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LETTER

Disentangling climatic and nest predator impact on reproductive output reveals adverse high-temperature effects regardless of helper number in an arid-region cooperative bird

Pietro B. D'Amelio^{1,2}  | André C. Ferreira^{2,3,4}  | Rita Fortuna^{3,4,5}  |
Matthieu Paquet⁶  | Liliana R. Silva^{3,4}  | Franck Theron^{2,3,4} | Claire Doutrelant^{1,2}  |
Rita Covas^{1,3,4} 

¹FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch, 7701, South Africa

²Centre d'Ecologie Fonctionnelle et Evolutive, CEFE, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, 34293, France

³BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Vairão, 4485-661, Portugal

⁴CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, Vairão, 4485-661, Portugal

⁵Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, 4099-002, Porto, Portugal

⁶Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, SE-75007, Sweden

Correspondence

Pietro B. D'Amelio, FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa.
Email: pie.damelio@gmail.com

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Abstract

Climate exerts a major influence on reproductive processes, and an understanding of the mechanisms involved and which factors might mitigate adverse weather is fundamental under the ongoing climate change. Here, we study how weather and nest predation influence reproductive output in a social species, and examine whether larger group sizes can mitigate the adverse effects of these factors. We used a 7-year nest predator-exclusion experiment on an arid-region cooperatively breeding bird, the sociable weaver. We found that dry and, especially, hot weather were major drivers of nestling mortality through their influence on nest predation. However, when we experimentally excluded nest predators, these conditions were still strongly associated with nestling mortality. Group size was unimportant against nest predation and, although positively associated with reproductive success, it did not mitigate the effects of adverse weather. Hence, cooperative breeding might have a limited capacity to mitigate extreme weather effects.

KEY WORDS

climate, cooperative breeding, environmental variability, maximum temperature, nest predation, offspring mortality, rain, social mitigation

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INTRODUCTION

Anthropogenic climate change is progressively exposing life on earth to warmer climates and increased frequency of extreme weather events such as floods and droughts (Diffenbaugh & Field 2013; Duffy et al. 2019). Weather affects species' survival and reproduction both directly, for example through the detrimental effects of extreme temperatures on animals' physiology (Oswald & Arnold 2012; Wingfield et al. 2017; Riddell et al. 2019), and indirectly, for example by altering foraging success (van de Ven et al. 2020b), predator–prey interactions (Allan et al. 2017) or intra- and interspecific competition (Ahola et al. 2007; Tylianakis et al. 2008). Understanding how weather influences reproduction, alongside the factors that can mitigate their negative effects, is therefore fundamental to predict how species will cope with the expected climate change (Conradie et al. 2019; Ratnayake et al. 2019).

Studying how climate affects reproductive output is, however, complex. First, the effects of climatic variables are likely to differ at different times of the year (i.e. they depend on specific climate windows; Bailey & van de Pol 2016). For example, rainfall is known to promote plant germination and invertebrate abundance, increasing food availability (Dean & Milton 2001; White 2008), but high rainfall can have negative effects on juvenile survival (Öberg et al. 2015; Gunderson et al. 2017; Juhasz et al. 2020), and while temperatures above seasonal averages can be beneficial in winter (Altwegg et al. 2014; Woodworth et al. 2017), they can be detrimental during breeding (van de Ven et al. 2019). Second, even when positive or negative effects of climate on reproduction are detected, the actual mechanisms are often unknown. For example, weather can directly affect the physiology of adults and offspring (van de Ven et al. 2020a, b) but also the activity of ectothermic predators (Cox et al. 2013). Snakes are important nest predators of birds and burrowing animals (Ricklefs 1969; Thompson 2007) and their impact may be stronger under dry and hot conditions when availability of alternative preys may be reduced (McShea 2000; Martin 2007). Therefore, disentangling the consequences of increasing temperatures on reproduction is challenging, as it increases predators' activity while subjecting prey to other types of stress (e.g. physiological stress) (Mainwaring et al. 2017).

Detrimental climatic effects can interact with mitigation mechanisms such as social factors (Covas et al. 2008; Rubenstein 2011) and to some extent, buffer them (Rubenstein & Lovette 2007; Shen et al. 2017). Mitigation effects may be pronounced in cooperative breeders where non-breeding individuals (helpers) assist breeding pairs in providing care to developing young, allowing parents to reduce their workload (Crick 1992; Hatchwell & Russell 1996) or increasing net food delivered when needed (Hatchwell 1999). This help was found to be associated with improved reproductive outcome under

adverse breeding conditions in two semi-arid zone birds (sociable weavers, *Philetairus socius*, Covas, Du Plessis, & Doutrelant, 2008; superb starlings, *Lamprolornis superbus*, Rubenstein, 2011), and a mammal (meerkats, *Suricata suricatta*, Groenewoud & Clutton-Brock 2021), but not in another bird (pied babblers, *Turdoides bicolor*, Bourne et al. 2020a). Together, these observations suggest that cooperatively breeding species may be better equipped to withstand the effects of weather extremes (Jetz & Rubenstein 2011) and hence could be more resilient against the ongoing climate change. Accordingly, on a global level, the incidence of cooperatively breeding species appears to be associated with high spatial and/or temporal variability in temperature and rainfall, such as most arid regions (Cornwallis et al., 2017, for birds; Firman et al., 2020 for rodents). Moreover, cooperative breeding can interact with nest predation, and either increase it, through the additional activity around the nest or den (Martin et al. 2000), or decrease it by improving surveillance and predator mobbing (Santema & Clutton-Brock 2013). Experimental approaches separating the mechanisms by which climatic variables influence reproduction, such as controlling predation pressure (Weatherhead & Blouin-Demers 2004), are fundamental to identify the specific mitigation mechanisms arising from cooperation (Shen et al. 2017).

Here, we used a 7-year nest predator-exclusion experiment (comprising 1906 breeding attempts) to disentangle the effects of climate and nest predation on nestling survival, and investigate whether these effects are mitigated by helpers' presence. Our study model is an arid-region cooperatively breeding bird, the sociable weaver. We use a recent approach (Bailey & van de Pol 2016) to identify the time windows where rain and mean maximum temperature have the strongest correlation with offspring survival. We predict that reproductive outcome should be positively associated with rainfall and negatively associated with maximum temperature, both directly and through a positive effect of temperature on nest predation. In addition, we expect larger cooperating groups to be irrelevant against nest predation, since snake mobbing seems ineffective in this species (pers. obs.), but able to mitigate negative effects of weather.

MATERIALS AND METHODS

Study site and system

Sociable weavers are small monomorphic passerines (Mean \pm SD, 27.8 ± 1.6 gr., $N = 5412$) endemic to the semi-arid Kalahari savannahs of southern Africa (Maclean 1973a). They feed mainly on insects and seeds (Maclean 1973c), resources highly dependent on rainfall in this climate type (Dean & Milton 2001; Yu et al. 2017; Hidalgo Aranzamendi et al. 2019). Sociable weavers build large communal colonies with several independent chambers,

hosting few to several hundred individuals, where birds breed and roost throughout the year (Maclean 1973b). The breeding season usually starts in September and continues for as long as conditions remain suitable, and it can pause and resume within the same season (in this study, 91.3% of breeding attempts were between September and April). Females lay two to five eggs (1 per day) and typically lay several clutches per breeding season (Covas et al. 2008). Incubation lasts ~15 days and nestling period up to 25 days (Maclean 1973c). Breeding pairs can breed with or without helpers (69.3% of breeding attempts ($N = 772$) in this study had helpers; group size, Mean \pm SD, 4.01 ± 1.09 , Figure S1). Most helpers are offspring from previous breeding attempts, but up to 20% of helpers are distant relatives or unrelated (Covas et al. 2006). In our population, nest predation from snakes, boomslangs (*Dispholidus typus*) and cape cobras (*Naja nivea*), is the major cause of nest failure (Covas et al. 2008, Figure S2). Snakes climb tree trunks to access colonies where they feed on eggs and nestlings.

This study was conducted at Benfontein Nature Reserve, ~6 km south-east of Kimberley (South Africa, 28°520 S, 24°500 E, 1190 m). Climatic data, daily rain and maximum temperature, were collected at Kimberly Airport weather station, which is located ~10 km from the study site (Mares et al. 2017). Mean daily maximum temperatures (hereafter, mean T_{\max}) and average rain for all studied time windows are reported in Table 1.

DATA COLLECTION

Most colonies in the study area have been captured since 1993 and birds were marked with numbered metal rings and unique colour combinations (Fortuna et al. 2021). The data set used here includes the breeding seasons of 2011/2012 and from 2013/2014 to 2018/2019. For group size, we used data until 2017/2018.

Reproductive outcome

We visited colonies at maximum every 3 days to search for new clutches and to record their fate dates (Fortuna et al. 2021). We scored three possible brood outcomes, that is fates: predated, fully fledged or ejection. 'Predated' was assigned when the full brood went missing and a snake was found in the colony or, in the absence of a snake encounter, when several neighbouring nests went missing simultaneously (as snakes usually predate multiple nests during a foraging event). 'Fully fledged' was assigned if all hatchlings were alive when the oldest chick reached 17 days (nest inspection at later dates would induce premature fledging). 'Ejection' was assigned when at least one chick was found dead or when it disappeared from the nest, with fate date corresponding to the first dead chick. Possible causes of ejection are starvation, disease

or infanticide by intruders (Covas R., Silva L. personal communication). Disappearance of single eggs or full clutches during the egg stage were not considered, as ejection caused may differ at this stage. We also excluded broods used in experiments that could have influenced the reproductive outcome, cases when a fate date could not be assigned and, for fates 'ejection' and 'predated', failed broods for which either of these fates could not be safely given (for frequency distributions of each brood outcome, see Figure S2).

Experimental predator exclusion

We experimentally decreased snake predation by wrapping the colony's tree trunk with plastic film (Figure S3). This treatment reduced confirmed cases of predated broods, from 22.5% to 8.3%, and in the subset of broods where we quantified group size from 16.2% to 3.2% (Figure S2). Hereafter, we will refer to 'natural' colonies when colony protection was absent and to 'protected' colonies when protection was present. We protected nine colonies for 1–6 consecutive years (details in 'Protection experiment' in Supporting Information).

Group size assessment

Group size was determined using video recordings (since 2014) and direct observations (before 2014) of birds feeding nestlings (details in Silva et al. 2018; Fortuna et al. 2021). Briefly, each nest was recorded or observed for at least 120 min on different days, and individuals were identified through their unique colour ring combination. Group size was defined as the total number of individuals (breeders and helpers) seen visiting the nest at least three times, after excluding non-feeding visits. We only counted individuals seen visiting the nest until the oldest chick was 12 days old to follow a similar procedure for all nests (as nests reaching fledging are recorded more times compared to those failing earlier and some helpers only appear late in the nestling period (Ferreira A., personal communication). The distribution of group sizes for all fates and experimental conditions is reported in Figure S1.

STATISTICAL ANALYSES

All analyses were performed in R v.3.5.3 (R Core Team 2019). To select the most influential climatic windows for each fate, we ran five batches of generalised linear mixed models with a binomial response ('yes'/'no'), corresponding to the three possible fates for natural colonies ('predated', 'fully fledged' or 'ejection') and the two possible fates for protected colonies ('fully fledged' or 'ejection'). To study the effects of group size, we ran models with the

TABLE 1 Summary table including all climwin models' window output and AIC for the climatic variables mean T_{\max} and rain

Climatic variable	Brood outcome	Treatment	Func.	Delta AICc	Median window (best)	Mean \pm SD (range) mean T_{\max} ($^{\circ}$ C) rain (mm/day)
Mean T_{\max}	Predated	Natural	lin.	-133	18-0 (8-0)	31.8 \pm 3 (22.4-36.9)
			quad.	-132	16-0 (13-0)	31.8 \pm 3.1 (21.7-36.7)
	F. fledged	Natural	lin.	-81	21-2 (20-0)	28.8 \pm 4 (21.3-36.5)
			quad.	-94	39-2 (39-0)	29 \pm 3.4 (20.2-35.1)
		Protected	lin.	-38	10-1 (4-1)	28.8 \pm 4.3 (17.8-37.4)
			quad.	-64	42-32 (42-34)	29.5 \pm 3.4 (15.6-37.5)
	Ejection	Natural	lin.	-12	79-38 (48-48)	30.3 \pm 4.1 (19-37.2)
			quad.	-31	73-48 (62-57)	30.2 \pm 4.3 (18.6-37.3)
		Protected	lin.	-23	7-2 (3-3)	30.3 \pm 4.5 (17.2-38.5)
			quad.	-25	10-3 (7-1)	30.2 \pm 4.3 (19.6-38.1)
Rain	Predated	Natural	lin.	-27	94-57 (98-59)	1 \pm 1 (0-4.7)
			quad.	-32	92-61 (90-64)	1 \pm 1.1 (0-4.4)
	F. fledged	Natural	lin.	-29	90-53 (82-53)	1.3 \pm 1.2 (0-4.7)
			quad.	-29	89-53 (82-53)	1.3 \pm 1.2 (0-4.9)
		Protected	lin.	-18	57-33 (96-95)	1.5 \pm 1.4 (0-5.1)
			quad.	-28	86-68 (89-68)	1.2 \pm 1.5 (0-6.7)
	Ejection	Natural	lin.	-14	71-28 (19-19)	1.5 \pm 1.1 (0-5.1)
			quad.	-17	37-9 (36-0)	1.5 \pm 1.3 (0-4.8)
		Protected	lin.	-17	92-58 (90-57)	1.2 \pm 1.1 (0-4.9)
			quad.	-25	90-62 (90-67)	1.1 \pm 1.1 (0-4.8)

Note: We present: brood outcome ('predated'—'fully fledged'—'ejection'); treatment (natural—protected); function (linear—quadratic); Delta AICc; Median windows, used for the subsequent analysis, and best window within brackets; Mean \pm SD refer to the median window and the range, within brackets, for each climatic variable (in $^{\circ}$ C for mean T_{\max} and mm/day for rain). The AICs within a specific fate and treatment (e.g. 'ejection'—'natural') are directly comparable.

same structure for each fate and climatic variable (mean T_{\max} and rain). Additionally, we also tested whether simply the presence/absence of helpers was associated with each fate probability, this also allowed comparison with a previous study (Covas et al. 2008). All models' estimates and relative confidence intervals, sample sizes and p -values are given as Supporting Information (Tables S2–S31).

Climatic time windows selection

We used the function 'slidingwin' from the R package 'climwin' (Bailey & van de Pol 2016; van de Pol et al. 2016) to identify for each fate the most influential weather time window and measure its reliability. This approach uses two separate data sets: one containing climate data (on a daily scale) and one containing the response variable (i.e. probability of a certain fate) and covariates (i.e. baseline model). Climwin fits all possible time windows, each time varying start and end, within a chosen range and compares the resulting models' output using information criteria, AIC (Akaike 1998), corrected for small sample sizes, AICc. Since sociable weavers can breed throughout the year, we tested windows relative to each fate date, with a maximum of 100 days before

the fate (i.e. assuming that weather events farther than 100 days did not strongly influence brood outcome). We used the averages of the climatic variables and we hypothesised that their relationship with the response variables (i.e. 'predated', 'fully fledged' and 'ejection') could be linear or quadratic (van de Pol et al. 2016), and therefore tested both. We considered as the most relevant time window not the absolute best window but the median window resulting from the top 95%, thus accounting for model uncertainty and avoiding spurious correlations (Bailey & van de Pol 2016). The baseline model for each fate contained three continuous explanatory co-variables (all scaled and centred, Schielzeth 2010): (1) colony size, assessed at season start, expecting larger colonies to have lower success (Spottiswoode 2009); (2) brood size (i.e. hatchlings' number), since larger broods should have higher probability of at least one ejection; and (3) activity ratio, the number of active nests (from eggs to fledging) divided by the season total number of occupied nests in that colony. We expected activity ratio to be important because when facing good conditions colonies become increasingly reproductively active and conflict should decrease, thus decreasing opportunity for ejections. Finally, we added two random effects: colony ID, to control for intrinsic variability between colonies, and season ID to control for differences

between seasons possibly due to the non-breeding period (austral winter). Results on these co-variables can be found in Tables S2–S32 and are not discussed in the main text.

The interactive effects of climate, predation and helpers

To test the effect of group size on reproductive success during the most relevant climatic window for each fate, we ran binomial linear mixed models using the package ‘lme4’ (Bates et al. 2015) with a logit link function. We ran one model for each fate (i.e. ‘predated’, ‘fully fledged’ and ‘ejection’) and each experimental condition (i.e. natural and protected—the ‘predated’ broods of the latter were excluded) and weather variable (i.e. temperature and rain) for a total of 10 models (Tables S12–S21). We had five explanatory variables, again all scaled and centred, the same three included in the baseline climatic models (i.e. colony size, brood size and activity ratio), the weather variable for the time windows determined during the climatic analysis and group size. To test for helpers' mitigation of harsh weather conditions, we added the interaction between weather and group size. We also added an interaction between colony size and group size because it was previously found that larger colonies are poorer reproductive environments (Covas et al. 2008; Spottiswoode 2009). Colony ID and season ID were included as random factors. The breeders' ID was not included as it would markedly decrease sample sizes, but follow-up analysis including them showed that these random factors did not explain any or negligible variance (data not shown). As indicated above, we repeated the same analyses with helpers' presence/absence instead of group size, which yielded qualitatively similar results (Figures S4, S5, Table S22–S31). Finally, to test if group size was associated with decreased nestling mortality within broods, we ran a finer analysis for ‘ejection’ in protected colonies. We built a binomial model with the outcome variable consisting of number of chicks' dead for causes other than predation versus number of fledged chicks, and kept all the other covariates as described (Table S32).

RESULTS

Comparison of weather variables and best functions

Both rain and mean T_{\max} were important predictors of brood fate within certain windows (Figure S6), but mean T_{\max} models were better supported than rain models, except for ‘ejection’ in protected colonies where models including mean T_{\max} or rain were similarly supported

(Table 1). In general, quadratic functions represented climatic effects better than linear ones, with the exceptions of temperature-‘predated’ and rain-‘fully fledged’ in natural conditions (Table 1).

Effects of temperature and predation reduction.

For ‘predated’ broods, mean T_{\max} strongest effects occurred over the 18 days prior to the fate date (Figure 1a). Mean T_{\max} was strongly positively associated with predation (estimated mean [95% CI], 1.32 [1.04–1.59], $p < 0.001$). This represents an increase in the probability of being predated from 13% [6–24] to 57% [38–75] when mean T_{\max} increases from 28 to 35 degrees.

For ‘fully fledged’ broods, in natural colonies, mean T_{\max} had its strongest influence in a time window lasting between 39 and 2 days before the fate date. Mean T_{\max} negatively associated with fledging probability (both linear, -0.92 [-1.13 to -0.71], $p < 0.001$ and quadratic effects, -0.36 [-0.52 to -0.20], $p < 0.001$; Figure 1b) thus, for example, the probability of fledging the full brood at 28 and 35 degrees was estimated to decrease from 39% [30–48] to 5% [3–9]. In protected colonies, the effect of mean T_{\max} on fledged clutches was quadratic and strongest between 42 and 32 days before fledging, hence just before egg laying, with extreme temperatures associated with decreased fledging probability (Figure 2c, Table S4). This was the only case where windows of linear and quadratic functions did not overlap (Table 1). The median window for the linear function was between 10 and 1 days, thus during chick rearing and overlapping with the natural conditions' window, again mean T_{\max} negatively correlated with ‘fully fledged’ probability (Figure S7a, Table S33).

For the fate ‘ejection’, mean T_{\max} effect in natural colonies was rather weak and undefined as shown by high window uncertainty (Figure 1d) and low precision of cumulative model weights (Figure S8d). The median window opened 73 days and closed 48 days before an ejection, mean T_{\max} had a non-significant linear effect (-0.01 [-0.23 to 0.22], $p = 0.940$) and a positive significant quadratic effect (0.33 [0.18 – 0.47], $p < 0.001$). In protected colonies, mean T_{\max} effects on ‘ejection’ were, however, strikingly different. The effects were marked and the most relevant window was short and near the fate date, starting 10 and closing 3 days before an ejection event (Figure 1e). High temperatures close to the fate date had a linear positive correlation with ‘ejection’ probability, reaching a maximum and stabilising at 38.2°C (linear 0.30 [0.12 – 0.48], $p = 0.001$, quadratic -0.07 [-0.23 to 0.09], $p = 0.368$).

Effects of rain and predation reduction

In both natural and protected conditions, rain windows for all fates, except ‘ejection’ in natural colonies, were

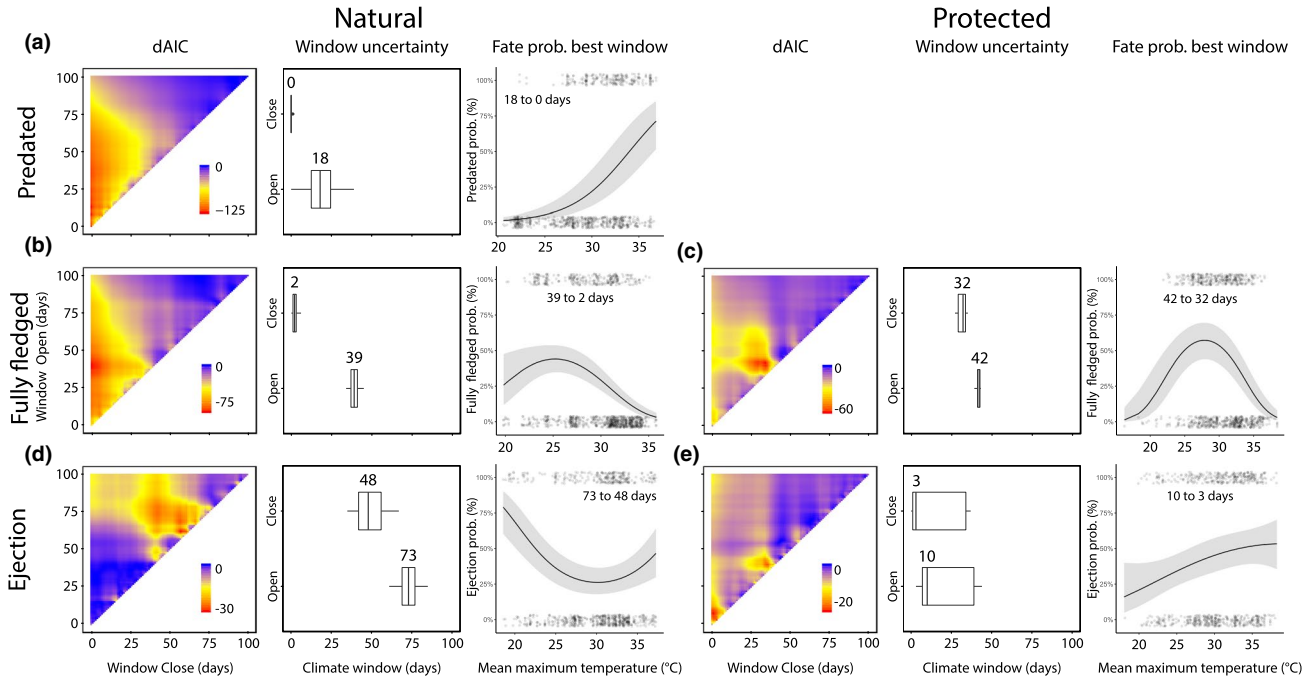


FIGURE 1 Influence of temperature. One fate per row, (a—top) ‘prenated’, (b, c—middle) ‘fully fledged’ and (d, e—bottom) ‘ejection’. Natural colonies (a, b, d—left) and protected (c, e—right). Three analyses are presented for each brood outcome and condition. First, left, a heatmap plot of model’s deltaAICc values (larger negative values indicate stronger models). DeltaAICc is the difference between AICc of each climate window model and the baseline model containing no climate data. Second, centre, two boxplots showing the start and end time for the 95% best climate windows, with values above boxplots representing the median values. Third, right, the results of the binomial model showing the effect of the most relevant time window on each fate (the line is the estimate and the shaded area the 95% confidence intervals), dots are raw values

found to be approximately between 3 and 2 months before the fate dates (Figure S6).

The most relevant window to explain the ‘prenated’ fate was between 92 and 61 days, and predation probability decreased with high precipitation (linear -0.74 [-1.01 to -0.47], $p < 0.001$, quadratic 0.28 [0.09 – 0.48], $p = 0.005$, but the positive quadratic effect was driven by a few values and thus unreliable; Figure 2a).

For the ‘fully fledged’ fate, the identified windows were similar in natural and protected colonies, 90 to 53 and 86 to 68 days respectively. In natural colonies, high precipitations were associated with increased probability of ‘fully fledged’ broods (0.34 [0.20 – 0.49], $p < 0.001$; Figure 2b). In protected colonies, rainfall had a quadratic effect, with low rain slightly increasing ‘fully fledged’ probability and high rains increasing it markedly (linear, -0.41 [-0.65 to -0.17], $p = 0.001$; quadratic, 0.24 [0.13 to 0.34], $p < 0.001$, Figure 2c).

For ‘ejection’, the window that we identified was between 37 and 9 days before the fate date in natural colonies, but with high uncertainty (Figure 2d, Figure S9d). Within this window, low and high precipitation had a weak and uncertain association with increased ‘ejection’ probability (linear, -0.22 [-0.45 to 0.01], $p = 0.058$, quadratic, 0.25 [0.02 to 0.48], $p = 0.030$). In protected colonies, the identified window was between 90 and 62 days, with increasing rain correlating with decreasing ‘ejection’ probability (linear, -0.25 [-0.51 to 0.00],

$p = 0.054$; quadratic, -0.10 [-0.22 to 0.03], $p = 0.128$, Figure 2e).

Social mitigation of adverse effects

In the subsample including data on group size, the effects of mean T_{\max} and rainfall closely matched the full data set analyses (Tables S12–S21).

‘Prenated’ probabilities were strongly positively associated with mean T_{\max} (between 18 and 0 days) but not with group size (Figure 3a, Table S12).

‘Fully fledged’ probabilities were strongly associated with mean T_{\max} in natural conditions (between 39 and 2 days), but group size and its interaction with mean T_{\max} did not have an overall statistically significant effect (Figure 3b, Table S13). However, when assessing mean effect sizes (Figure 3b), we observed that larger group sizes were associated with increased success at medium-low temperatures. For example, at 25°C , the probability of fledging a full brood was estimated to be 25% [10, 50] for group size 2 (i.e. pairs without helpers) and 55% [27, 85] for group size 6. This difference was considerably lower at high temperatures: at 34°C , ‘fully fledged’ probability was 11% [4, 26] and 15% [4, 41] for group sizes 2 and 6 respectively. In protected colonies (window from 42 to 32 days), group size significantly positively correlated with ‘fully fledged’

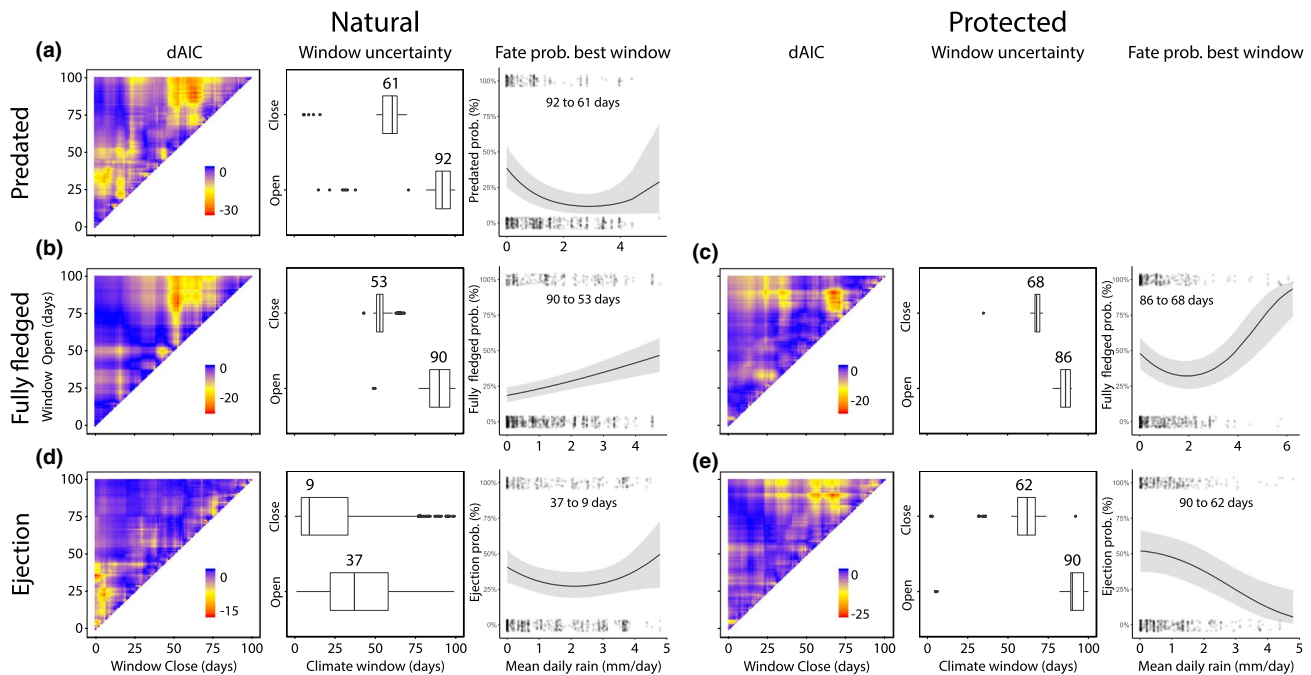


FIGURE 2 Influence of rain. One fate per row, (a—top) ‘predated’, (b, c—middle) ‘fully fledged’ and (d, e—bottom) ‘ejection’. Natural colonies (a, b, d—left) and protected (c, e—right). Three analyses are presented for each brood outcome and condition. First, left, a heatmap plot of model’s deltaAICc values (larger negative values indicate stronger models). DeltaAICc is the difference between AICc of each climate window model and the baseline model containing no climate data. Second, centre, two boxplots showing the start and end time for the 95% best climate windows, with values above boxplots representing the median values. Third, right, the results of the binomial model showing the effect of the most relevant time window on each fate (line is the estimate and shaded area 95% confidence intervals), dots are raw values

(0.52 [0.21–0.82], $p = 0.001$, Figure 3c) but not in interaction with temperature (Table S14), and the same was observed for the linear window (10 to 1 day, Figure S7b, Table S34). When considering the effect sizes, we noticed that differences between estimated probabilities were again higher for medium than for extreme temperatures (Figure 3c).

For ‘ejection’ in natural colonies, the found mean T_{\max} window was far from the fate date (73 and 48 days) and the group size effect was weak (Figure 3d, Table S15). In contrast, in protected colonies, the identified window was between 10 and 3 days before the fate date, and group size significantly negatively correlated with ‘ejection’ probability ($-0.49 [-0.85 \text{ to } -0.14]$, $p = 0.007$). The interaction between group size and mean T_{\max} was not significant (Figure 3e, Table S16). Furthermore, the finer scale analysis designed to examine if group size was associated with increased probability that at least part of the brood fledged, yielded a similar result. Group size significantly negatively correlated with ejections’ number per brood (Table S32) and the interaction between group size and mean T_{\max} was weak and not significant ($0.07 [-0.12 \text{ to } 0.26]$, $p = 0.489$, Figure S10).

Concerning the effects of rainfall, for all brood outcomes except ‘ejection’ in natural colonies, the strongest effects were ~30 days long and between 3 and 2 months before the fate date (Figure S6). Group size significantly negatively correlated with predation

probability ($-0.75 [-1.33 \text{ to } -0.17]$, $p = 0.01$, Figure S11a), and both linear and quadratic interactions were significant (linear, $-0.60 [-1.12 \text{ to } -0.09]$, $p = 0.023$; quadratic $0.38 [0.00-0.76]$, $p = 0.050$). However, these results seemed to be driven by a few data points for high rainfall (Figure S11a) and therefore should be interpreted with caution.

Group size also positively correlated with the probabilities of successfully fledging a full brood in natural ($0.28 [0.05-0.50]$, $p = 0.015$, Figure S11b) and in protected colonies ($0.72 [0.41-1.03]$, $p < 0.001$, Figure S11c), but no interaction with rainfall was detected (Table S18, S19).

For ‘ejection’ in natural colonies (time window 37–9 days), we did not find significant interactions of group size with rain for either linear or quadratic terms (Figure S11d, Table S20). In protected colonies, group size was correlated with reduced ejections ($-0.58 [-0.91 \text{ to } -0.25]$, $p = 0.001$, Figure S11e), but the interaction with rain was not significant (time window 90–62 days; Table S21).

DISCUSSION

By using a nest predator exclusion experiment, we separated the effects that climate has on reproduction through nest predation from the remaining effects (e.g. physiological stress or food abundance). In addition, we evaluated the potential for a social factor (breeding

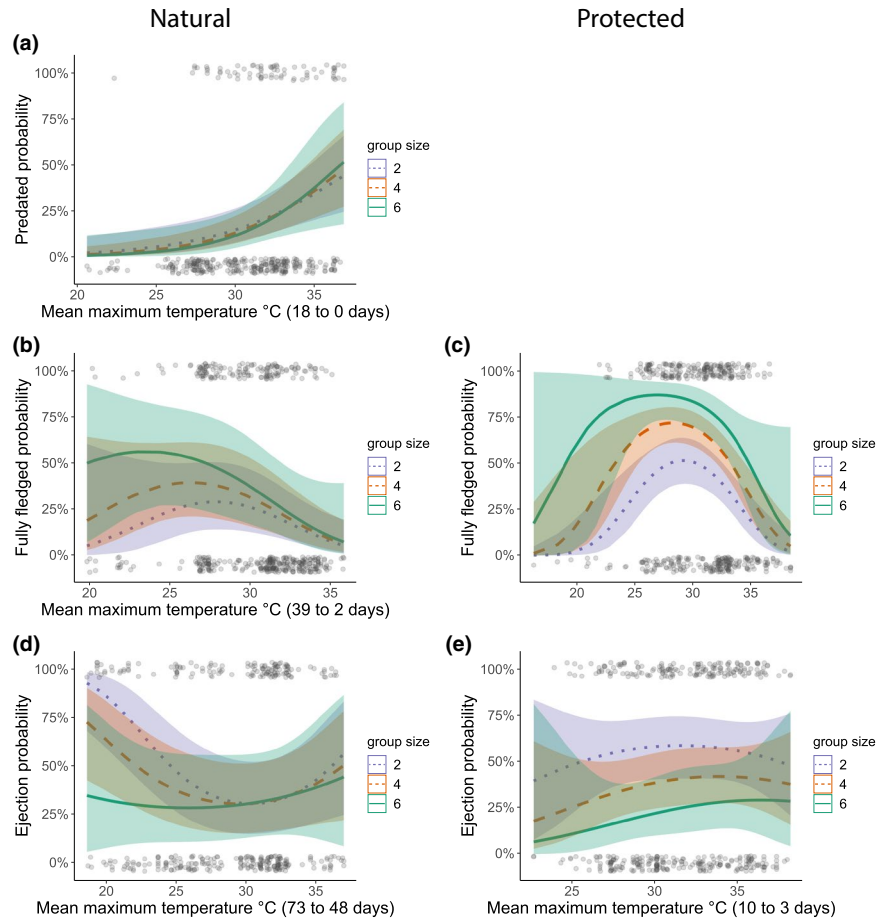


FIGURE 3 Group size influence on mean T_{\max} effects. Probabilities of the three broods' outcome for different possible group sizes for the most influential windows identified for mean T_{\max} . One fate per row, (a—top) 'predated', (b, c—middle) 'fully fledged' and (d, e—bottom) 'ejection'. Natural colonies (a, b, d—left) and protected (c, e—right). Each graph represents a binomial model and in each three possible group sizes (range 1–8) are represented in different colours and line types (2, 4, 6, i.e. no helpers, two helpers, four helpers). Lines represent estimated means, shaded area 95% confidence intervals and black dots raw values

group size) to mitigate the effects of predation and adverse weather. We found that, generally, temperature had stronger effects on reproductive output close to the fate date, whereas rain had a longer term influence. High mean T_{\max} was linked to high predator-related mortality, but when we experimentally reduced predation, temperature still had a strong negative effect on nestling mortality. Group size was generally positively associated with successful reproduction, but there was little evidence that it could decrease predation and it did not mitigate the effects of warm temperatures and low rainfall on nestling mortality.

The effects of temperature

Nest predation probability markedly increased with mean T_{\max} , with the strongest effects during chick rearing. This was expected as snakes, sociable weavers' main nest predators, are ectotherms and their activity pattern is influenced by ambient temperature (Brown & Shine 2002). Under this naturally high level

of nest predation, high temperatures were also associated with low probabilities of fledging a full brood, but this was not paralleled by an increase in nest ejections. However, when we experimentally decreased predation, ejection probability strongly increased with mean T_{\max} (over a short time window close to the fate date). This indicates that, besides increasing nest predation, high temperatures have a detrimental short-term effect on nestling survival. This finding is consistent with negative effects of high temperatures on reproduction found in other arid-region vertebrates (e.g. common fiscals *Lanius collaris* [Cunningham et al. 2013], southern yellow-billed hornbills *Tockus leucomelas* [van de Ven et al. 2020b], meerkats [van de Ven et al. 2020a] and wild dogs *Lycaon pictus* [Woodroffe et al. 2017]). Low reproductive outcome under high temperatures can be a consequence of physiological stress acting on nestlings (van de Ven et al. 2020b, a), decreased body condition (van de Ven et al. 2020a) or impaired breeders' foraging success (du Plessis et al. 2012; van de Ven et al. 2019). However, to what extent the negative effect of temperature on reproduction is mediated by

predator–prey interactions as found here requires further scrutiny in other species (Oswald et al. 2020).

The effect of rain

In contrast to temperature, rainfall was important several weeks before breeding initiation (3 to 2 months before the fate date), supporting earlier findings that rainfall exerts a long-term influence over the breeding season (Mares et al. 2017), presumably through its lasting effects on plant germination and growth and insect abundance (Dean & Milton 2001; Hidalgo Aranzamendi et al. 2019). High rainfall over this period was also associated with low nest predation. This effect might arise from a dilution effect, as higher rainfall is associated with generally increased breeding activity in arid regions (Lloyd 1999) and hence higher abundance of preys (Layloo et al. 2017; Smith et al. 2019).

Our models including rain were generally less supported than models including mean T_{\max} , and this effect was particularly marked for predated clutches, which is expected given the influence of temperature on ectotherms' activity. However, this difference was present also for the other fates. Notwithstanding the importance of rainfall for food availability and reproduction, recent work in arid-region birds has demonstrated detrimental effects of heat on physiology (Cooper et al. 2020; van de Ven et al. 2020b), foraging efficiency (du Plessis et al. 2012; van de Ven et al. 2019) and reproduction (Cunningham et al. 2013; Conradie et al. 2019). This stronger negative impact of mean T_{\max} compared to rain on reproduction is especially relevant under the current and projected temperatures increases in arid regions (Iknayan & Beissinger 2018; Conradie et al. 2019; Riddell et al. 2019), particularly in southern Africa where rainfall, necessary to trigger breeding, is higher during the austral summer, the hottest season.

Social mitigation of adverse effects

Cooperative breeders are generally more common in environmentally unpredictable conditions (birds [Cornwallis et al. 2017], rodents [Firman et al. 2020] and humans [Martin et al. 2020]). It has been suggested that the additional food provided by helpers in cooperatively breeding systems is important to overcome difficult conditions associated with dry and hot weather (Rubenstein & Lovette 2007; Covas et al. 2008; Jetz & Rubenstein 2011; Rubenstein 2011). Moreover, cooperation among group members can provide additional benefits in variable environments and the relative importance of each factor is still unclear (Shen et al. 2017). Here, by manipulating a critical ecological variable—nest predation—we were able to directly evaluate the importance of cooperation in mitigating nest predation and non-predation-related

weather effects (Shen et al. 2017). For temperature, which had the strongest effect during rearing, larger breeding groups (or presence of helpers) did not prevent predation, but were associated with lower nest ejections and, in accordance, higher fledging probability. This suggests a direct positive effect of helpers-at-the-nest on brood survival, via increased food provisioning, and not through anti-predatory effects.

For rainfall, interpreting the mechanisms underlying the helpers' effect is more complex because the most influential windows occurred several weeks before the fate date. Group size was negatively associated with nest predation and ejections and positively with fledging success. However, given the paucity of data for high rain and the small effect sizes, we consider that any interpretation of indirect group size effects far from the fate date would be speculative.

Despite the helpers' overall positive effects, we found no indication of helpers' mitigation against the observed negative effects of high temperatures or low rainfall on nestling survival. Specifically, when nest predation was artificially reduced, we did not find an interaction between group size (or helpers' presence) and temperature or rainfall for either 'fully fledged' or 'ejection' fates. Similar results were obtained when looking at the number of fledged/ejected chicks per brood. A previous study on the same population (Covas et al. 2008) found buffering effects of helpers on fledgling mass under low rainfall (over the previous 30 days) and on nestling survival in larger colonies (which represented poorer breeding environments; Covas et al. 2008; Spottiswoode 2009, but not here). This previous study, however, covered only two breeding seasons and short-term analyses might only provide limited insights into inconstant ecological processes (Cockburn 2014). Mitigation effects of helpers during reproduction have been found in other arid-region cooperative vertebrates under varying rainfall conditions (Rubenstein 2011; Groenewoud & Clutton-Brock 2021), but not in relation to high temperatures (Bourne et al. 2020a) and comparable results were found for inter-annual group survival (Bourne et al. 2020b; Guindre-Parker & Rubenstein 2020). Taken together, these results suggest that detrimental effects of high temperature deserve particular attention, as they might not just reflect lack of food that can be compensated by larger group size, but inability for carers (and offspring) to maintain an adequate body temperature and hydration, leading to physiological stress (Salaberria et al. 2014; Smit et al. 2018).

CONCLUSION

Our study revealed that temperature is a major driver of nestling mortality in sociable weavers through its influence on nest predation. However, when we experimentally excluded nest predators, high temperatures were

still strongly associated with nestling mortality. Under the current climate change, intensity and frequency of hot and dry weather are predicted to increase (Duffy et al. 2019), and our results indicate that this will lead to a significantly lower reproductive output altering both predator–prey interactions and non-predator-related mortality (Mainwaring et al. 2017), which is likely to have population-level detrimental effects (Román-Palacios & Wiens 2020). Despite previous indication that helpers could contribute to mitigate the effects of adverse breeding conditions, our results (in line with others from the Kalahari region; e.g. Bourne et al. 2020a), show that the beneficial effects of helpers appear ineffective against extreme temperatures. Given that the global distribution of cooperative breeding is thought to arise largely from the mitigation effects of helpers on reproduction under adverse conditions (Jetz & Rubenstein 2011; Shen et al. 2017), we need studies on other systems integrating different ecological and social factors to determine whether helpers mitigation effects are indeed widespread, limited to specific conditions, or uncommon.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

PD, RC, CD, RF, AF and LS designed the study. MP, RC, CD, RF, FT, AF and LS contributed to collecting the data. RF, AF, FT and LS processed and stored the data. PD analysed and interpreted the data with input from all the authors. PD wrote the first manuscript draft and all authors contributed substantially to every

draft since. RC and CD initiated the data collection and supervised the work.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13913>.

OPEN RESEARCH BADGES



This article has earned an Open Data badge for making publicly available the digitally shareable data necessary to reproduce the reported results. The data are available at: <https://doi.org/10.6084/m9.figshare.16803229.v1>.

DATA AVAILABILITY STATEMENT

The data supporting the results, the R scripts for all models and of all figures have been archived under the DOI: <https://doi.org/10.6084/m9.figshare.16803229.v1>

ORCID

Pietro B. D'Amelio <https://orcid.org/0000-0002-4095-6088>

André C. Ferreira <https://orcid.org/0000-0002-0454-1053>

Rita Fortuna <https://orcid.org/0000-0002-6049-3690>

Matthieu Paquet <https://orcid.org/0000-0003-1182-2299>

Liliana R. Silva <https://orcid.org/0000-0003-4475-8035>

Claire Doutrelant <https://orcid.org/0000-0003-1893-3960>

Rita Covas <https://orcid.org/0000-0001-7130-144X>

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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