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High temperatures drive offspring mortality in a cooperatively breeding bird

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An improved understanding of life-history responses to current environmental variability is required to predict species-specific responses to anthopogenic climate change. Previous research has suggested that cooperation in social groups may buffer individuals against some of the negative effects of unpredictable climates. We use a 15-year dataset on a cooperative breeding arid zone bird, the southern pied babbler *Turdoides bicolor*, to test (i) whether environmental conditions and group size correlate with survival of young during three development stages (egg, nestling, fledgling) and (ii) whether group size mitigates the impacts of adverse environmental conditions on survival of young. Exposure to high mean daily maximum temperatures (mean T_{max}) during early development was associated with reduced survival probabilities of young in all three development stages. No young survived when mean $T_{max} > 38°C$, across all group sizes. Low survival of young at high temperatures has broad implications for recruitment and population persistence in avian communities given the rapid pace of advancing climate change. Impacts of high temperatures on survival of young were not moderated by group size, suggesting that the availability of more helpers in a group is unlikely to buffer against compromised offspring survival as average and maximum temperatures increase with rapid anthropogenic climate change.

1. Introduction

Anthropogenic climate change has altered weather patterns in every ecosystem on Earth [1,2], with far-reaching consequences for population dynamics across taxa [3]. An improved understanding of life-history responses to current environmental variability is required to predict species-specific responses to climate change [4]. While cooperative breeders occur in diverse habitats [5,6], comparative research has demonstrated that both cooperatively breeding birds [7] and mammals [8] occur with disproportionate frequency in regions characterized by high spatial and temporal variability in environmental conditions. This implies that group living enhances the ability to persist in challenging environments [9]. To date, however, there are few empirical studies that explicitly test the extent to which group living mitigates the effects of climate variability on reproduction [10–14]. Some of these studies [10,11,14] explore impacts of temperature alongside variation in group size, but only Covas *et al.* [13] consider offspring survival across more than one development stage. This latter point is important, because specific drivers of survival can differ substantially between development stages [15–17].

Recent changes in temperature and rainfall patterns have led to adjustments to the timing and success of breeding in some bird species [18,19]. For birds in arid environments, higher rainfall is often associated with improved offspring survival [20,21], droughts with reduced offspring survival [22,23], and periods of very hot weather with lower nest survival rates [15] and nestling growth rates [24–26]. Offspring survival and population persistence of birds in arid environments will be further impacted as regions become hotter and drier under climate change [27,28].

Cooperative breeding, where more than two individuals rear a single brood [29], occurs in approximately 9% of bird species [30]. Benefits of cooperation include earlier fledging age and more broods raised per season [31], reduced costs of breeding for females [11,32], enhanced egg investment [33], increased fledgling recruitment [17,34], and the ability to raise overlapping broods [12,35]. Global comparative studies suggest that cooperative breeding evolved in unpredictable environments [36], facilitated the colonization of such environments [37] or prevented extinction under increasingly harsh conditions [38]. One prominent explanation for the occurrence of cooperative breeding in birds in variable environments is that it represents a 'bet-hedging' strategy [36], reducing interannual variation in offspring survival in response to unpredictable rainfall and food availability [9]. This implies that cooperation might buffer breeding attempts from failure during adverse environmental conditions [13,39], via load-lightening [40].

Load-lightening refers to individual reductions in workload in response to the presence of additional group members. Load-lightening has been observed in a number of cooperatively breeding species [11,16,41] and may operate via task-partitioning [35,42] or improving access to resources [43]. In larger groups, more individuals can assist with breeding attempts, leading to either load-lightening among individual group members [11,35] or cumulatively greater investment in young [34,44]. Both are potential benefits of group living that may be particularly advantageous when unfavourable rainfall or temperature conditions are experienced. Specifically, larger groups may be better able to maintain adequate levels of parental care to eggs, nestlings and/or fledglings at high temperatures or during periods of low rainfall, despite individual declines in investment in parental care behaviours.

We use a comprehensive 15-year dataset on southern pied babblers *Turdoides bicolor* (hereafter 'pied babblers'), a cooperatively breeding passerine endemic to the Kalahari in southern Africa, to explore the impacts of temperature, rainfall and group size (the number of adults in the group, indicating the potential for the breeding pair to receive help) on the survival of young, including fledgling survival. Specifically, we test for effects of these parameters on survival of young from (i) initiation of incubation to hatching, (ii) hatching to fledging and (iii) fledging to nutritional independence at 90 days of age. We expected high temperatures to reduce survival and high rainfall and larger group sizes to enhance survival during each development stage. If the presence of helpers buffers the effect of environmental variation on reproduction [9], then we would expect an interaction between environmental factors and group size, such that weaker impacts of adverse climatic conditions on reproduction are observed in larger groups.

2. Material and methods

(a) Study site and system

Fieldwork was conducted at the Kuruman River Reserve (33 km^2, KRR; 26°58′S, 21°49′E) in the southern Kalahari. Mean summer daily maximum temperatures at the study site, from 1995 to 2015, averaged 34.7 ± 9.7°C and mean annual precipitation averaged 186.2 ± 87.5 mm [45]. The Kalahari region is characterized by hot summers and periodic droughts [46], with extremely variable rainfall between years [47], and increases in both the frequency and severity of high temperature extremes over the last 20 years [48]. Pied babblers weigh 60–90 g and live in territorial groups ranging in size from 3 to 15 adults [49]. Groups consist of a single breeding pair with subordinate helpers [50], and all adult group members (individuals greater than 1 year old) engage in cooperative behaviours, including territory defence and parental care [51,52]. Pied babblers breed during the austral summer, from September to March [51]. Previous research has shown that high temperatures and drought negatively affect many aspects of this species's ecology, including foraging efficiency, body mass maintenance, interannual survival and provisioning of young [53–55].

Birds in the study population are marked as nestlings with a metal band (engraved with a unique number) and a unique combination of up to three colour rings for individual identification and are habituated to observation at distances of 1–5 m [52]. Habituated groups are visited weekly during the breeding season to check group composition and record life-history events, including breeding activity.

(b) Data collection

Data were collected for each austral summer breeding season from September 2005 to February 2019 (14 breeding seasons in total).

(i) Nest life-history data

Nest monitoring (locating nests, determining incubation, hatch and fledge or failure dates, recording group size and brood size) followed Ridley & van den Heuvel [31]. Nests were located by observing nest-building, and incubation start, hatch and fledge dates were determined by checking nests every 2–3 days. Breeding attempts were considered to have failed when nests were no longer attended, or when dependent fledglings were not seen on two consecutive visits. Failure dates were calculated as the midpoint between the date of the last pre-fail nest/group check and the date when the nest was no longer attended or the fledgling was missing. In most cases, it was not possible to determine the proximate cause of nest failure or death, although common causes of nest failure in this species include predation, abandonment and nestling starvation [49,56].

Group size (mean = 4.2 ± 1.5, range: 2–10 adults) was recorded for each nest incubated. Brood size (mean = 2.7 ± 0.8, range: 1–5 nestlings) was recorded 11 days after hatching, when nestlings were ringed. We defined early development as the period between initiation of incubation and nutritional independence at 90 days of age [52]. Average time from initiation of incubation to hatching is 14 ± 1.2 days and from hatching to fledging is 15.4 ± 1.7 days. Pied babblers are nutritionally independent (receiving less than 1 feed per hour) by 90 days of age [52].

(ii) Sexing and nestling mass

Pied babblers are sexually monomorphic [51] and molecular sexing was used to determine the sex of individuals (*sensu* Fridolfsson & Ellegren [57]). Blood samples were collected by brachial venipuncture and stored in Longmire's lysis buffer. Nestlings were ringed, blood sampled and weighed to 0.1 g (Mass$_{11}$) on a top-pan scale 11 days post-hatching.

(iii) Temperature and rainfall

Daily maximum temperature (°C) and rainfall (mm) data were collected from an on-site weather station (Vantage Pro2, Davis Instruments, Hayward, USA). Missing weather data from 2009, 2010 and 2011 were sourced from a nearby South African Weather Services weather station (Van Zylsrus, 28 km away), which produces significantly repeatable temperature measurements and moderately repeatable rainfall measurements, adequately detecting wet versus dry periods, in comparison with the on-site weather station [58].

Daily minimum (T_{min}) and maximum (T_{max}) temperatures, and daily temperature variation ($T_{max} - T_{min}$), were averaged for each development stage: incubation (mean T_{minInc}, mean T_{maxInc}, mean T_{varInc}), nestling (mean $T_{minBrood}$, mean $T_{maxBrood}$, mean $T_{varBrood}$) and fledgling (mean T_{min90}, mean T_{max90}, mean T_{var90}). Rainfall was summed for the 60 days prior to initiation of incubation ($Rain_{60}$), and for the period between fledging and independence ($Rain_{90}$).

(c) Statistical analyses

Statistical analyses were conducted in R version 3.6.0 [59]. All continuous explanatory variables were scaled by centreing and standardizing by the mean [60,61]. All explanatory variables were tested for correlation with one another [62]. Mean T_{max90} and mean T_{min90} were correlated (VIF = 2.8, correlation coefficient = 0.77) and all other explanatory variables were not correlated with each other (all VIF < 1.3, correlation coefficients less than 0.30). Correlated variables were not included in the same additive models. Unless otherwise indicated, summary statistics are presented as mean ± one standard deviation. Analyses exclude groups greater than 8 due to small sample sizes for groups of 9 ($n = 5$) and 10 ($n = 1$) over 15 years of records. A quadratic term for temperature (T^2) was included as a predictor variable only when no main linear effect of temperature was found and visual inspection of the data suggested a nonlinear relationship. Sensitivity power analyses, using the package *pwr* [63], indicated sufficient statistical power to detect effects of two-way interactions given our sample sizes [64,65], see electronic supplementary material table S1. We tested for temporal trends in environmental (temperature and rainfall) and reproductive (nest success, fledgling survival) parameters using univariate linear models with breeding season as the only predictor. Covariates exhibiting temporal trends were detrended using the *detrend* function in the package *pracma* [66].

(i) Survival probabilities during each development stage

Pied babbler survival probabilities are not constant across time during early development [51] (see electronic supplementary material, figure S1), and covariates are unlikely to have the same relationship with survival during all three early development stages. We used generalized linear mixed effects models (GLMMs) with a binomial distribution and a logit link function in the package *lme4* [67] to determine which variables best predicted survival probabilities during each development stage. These analyses were undertaken at the level of the breeding attempt (i.e. clutch or brood) because individual offspring were only ringed for individual identification from the 11th day after hatching, by which time approximately 60% of monitored breeding attempts had failed. Model selection using Akaike's information criterion corrected for small sample size (AICc) with maximum-likelihood estimation was used to test a series of models to determine which best explained patterns of variation in the data [60]. Where several models were within five AICc of the top model, top model sets were averaged using the package *MuMIn* [68]. Model terms with confidence intervals not intersecting zero were considered to explain significant patterns in our data [69]. Binomial model fits were tested against the dispersion parameter in the package *RVAideMemoire* [70].

We considered the influence of the following parameters on (i) the probability of at least one egg per clutch surviving to hatch, (ii) the probability of at least one nestling per brood surviving to fledge and(iii) the probability of at least one fledgling per brood surviving to nutritional independence: for (i) group size, $Rain_{60}$, mean T_{minInc}, mean T_{maxInc} and mean T_{varInc}, (ii) group size, $Rain_{60}$, mean $T_{minBrood}$, mean $T_{maxBrood}$, mean $T^2_{maxBrood}$ and mean $T_{varBrood}$, and (iii) group size, $Rain_{90}$, mean T_{min90}, mean T_{max90}, mean T^2_{max90} and mean T_{var90}. We tested two-way interactions between rainfall, T_{max}, and group size variables in each analysis, and, in order to account for non-independence of data, included group identity as a random term in all three analyses.

In order to contribute data that can be incorporated into mechanistic modelling of the effects of climate change on avian populations [4], we further sought to identify the threshold T_{max} (breakpoints) above which survival was compromised during each development stage. We used the package *segmented* [71] to apply a Davies test for a non-zero difference-in-slope and, when the regression parameter in the linear predictor was non-constant, to identify a point estimate and 95% confidence interval for the breakpoint. We then fitted simple linear regression models for the data above and below the identified breakpoints with temperature (mean T_{maxInc}, mean $T_{maxBrood}$ and mean T_{max90}, respectively) as the only predictor, and survival per breeding attempt as the response. In the segmented regressions, we used a continuous form of the survival response, specifically the number of days between (i) initiation of incubation and either the hatching of at least one egg or failure of the breeding attempt before hatching (age at hatch/fail), (ii) hatching and fledging at least one nestling from a brood or failure (age at fledge/fail) and (iii) fledging and at least one fledgling surviving to nutritional independence or failure (age at survival/fail).

(ii) Influence of nestling mass on fledgling survival

In addition to survival data at the scale of the breeding attempt, we have detailed individual-level survival data for 372 fledglings weighed and banded as 11-day-old nestlings. Larger nestling mass is commonly associated with higher survival probabilities in birds [16,72]. Prior research on pied babblers has shown that nestling mass is influenced by environmental factors such as temperature and rainfall [54]. We therefore used a confirmatory path analysis [73,74] to test for indirect effects of environmental and group size factors on survival to nutritional independence in known individual fledglings mediated via their mass as a nestling ($Mass_{11}$). We computed the path analysis using the R package *piecewiseSEM* [75], which can accommodate multiple error structures. This capacity is important because the response terms of our component models have different distributions (see below). Path analysis allowed us to specify and simultaneously quantify all hypothesized relationships of interest, including the indirect effects of weather and group size on survival via nestling mass. Path coefficients are partial regression coefficients and can be interpreted similarly to simple and multiple regression outputs. Statistical significance was taken as $p < 0.05$. We hypothesized that:

Survival would be negatively affected by (i) high temperatures during the nestling and fledgling stages, (ii) low rainfall between fledging and independence, (iii) smaller group size and (iv) low nestling body mass (model with binomial error structure).

Nestling body mass would be negatively affected by (i) high mean temperatures during the nestling period, (ii) low rainfall prior to the nestling period and (iii) smaller group size (model with Gaussian error structure).

3. Results

(a) Temporal patterns in temperature, rainfall and reproduction

Most rain falls between December and February (72%), when temperatures are high (figure 1). Most pied babbler breeding activity occurs between October and December (68%), when conditions are generally drier and cooler than later in the season

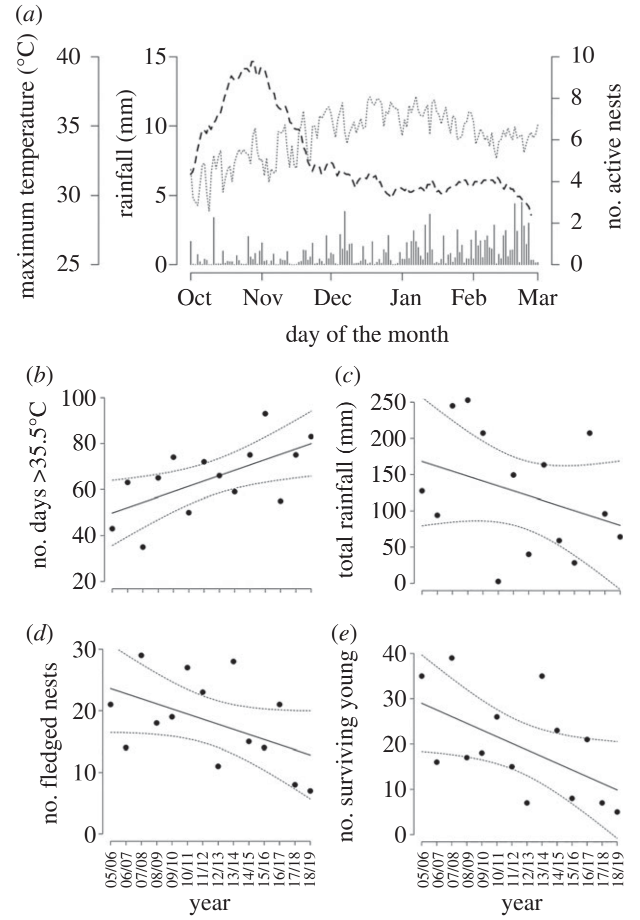

Figure 1. (*a*) Breeding activity between October and March (average number of active nests per day: dashed line), relative to temperature (average daily maximum temperature in °C per day: dotted line) and rainfall (average rainfall in mm per day: vertical bars). (*b*) the number of days >35.5°C at the study site (*c*) total summer rainfall, (*d*) number of southern pied babbler *Turdoides bicolor* nests fledged in the study population and (*e*) number of surviving young produced in the study population per breeding season per year (austral summer: 1 October to 1 March) since 2005. Black lines in (*b–e*) represent predictions from the linear regression models, and dashed lines the 95% confidence intervals.

(figure 1*a*). The total number of days (Oct–Mar) exceeding 35.5°C, identified as a critical temperature threshold in pied babblers [53,54], has increased significantly at the study site since 2005 ($F_{1,12} = 7.448$, $p = 0.018$; figure 1*b*). Total summer rainfall (Oct–Mar) over the same time period was highly variable but showed a declining, non-statistically significant trend ($F_{1,12} = 1.616$, $p = 0.228$; figure 1*c*). Both the number of nests fledged (a non-significant trend; $F_{1,12} = 3.747$, $p = 0.077$; figure 1*d*) and the number of surviving young produced ($F_{1,12} = 5{,}285$, $p = 0.040$; figure 1*e*) have declined at the study site since 2005, despite the number of groups monitored remaining relatively constant between years (coefficient of variation = 0.17).

(b) Survival probabilities during each development stage

Overall, 31.4 ± 10.9% of breeding attempts produced at least one fledgling that survived to nutritional independence. Mean (±s.e.) survival probabilities of young differed between life stages (incubation, nestling, dependent fledgling), with lower survival probabilities during early development in the nest than post-fledging (electronic supplementary material, figure S1c).

Of 489 breeding attempts by 50 groups over 14 breeding seasons, 339 hatched (69.3%). The probability of at least one egg per clutch hatching decreased as mean T_{maxInc} increased (electronic supplementary material, table S2a). We found no evidence that mean T_{minInc}, mean T_{varInc}, Rain_{60} or group size, or interactions between environmental conditions, influenced the probability of hatching (see electronic supplementary material, table S3 for full model output). For the period between initiation of incubation and hatching, a breakpoint was detected at 35.4°C (95% CI: 33.9, 36.9): there was no effect of mean T_{maxInc} on age at hatch/fail below 35.4°C ($F_{1,399} = 0.008$, $p = 0.926$), whereas above 35.4°C, age at hatch/fail significantly declined with increasing temperature ($F_{1,85} = 9.490$, $p = 0.003$, figure 2*a*).

Of 339 hatched nests by 46 groups over 14 breeding seasons, 210 fledged at least one chick (61.9%). The probability of at least one nestling per brood surviving to fledge increased with increasing mean T_{maxBrood} until approximately 33.1°C, above which survival probability decreased (electronic supplementary material, table S2b). We found no evidence that mean T_{minBrood}, mean T_{varBrood}, Rain_{60} or group size, or interactions between group size and environmental conditions, influenced the probability of fledging (see electronic supplementary material, table S4 for full model output). For the period between hatching and fledging, a breakpoint was detected at 37.3°C (95% CI: 36.5, 38.0). Age at fledge/fail tended to increase with increasing mean T_{maxBrood} until 37.3°C ($F_{1,317} = 3.239$, $p = 0.073$), above which age at fledge/fail declined significantly with increasing temperature ($F_{1,20} = 13.370$, $p = 0.002$, figure 2*b*). At mean $T_{\mathrm{maxBrood}} >$ 38°C ($n = 12$), no nests fledged young.

Of 198 fledged broods with complete weather data by 36 groups over 14 breeding seasons, 160 produced at least one fledgling that survived to nutritional independence (80.8%). The probability of surviving to nutritional independence increased as Rain_{90} increased (electronic supplementary material, table S2c). We found no evidence that mean T_{min90}, mean T_{max90}, mean T_{var90}, group size or interactions between group size and environmental conditions influenced the probability of fledgling survival to independence (see electronic supplementary material, table S5 for full model output). We also found no evidence for a breakpoint in the data related to variation in mean T_{max90} for the period between fledging and independence (Davies test $p = 0.288$). While temperature was not a significant predictor of survival to nutritional independence overall, no breeding attempts produced surviving young at mean $T_{\mathrm{max90}} > 38$°C ($n = 8$).

(c) Influence of nestling mass on fledgling survival

The confirmatory path analysis model explained 47% of the variation in survival from fledging to independence (figure 3; $X^2 = 0.689$, $p = 0.708$). Higher Rain_{90} was directly associated with an increased probability of surviving to independence, and larger group sizes were indirectly associated with increased survival via the positive effect of larger group size on nestling Mass_{11}. High mean T_{maxBrood} was associated with reduced survival both directly and indirectly (high mean T_{maxBrood} was associated with reduced nestling mass, which in turn predicted reduced survival). There was no evidence for a direct effect of either mean T_{max90} or natal group size on survival to independence, or an effect of Rain_{60} on Mass_{11}.

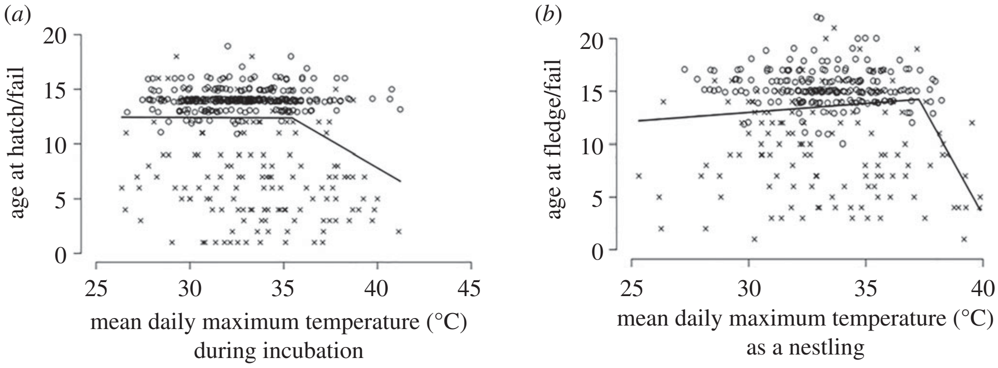

Figure 2. Survival from (*a*) initiation of incubation to hatch and (*b*) hatch to fledge as a function of mean daily maximum air temperature during the corresponding time period. Lines represent segmented linear regressions for the relationship between survival age and air temperature above and below the detected temperature thresholds. Open circles indicate that the clutch (*a*) or brood (*b*) transitioned to the next development stage; crosses indicate failure of the clutch (*a*) or brood (*b*).

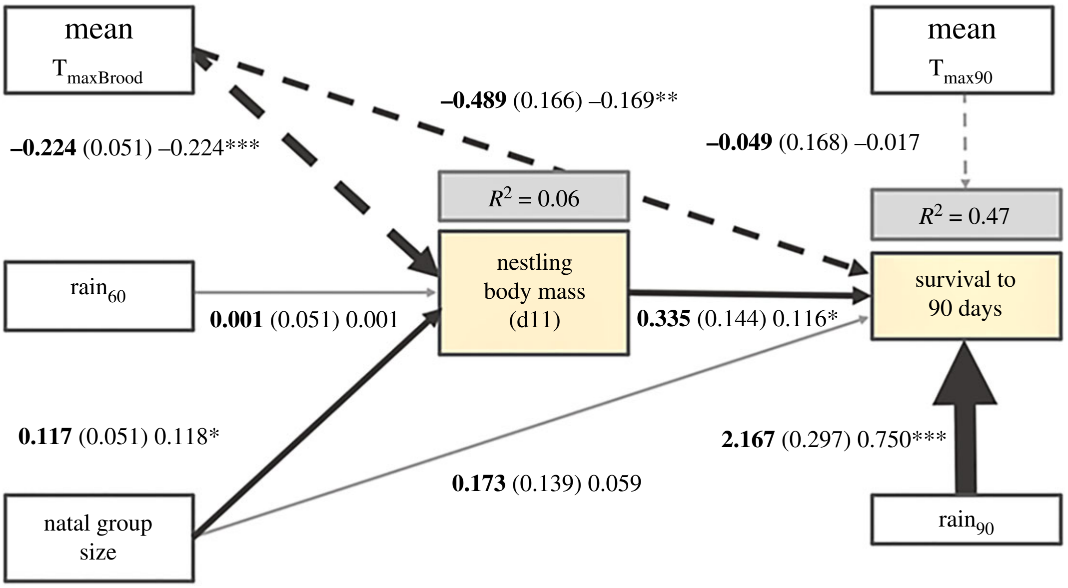

Figure 3. Confirmatory path analysis exploring the effects of environmental factors (temperature and rainfall) and group size on nestling body mass and survival to nutritional independence (90 days). Boxes represent measured variables. Arrows represent hypothesized unidirectional relationships among variables. Solid arrows denote positive relationships, dashed arrows negative relationships. Unstandardized path coefficients are shown in bold, followed by standard errors in parentheses, standardized estimates and an indicator of statistical significance of the effect (asterisks). Non-significant paths are grey. The thickness of significant paths has been scaled relative to the absolute magnitude of the standardized estimates, such that stronger effects have thicker arrows. R^2 for component models are given (grey shaded boxes) in the grey boxes above response variables (orange shaded boxes). (Online version in colour.)

Specifically, larger nestlings were more likely to survive to independence (Est = 0.116, $p = 0.019$), as were fledglings that experienced higher $Rain_{90}$ (Est = 0.750, $p < 0.001$). However, fledglings were less likely to survive (Est = −0.169, $p = 0.003$) when they had experienced higher mean $T_{maxBrood}$. Nestlings were heavier when raised by larger groups (Est = 0.118, $p = 0.021$) and lighter when they experienced higher mean $T_{maxBrood}$ (Est = −0.224, $p < 0.001$). There was an indirect negative effect of mean $T_{maxBrood}$ on survival via nestling mass [Est = −0.026 (calculated by multiplying standardized estimates for each component of the indirect path: −0.244 × 0.116; figure 3)]. The combined direct and indirect effect of mean $T_{maxBrood}$ (via nestling mass) on survival was negative [−0.195, calculated by summing standardized estimates for direct and indirect paths: −0.169 + (−0.026); figure 3]. The direct effect of mean $T_{maxBrood}$ was more prominent (approx. 87% of the combined effect) than the indirect effect via nestling mass (approx. 13% of the combined effect). Natal group size had an indirect positive effect on survival via nestling mass [Est = 0.014 (=0.118 × 0.116)], with an overall effect of natal group size = 0.132 (0.059 + 0.014).

4. Discussion

We investigated the impacts of environmental conditions and the potential for larger group sizes to buffer against these impacts in a cooperatively breeding bird, focusing on egg, nestling and fledgling survival. Exposure to high mean daily maximum temperatures during early development was associated with significant reductions in survival probabilities, in keeping with other recent studies [23,24,26]. Both environmental (largely direct) and social (indirect) factors were important for predicting survival during different development stages. Contrary to our expectations, we found no evidence that effects of T_{max} and rainfall on reproduction were moderated by group size, despite considerable statistical power to detect such interactions. Taken together with evidence that temperatures are increasing and rainfall decreasing at the study site, and that the number of surviving young produced in the study population showed similar declines, the impacts of high temperatures on mortality during early development are concerning.

(a) Impacts of high temperatures during early development

In pied babblers, high mean daily maximum temperatures during early development were associated with a significantly increased risk of mortality. Adverse weather is known to impair egg [76] and nestling development [77]. For example, survival to fledging can be compromised both by sub-optimally cool [78] and sub-optimally hot conditions [24,26]. For the early development stages before fledging, we identified temperature thresholds in the mid- to high-30 s (35.4°C during incubation, and 37.3°C for nestlings) above which survival of eggs and young became significantly less likely. These temperatures are within approximately 2°C of an apparent upper limit (38°C) above which we recorded no successful breeding in this species over 15 years of research. While we did not detect a direct effect of high temperatures on post-fledging mortality (i.e. between fledging and independence) at the brood scale, path analysis revealed that the probability of individual fledglings surviving to independence was influenced by high temperatures experienced as a nestling (Mean $\mathrm{T}_{\mathrm{maxBrood}}$), both directly and indirectly via the effect of high temperatures on nestling Mass_{11}. This suggests that dependent pied babbler fledglings, similar to the young of other species [79,80], are influenced by carryover effects of high temperatures they experienced while still in the nest. With temperatures increasing rapidly in the Kalahari [28,46], the 38°C limit for successful breeding in this species suggests that pied babblers may increasingly experience conditions that do not allow successful breeding. This could undermine population growth and ultimately lead to local extinctions for this species, although the effect may be mitigated by behavioural adjustments such as breeding earlier in the season or engaging in compensatory breeding during good years [58].

(b) Different drivers of survival for each early development stage

The primary climatic (temperature and rainfall) and social (group size) drivers of survival probability were different across the three development stages. Mean daily maximum temperature was the strongest predictor of survival probability during both the incubation and nestling development stages. At high temperatures over prolonged periods, incubating birds may not be able to sustain nest attendance to regulate egg temperature [81], leaving eggs vulnerable to overheating and becoming unviable [15,76]. Likewise, several studies have reported that high temperatures constrain nestling growth [24,77,82], result in smaller nestlings overall [25,83,84], alter corticosterone levels [85,86] and reduce nestling survival probabilities [87,88].

Rainfall was the strongest predictor of survival probability during the dependent fledgling stage. Higher rainfall periods are associated with greater food availability [20,89], which likely enhanced both provisioning rates to fledglings [90] and their ability to find food for themselves [91,92]. In cooperative breeders, survival of young during this stage often improves with increasing group size [34,51]: larger groups may provision more regularly [17] (but see [54]), better detect and repel predators [49], or access higher quality territories or nest sites [16]. We did not find a direct effect of group size on survival to independence at the brood scale. However, path analysis indicated that group size influenced individual fledgling survival probabilities indirectly, via a positive effect on nestling mass. Larger nestlings are more mobile and better developed at fledging, enabling them to forage more effectively, avoid predators and survive longer [93]. The presence of both direct and indirect (via negative effects on nestling Mass_{11}) effects of mean $\mathrm{T}_{\mathrm{max}}$ during the nestling period on survival to independence suggests that carryover effects of high temperatures during early development continue to impact individual survival probabilities post-fledging [94,95].

(c) Buffering effect of group size

We found a lack of a buffering effect of group size on the effects of high mean $\mathrm{T}_{\mathrm{max}}$ on offspring survival. While, as discussed above, we found an indirect positive effect of larger group size on survival from fledging to independence, group size did not interact with the large and persistent negative effects of high mean $\mathrm{T}_{\mathrm{max}}$ on survival observed across all development stages to buffer the detrimental effects of high temperatures on survival from one early development stage to the next. This suggests that physiological tolerance limits [96] and resource constraints [97] at high temperatures may exceed any potential buffering effect of group size on offspring survival in cooperative breeders in arid and semi-arid environments [10].

5. Conclusion

In this study, negative effects of adverse climate conditions on breeding success in a cooperative breeder were not moderated by group size, suggesting that reproduction in pied babblers is constrained by available resources and physiology at high temperatures and low rainfall, regardless of group size. Climate change is one of the defining challenges of our time, posing a serious threat to biodiversity [3] and society [1]. Hot extremes will continue to become more frequent, and the length, frequency and intensity of heatwaves will continue to increase over most land masses [28,98]. At higher average and extreme temperatures, arid zone birds may increasingly experience temperatures that preclude successful breeding. We have observed both increasing temperatures and declining rainfall, along with declining offspring survival rates, at the study site over the last 15 years. Over time, the negative effects of these high temperatures on offspring survival could limit population recruitment and lead to local extinctions. Despite the intuitive appeal of the hypothesis that cooperative breeding may buffer against some of these effects, we found no evidence this will be the case in pied babblers. Our findings suggest that the presence of more helpers in a group is unlikely to provide a buffer against reproductive failure as average and maximum temperatures increase with advancing anthropogenic climate change and raise concerns for the long-term persistence of arid zone species in the face of rapidly changing environmental conditions.

Ethics. All data were collected under animal ethics permit numbers R2012/2006/V15/AR and 2016/V6/SC from the University of

Cape Town and 1216/2016 from the Department of Environment and Nature Conservation, and blood samples were collected and birds banded by licenced professionals [blood sampling was authorised by the South African Veterinary Council (AL17/15885) and bird banding licences were issued by SAFRING (11663)].

Data accessibility. The datasets underlying all analyses presented in this study have been archived at the University of Cape Town's open access institutional data repository, ZivaHub (a figshare platform), where they are publicly available at doi:10.25375/uct.12441899.v1.

Authors' contributions. A.R.R., S.J.C., A.R.B. and C.N.S. conceived the study and secured funding. A.R.R. started habituation of the study animals and collection of life-history data in 2003 and has maintained it ever since; this was central to making the study possible. A.R.B. undertook all fieldwork from 2016 onwards. A.R.B. and A.R.R. analysed the data. A.R.B. drafted the manuscript. All authors contributed substantially to revisions and gave final approval for publication.

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