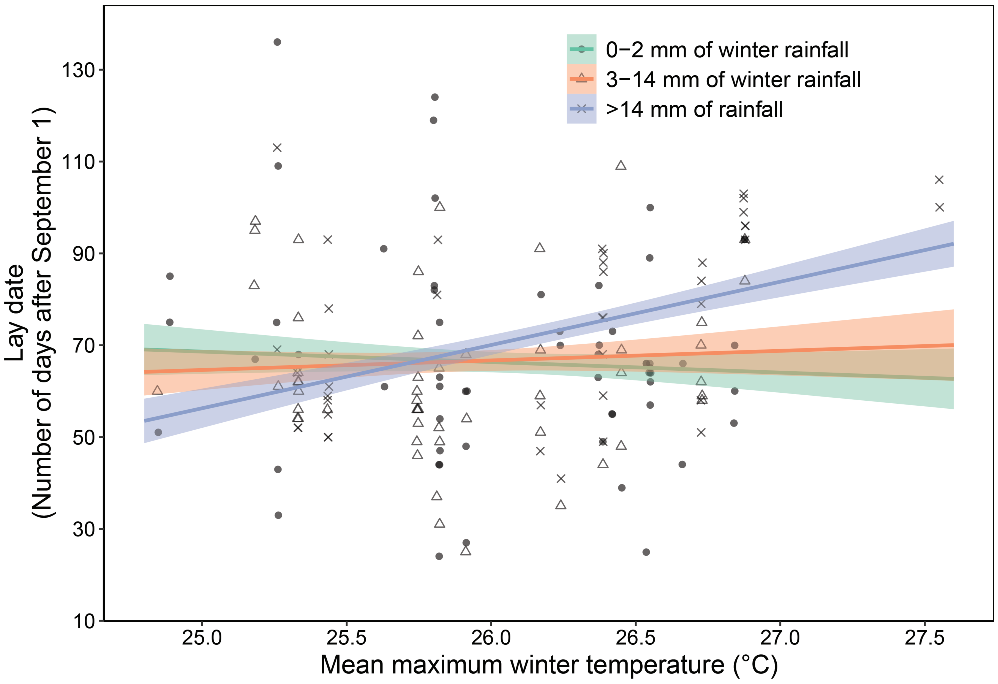

Figure 4: Interactive effect of mean maximum winter temperature and rainfall on lay date. For ease of visualization, rainfall is separated into three categories but was continuous in the main analysis. Lines represent the model-predicted relationship with 95% confidence intervals.

Table 1: Top five models for nestling fledging success

Model	*k*	Dev	AICc	ΔAICc	Model weight
Null model	3	181.9	188.06	0	.78
AM + SA + Juv + lay date	7	177.4	192.20	4.14	.10
AM + SA + Juv	6	180.5	193.14	5.08	.06
AM + SA + Juv + lay date + AM × lay date	8	177.3	194.36	6.31	.03
AM + SA + Juv + lay date + nest height	8	177.3	194.43	6.37	.03

Note: Random terms: group identity and year. AICc = Akaike information criterion corrected for small sample size; AM = number of adult males; SA = number of subadults; Juv = number of juveniles; Dev = model deviance.

between tarsus length and nestling mass (estimate = 172.01 ± 41.46, 95% CI = 86.01 to 256.58; table S14). The fixed and random effects explained 37.1% of the variation (conditional R^2), and fixed effects alone explained 25.1% of the variation (marginal R^2). The term year explained most of the variation from the random effects (for model output of the random variables, see table S15).

Nestling tarsus length. Mean tarsus length ± SD was 150.85 ± 10.07 mm (range: 128–179 mm). There were two best-fit models with ΔAICc < 2 and similar model weights (0.47 and 0.28), differing only in the replacement of variable mean maximum temperature with rainfall (for top five models, see table S16). Since these two variables were correlated, we present the top model only, which contained group composition, mean maximum temperature for the nestling growth period, and nestling age, with no interactions among them. No clear effects were detected for the number of subadults and mean maximum temperature (for full model outputs, see table S17). Tarsus length was positively associated with the number of adult males (estimate = 2.58 ± 0.98, 95% CI = 0.59 to 4.55; table S17; fig. 6*A*) and the number of juveniles (estimate = 2.90 ± 1.07, 95% CI = 0.62 to 5.20; table S17; fig. 6*B*). As expected, increases in nestling age were positively associated with tarsus length (estimate = 2.30 ± 1.13, 95% CI = 0.01 to 4.62; table S17). The fixed and random effects explained 37.2% of the variation (conditional R^2), and fixed effects alone explained 18.1% of the variation (marginal R^2). The

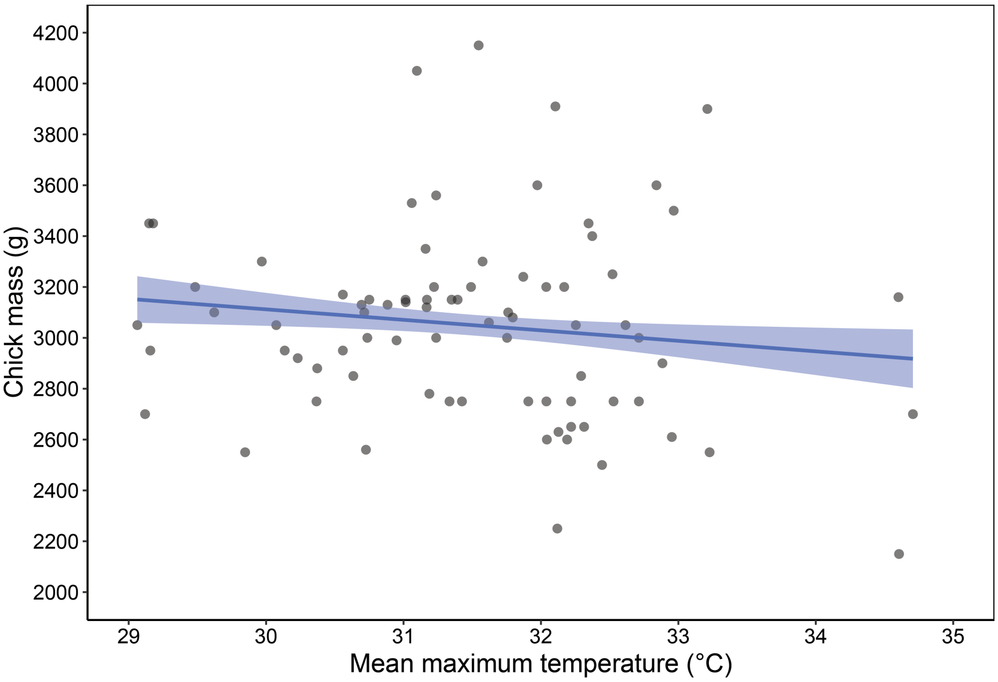

Figure 5: Relationship between mean maximum temperature (measured during the nestling period) and nestling mass. Data points represent different nests, and the blue line and confidence interval represent the model-predicted relationship.

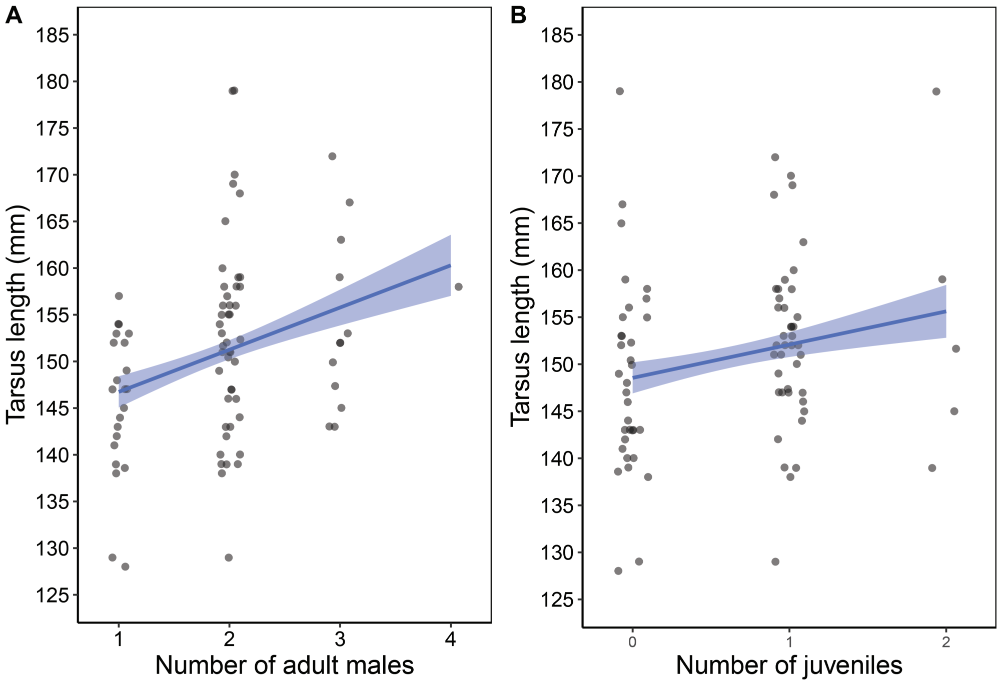

Figure 6: Tarsus length of nestlings in relation to the number of adult males in the group (*A*) and the number of juveniles in the group (*B*). Jittered data points represent individual nests, and blue lines and confidence intervals represent the model-predicted relationship.

term year explained most of the random effects variation (for model output of the random variables, see table S18).

Discussion

We proposed that a species' life history may influence the extent to which helpers buffer the reproductive outcomes under harsh conditions and explored this idea in the context of a long-lived cooperative breeder. We investigated whether climatic factors and group composition were associated with reproductive outcomes in the southern ground-hornbill and whether social factors could mitigate the effects of unfavorable breeding conditions. First, our data showed that, as expected, high temperatures and low rainfall were usually associated with poorer reproductive outcomes. Second, the number of adults, subadults, and juveniles were, in general, positively associated with the reproductive process, but the effects were often statistically unclear. Third and also as expected for this long-lived species (see fig. 1), there was no evidence that having more group members mitigates (or, for juveniles, exacerbates) the adverse effects of high temperatures and low rainfall. Hence, despite ground-hornbills inhabiting semiarid environments, larger groups do not appear to reproduce better under adverse conditions. Our results are consistent with comparative analyses suggesting that in the hornbill family, additional group members may not be relevant for reproductive outcomes under adverse conditions and instead likely contribute to other group behaviors (Gonzalez et al. 2013). Taken together, these findings suggest that life history and group benefits besides reproduction need to be considered when investigating the evolution and biogeography of cooperative breeding and when making predictions about how cooperative breeders might respond to climate change.

Temperature and Rainfall

As expected, reproduction was poorer under higher mean maximum temperatures, which were the strongest predictors of laying date and nestling mass at fledging. Warmer winters were followed by delayed laying, but this effect was modulated by winter rainfall, indicating that reproduction suffered specifically under warm and wet conditions. The negative effects of high temperatures on bird reproduction have mostly been studied during warmer summer months (e.g., Cunningham et al. 2013; Bourne et al. 2021). However, in our study area, mean maximum winter temperatures can reach 26°C (with daily maxima frequently exceeding 30°C), which can be detrimental since 26°C is the temperature at which southern ground-hornbills commence heat dissipation behaviors (Janse van Vuuren et al. 2020). Rainfall increases humidity, reducing the potential for evaporative heat loss (Gerson et al. 2014; van Dyk et al. 2019), which may be further compounded by the lack of shade and increase in bare ground solar radiation arising from lack of foliage during the dry season (Abdu et al. 2018; Pattinson et al. 2020). If these conditions lead to birds spending more time seeking shade and performing heat dissipation behaviors, trade-offs with foraging may result (Conradie et al. 2019; Cunningham et al. 2021), leading to poorer body condition of breeders and longer recovery periods prior to laying. However, our model had low predictive power, suggesting that other factors also influence laying dates.

We also found that high mean maximum temperatures were strongly associated with reduced nestling body masses at fledging. Our results are consistent with similar studies showing adverse effects of high temperatures on offspring development (Cunningham et al. 2013; Andreasson et al. 2018; Bourne et al. 2021). Although the underlying mechanisms are uncertain, nestlings are likely affected by increased temperature both directly through increased thermoregulatory demands and indirectly through possible effects of reduced provisioning rates from carers (Bourne et al. 2020*b*, 2021; van de Ven et al. 2020; Corregidor-Castro and Jones 2021; Middleton 2022). Since fledging mass should impact postfledging survival (Maness and Anderson 2013; Perrig et al. 2017; Bourne et al. 2020*b*), our results raise concerns about how recruitment in this species might be affected by increases in temperature predicted under current climate change scenarios and so impact its current vulnerable conservation status.

In semiarid regions, rainfall is expected to strongly improve avian reproduction by aiding vegetation growth and associated increase in phytophagous insects (Bolger et al. 2005; Jamieson et al. 2012). Here, we found that winter rainfall was associated with increased breeding probability, an effect likely due to increased food abundance leading to improved body condition. Although there were no effects of rainfall on other parameters, attempting to breed is a major determinant of reproductive outcome in this species (see below), and hence our study confirms the importance of rainfall for this process.

Group Composition

Studies of the effects of helpers on reproductive outcomes expect these to be positive, as the evolution of helping behavior is thought to be favored by increased production of nondescendent kin (Koenig and Dickinson 2004) or group augmentation (Kingma et al. 2014). In most cooperative breeders, a significant number of group members are retained young from previous broods (Riehl 2013), which leads to a long-established difficulty in separating the effects of breeder and territory quality from those of helper presence (i.e., retained young). By analyzing the effects of group members of different ages separately, we found that groups were more likely to breed, and bred earlier, when they included juvenile members. With less clarity, the presence of subadults was also associated with increased breeding probability. However, these associations are unlikely to arise causally from the direct contributions of juveniles and subadults, as these birds have extended dependency periods (Kemp 1988) and contribute little to feeding the incubating female and developing nestling (Middleton 2022). Since most subadults were also retained offspring, their observed associations with breeding parameters likely arise from a positive correlation with parental (or territory) quality or experience. This is supported by a significant random effect of group identity on breeding probability and chick condition, showing consistent differences between groups (see table S19).

The only clear positive association between number of group members and reproduction was between the number of adult members and nestling tarsus length. Adult group members provision most of the food to the nestling (Middleton 2022), and this effect suggests that adults' provisioning efforts are additive and improve nestling structural development. However, the number of adult birds did not predict nestling mass, perhaps because ground-hornbill nestlings reach peak mass just past halfway through the nestling period (C. Hickman, unpublished data), whereas tarsus lengths continue to grow throughout (correspondingly, nestling age was associated with tarsus length but not mass). Any possible effects of adult male helpers on body mass might therefore be more important during earlier developmental stages.

Surprisingly, group composition variables were unrelated to fledging success. This is likely explained by predation being the main cause of nesting failure after hatching: our camera trap data indicate that ~60% of failed breeding attempts were from predation by large species adept at climbing, such as genets (*Genetta* spp.), leopards (*Panthera pardus*), and chacma baboons (*Papio ursinus*; unpublished data; see also Carstens et al. 2019). Studies of other cooperative breeders have shown that group members can decrease predation on young (Clutton-Brock et al. 1999; Santema and Clutton-Brock 2013). However, given ground-hornbills' large body size and energy requirements, much of their time is spent away from the nest foraging as a group (Zoghby et al. 2015), leaving nestlings vulnerable to predation. Furthermore, this limited nest attendance may be exacerbated under hot and dry conditions that increase the thermoregulatory demands of individuals, extend foraging times, and reduce prey availability (Bourne et al. 2020*b*, 2021; van de Ven et al. 2020; Corregidor-Castro and Jones 2021; Middleton 2022).

While helpers had no strong benefits for reproduction, juvenile and subadult group members may provide additional benefits not directly revealed by the reproductive outcomes. For instance, in different species helper roles also extend beyond nest provisioning to include other behaviors, such as lightening the workload of breeders (Russell et al. 2007; Paquet et al. 2015), territory defense (Radford 2003; Mosser and Packer 2009; Cassidy et al. 2015), and predator deterrence (Clutton-Brock et al. 1999; Arroyo et al. 2001; Jungwirth et al. 2015) during group foraging. By reducing predation or enhancing control of crucial resources (such as nesting sites or burrows/dens; Gonzalez et al. 2013; Shen et al. 2017), helpers can support the persistence of cooperation even in the absence of any immediate reproductive advantages (see fig. 1).

Mitigating Effects of Helpers and Life History

Given the slow life history of our study species, we expected that additional group members would not mitigate the negative effects of adverse environmental conditions (fig. 1) and found that accordingly they did not. Specifically, since high temperatures could lead to physiological stress impacting nestlings and/or their carers as well as to lower foraging efficiency (du Plessis et al. 2012) and reduced prey availability (Visser et al. 2012), we expected that carers should postpone their investment until conditions improve rather than incur high costs of nestling provisioning under adverse conditions. This is in line with the broader life history theory that predicts that the physiological costs of helping and general risk taking associated with nestling care should be minimized in species with high life expectancy and slow life history (see Ghalambor and Martin 2001).

Our results thus indicate that helpers do not mitigate the effects of harsh conditions on these reproductive outcomes, but there may still be indirect or delayed benefits of larger groups. For example, if helpers reduce the workload of the breeders through load-lightening, it may potentially enhance future survival and lifetime reproductive output of the breeders (Hatchwell 1999; Meade et al. 2010; see fig. 1). This may be especially relevant in long-lived species such as ground-hornbills, where maintaining body condition could be a more important factor in lifetime fitness than maximizing current breeding outcomes.

The hypothesis that cooperative breeders are more common in areas that experience greater climatic variation because additional group members allow sustained reproduction under poor conditions became a prominent explanation for the evolution and geographical distribution of cooperative breeding (Rubenstein and Lovette 2007; Covas et al. 2008; Jetz and Rubenstein 2011; Rubenstein 2011). This hypothesis has also gained additional relevance under current climate change and the associated increased variation in environmental conditions, as cooperative species could be more resilient to such variation. However, our results here add to recent studies in birds that did not find support for such mitigating effects on reproduction (Bourne et al. 2020*a*, 2020*b*; D'Amelio et al. 2022; Borger et al. 2023; but see Rubenstein 2011; Capilla-Lasheras et al. 2021). Most studies investigating mitigating effects of helpers have been conducted in small insectivorous birds from arid to semiarid regions. Additional studies of different systems and environments are needed to test whether our findings indicating no modulating effects of helpers on reproduction in a long-lived bird are more general, as expected according to predictions of life history theory.

Conclusion

Our study of the effect of helpers on reproduction in ground-hornbills found that hot and dry conditions are associated with poor reproductive outcomes and that the presence of helpers, while positively associated with some breeding parameters, did not mitigate the negative effects of adverse weather on reproduction. These results concur with a previous comparative study in the hornbill family (Gonzalez et al. 2013) that found that cooperation is more likely to be associated with group benefits, such as territory defense or predator vigilance while foraging, than with enhanced reproduction. Taken together, these results first suggest that the benefits of cooperation away from the nest may be important to understand the evolution of cooperative breeding and its biogeographical correlates. Second, they suggest that the reproductive outcomes of longer-lived species might not be buffered by group members under harsh conditions. Finally, life history needs to be formally integrated into studies addressing the evolution of cooperative breeding to help us predict when reproductive or nonreproductive benefits are more likely to occur. Further analyses across species with different life histories focusing on different cooperative behaviors and fitness outcomes are needed to examine these hypotheses. In addition, such analyses will shed light on the increasingly relevant question of how cooperative breeders will respond to current intensification in climatic variation arising from climate change.

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Statement of Authorship

R.C. and K.-M.M. conceived the study with input from C.N.S. K.-M.M. and C.H. curated the long-term data and collected additional data in the field. K.-M.M. processed and analyzed the data with input from R.C. K.-M.M. wrote the manuscript with input from R.C., C.N.S., and F.R. All authors commented on the manuscript and read and approved the final manuscript.

Data and Code Availability

All data and code are publicly available via the University of Cape Town's Zivahub (a Figshare platform; https://doi.org/10.25375/uct.27980420.v2; Middleton et al. 2024). The dataset includes all breeding records, and the code contains R scripts for statistical analyses.

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