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Under the weather: Corticosterone levels in wild nestlings are associated with ambient temperature and wind

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A B S T R A C T

Animals time reproductive events to overlap with periods of favorable environmental conditions. However, weather conditions can be unpredictable. Young animals may be particularly susceptible to extreme weather during sensitive developmental periods. Here, we investigated the effects of adverse weather conditions on corticosterone levels (a hormone linked to the avian stress response) and body condition of wild nestling zebra finches (*Taeniopygia guttata*). We sought to tease apart the direct versus indirect (i.e. parental) effects of weather on nestling physiology and condition by increasing parental work load with a clutch manipulation experiment. We found that high temperatures were associated with lower levels of restraint-induced corticosterone and high wind speeds were associated with higher levels of baseline corticosterone. We found no associations between weather and nestling body condition. However, clutch manipulation did affect body condition, with nestlings from experimentally enlarged clutches in worse condition compared to nestlings from experimentally reduced clutches. Our findings suggest that weather can directly affect wild nestlings via changes in corticosterone levels. Further research is needed to understand how changes in corticosterone levels affect phenotype and survival in wild nestlings. Understanding how developing animals respond to changes in environmental predictability and extreme weather is vital for understanding the potential for rapid adaptation in the face of changing climatic conditions.

1. Introduction

Animals are under selection to breed when environmental conditions are optimal (Visser and Both, 2005). However, weather can be unpredictable and have significant consequences on reproductive outcomes (e.g. Breuner and Hahn, 2003; Martin and Wiebe, 2004). In birds, rainfall, wind, and high or low temperatures can affect nestling development, morphology, body condition, and survival (Conrey et al., 2016; Oberg et al., 2015). Developing animals can be particularly sensitive to perturbations in their environment and developmental effects can have sustained effects on phenotype and fitness across life-history stages and even generations (reviewed in Crino and Breuner, 2015; Monaghan and Haussmann, 2015; Schoech et al., 2011). Consequently, exposure to extreme weather conditions during development could have profound and potentially long-lasting effects on nestlings via direct and/or indirect mechanisms (i.e. parental effects). Understanding how developing birds respond to extreme weather conditions is of relevance for predicting how they will cope with rapidly changing global conditions.

Although the effects of weather on nestling condition and survival have been well described (e.g. Christensen-Dalsgaard et al., 2018; Geiser et al., 2008; Sicurella et al., 2015), the physiological mechanisms that modulate such changes in wild birds are less well-known. The glucocorticoid hormone corticosterone (CORT) is an important modulator of the physiological stress response (Romero, 2004) and is thought to be an important mechanism that promotes adaptive responses during inclement weather (reviewed in de Bruijn and Romero, 2018). CORT promotes physiological and behavioral changes that allows birds to cope with environmental perturbations (Breuner et al., 2008; Sapolsky et al., 2000; Wingfield and Kitaysky, 2002). Studies from poultry science have established a well-supported link between high temperatures and elevated CORT levels in developing and adult

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chickens (e.g. Najafi et al., 2015; Star et al., 2008). Additionally, numerous studies have linked exposure to cold ambient temperatures to elevated CORT levels in nestlings (Bize et al., 2010; Lopez-Jimenez et al., 2016; Lynn and Kern, 2014). In nestlings, prolonged elevation of CORT levels can have negative effects on body size and condition (e.g. Crino et al., 2014; Kraft et al., 2019) and can cause life-long changes to the hypothalamic-pituitaryadrenal (HPA) axis (the neuroendocrine pathway that modulates the release of CORT; Spencer et al., 2009).

Weather could affect nestling physiology and condition through both direct and indirect mechanisms. Extreme temperatures can directly affect nestlings through increased energetic costs required to maintain body temperature within an optimal zone (Angilletta et al., 2010). Weather could also affect nestlings indirectly by reducing the ability of parents to feed and incubate their nestlings. In zebra finches (*Taeniopygia guttata*), the level of foraging activity by adults is reduced by half during hot conditions (> 35 °C) and spatially restricted to areas closest to water (Funghi et al., 2019). Additionally, adult zebra finches increase heat dissipations behaviors (e.g. panting, holding wings away from body) at temperatures above 35 °C suggesting that changes in foraging patterns at and above this temperature are driven by physiological constraints (Funghi et al., 2019). Windy conditions affect reproductive outcomes in birds by adversely affecting foraging ability in situations where extremely high winds increase the costs of foraging (e.g. Evans, 1976). Adult birds may also face increased costs of incubation and brooding in windy conditions (Hilde et al., 2016), likely due to the rate of water loss and thermostatic costs in hot or cool environments respectively (Wolf and Walsberg, 1996). Low levels of parental provisioning and nest attendance have been associated with elevated levels of CORT in nestlings suggesting that parental behavior contributes to nestling stress physiology (Rensel et al., 2010).

The effects of weather on nestling physiology and survival have been well described in temperate bird species. However, no study has examined the effects of ambient temperature on nestling physiology in arid environments that are prone to unpredictable elevations in temperature. A recent comparative study of over 300 Australian birds found that the peak of reproduction in the arid zone occurs earlier than in other biomes and the breeding of desert birds appears to be constrained by extreme weather in the late spring and summer (Duursma et al., 2019). The arid zones in Australia are predicted to be some of the most vulnerable in the world to global climate change (Loarie et al., 2009; Williams et al., 2007). To our knowledge, no study to date has examined how weather conditions affect nestling physiology in arid environments, and yet such information is important in developing an understanding of species resilience to a changing climate (Urban et al., 2016).

Here, we examined associations between weather, CORT levels, and body condition in wild zebra finch nestlings in the arid Australian outback. Zebra finch nests in the arid zone of Australia are an average of 2 °C hotter than ambient temperatures and regularly reach temperatures exceeding 40 °C, and sometimes 50 °C for short periods of time (Griffith et al., 2016). Wild and captive-bred zebra finches attain a smaller adult body size when reared during hot ambient conditions (Andrew et al., 2017; Mariette and Buchanan, 2016). The arid Australian outback is also regularly exposed to winds that peak during the hotter months of the year, with daily wind runs between an average low of 250 km in May and a peak of 393 km in January (average data for Fowlers Gap (AWS 046128, between 2004 and 2019: Australian Bureau of Meteorology).

We predicted that nestlings would exhibit elevated baseline and restraint-induced levels of CORT in high temperatures and windy conditions. Furthermore, we predicted negative relationships between CORT levels and weather variables with body size. We also sought to tease apart the direct versus indirect (i.e. parental) effects of weather conditions on nestlings by experimentally altering parental effort with a clutch size manipulation. We predicted that nestlings from enlarged clutches would be smaller and have higher CORT levels compared to nestlings from control or reduced clutches and that these effects would be greater during hotter and windier weather. Consistent with the results from previous studies in this species (Naguib et al., 2004), we predicted that nestlings from experimentally enlarged clutches would have higher levels of CORT and lower body condition compared to nestlings from smaller clutches.

2. Material and methods

2.1. Study site and clutch size manipulation

This study was conducted on a population of zebra finches breeding in nest boxes at Fowlers Gap, New South Wales, Australia (31° 05′ S, 142° 42′E) from 9th October to 12th December 2015 (Griffith et al., 2008). Throughout the experiment, we provided zebra finches with supplementary seed via feeders in order to ensure that natural food availability did not limit parental provisioning. The feeders were located in the center of each breeding area and were checked daily and filled when necessary. A previous study on this population showed that food availability did not determine nest site choice on small scales (in areas 1–2 km wide; Mariette and Griffith, 2012).

Nest boxes were monitored regularly to determine nesting activity and hatch date of each nestling. We manipulated clutch size with one of three treatments: enlarged (n = 25), reduced (n = 38), or no change (n = 22). We manipulated clutch size six days after clutch completion (± 2 days) by reducing (minus 3 eggs) or enlarging (plus 3 eggs) clutches. We matched nests with eggs at the same developmental stage and transferred eggs from reduced clutches to nests with enlarged clutches (methods as per Brandl et al., 2018). We were unable to use nestlings from all manipulated nests in this study because of logistical constraints of another study. Nestlings were individually marked by cutting down feathers in a unique combination when clutches were manipulated and then ringed with a numbered aluminum ring at 11 days post-hatching. We collected blood samples to measure CORT when nestlings were 11 days post-hatching (see below). The mean brood sizes for each treatment at the time of sampling were: enlarged clutches (mean = 4.84, s.d. = 1.17), control clutches (mean = 3.79, s.d. = 1.37), and reduced clutches (2.64, s.d. = 1.17).

2.2. Blood collection and morphological measurements

We sampled 169 nestlings from 85 nests for hormone analyses and body size measurements. We collected blood from the first two nestlings that hatched in each nest box at 11 days post-hatching between the hours of 6:30 and 12:00. A baseline sample was collected within three minutes of first disturbing the nest box (mean = 125.8 ± 51.0 s). The nestling was then held in a cloth bag out of direct sun exposure for 15 min, at which time a second blood sample was collected to quantify restraint-induced CORT (mean = 985.0 ± 54.9 s; as per Crino et al., 2017). To collect blood, we punctured the alar vein with a 27-gauge needle and collected 25–50 µl of blood with heparinized microcapillary tubes. We stored the blood on ice until it could be centrifuged to separate plasma from red blood cells (7000 rpm for ten minutes) within three hours of collection. After separation, the plasma was isolated and stored at −20 °C until the samples were transported to Deakin University on dry ice and stored at −80 °C until assayed. After collecting blood samples, we weighed nestlings and measured tarsus length. We calculated nestling body condition using the scaled mass index derived from mass and tarsus length (Peig and Green, 2009).

This research was conducted under approval of Macquarie University Animal Ethics Committee.

2.3. Corticosterone assays

We quantified CORT levels from extracted plasma using Enzyme Immunoassay (EIA) kits (Cat No. ADI 900-097, Enzo Life Sciences,

USA). Samples were spiked with one pg of tritiated CORT (1,2,6,7-^{3}H; Perkin Elmer, Australia) prior to steroid extraction to determine recovery percentage. We extracted CORT from raw plasma using a double wash of dichloromethane. Samples were then dried under nitrogen gas and reconstituted in buffer solution (1:20 ratio). We adjusted hormone values for the average sample recovery (70.7%). We used an adjusted protocol to assay the reconstituted samples using half the volume of all the reagents supplied with the EIA kits (as per Crino et al., 2017). An external standard of 500 pg/ml was run on every plate and used to calculate inter-plate variation. All samples and standards were run in triplicate. Plates were read on a VarioskanLUX microplate reader (Cat. No. N16046, Finland) at 405 nm corrected at 580 nm. Levels of CORT were determined from a six point standard curve ranging from 20,000 to 15.53 pg/ml. Intra- and inter-plate variation was 5.9 and 17.8% respectively. The detection limit of the assay was 0.02 ng/ml.

2.4. Weather data

Weather data were downloaded from the Australian Bureau of Meteorology automated weather station at Fowlers Gap (within 20 km of the study site). Temperature and wind speed were taken from the hourly reading closest to the time the first blood sample was collected to examine short-term associations between weather conditions and nestling physiology (hereafter: *immediate weather*). To examine sustained effects of weather conditions on nestlings, we averaged the maximum daily temperature and wind speed for the ten days prior to collecting blood from nestlings and used the means in separate analyses (hereafter: *sustained weather*). We averaged across the ten days prior to sampling (on nestling age 11 days), to account for the conditions experienced by the nestling during the whole period since hatching.

2.5. Statistical analyses

We analyzed data using the lme4, MuMIn, and lsmeans packages in R 3.4.1 (Barton, 2009; Bates et al., 2015; Lenth, 2016). We used generalized linear mixed models with gamma distributions and log link functions to examine the effects of immediate and sustained weather on CORT levels. We used baseline CORT and restraint-induced CORT as dependent variables and wind speed, temperature, and clutch manipulation treatment as fixed factors, and nest identity as a random factor. We estimated p-values from Wald's test statistic. The time to collect blood samples was correlated with baseline CORT levels ($P < 0.001$). The time to collect blood samples was used as a covariate in all models that utilized a gamma distribution with baseline CORT as a variable. For linear models, we used the residuals obtained from regressing baseline CORT against collection time as an explanatory variable. To examine associations between weather and body condition, we used linear mixed models with condition as the dependent factor and baseline CORT residuals, restraint-induced CORT, wind speed, temperature, and clutch manipulation as fixed factors and nest identity as a random factor. We compared differences in body condition between clutch manipulation treatments using post-hoc Tukey's HSD tests. We estimated p-values using the normal approximation. Normality and homoscedasticity of GLM models of best fit were tested and confirmed using Kolmogorov-Smirnoff tests, and visual examination of residual plots and histograms.

For all models, we used backward stepwise regression to remove the greatest non-significant term ($p > 0.10$) until arriving at models with the lowest AIC scores. We present the results from the most parsimonious models for each factor; however, the significant results for full and parsimonious models are identical. A small number of samples were lost due to collection problems. Sample sizes are n = 156 and 147 for baseline and restraint-induced CORT respectively and n = 169 for scaled mass measurements. To compare candidate models that had both baseline and restraint-induced CORT as explanatory variables, we used data from individuals with complete hormone measures (n = 145). Full results from all models are presented in Supplemental Table 1.

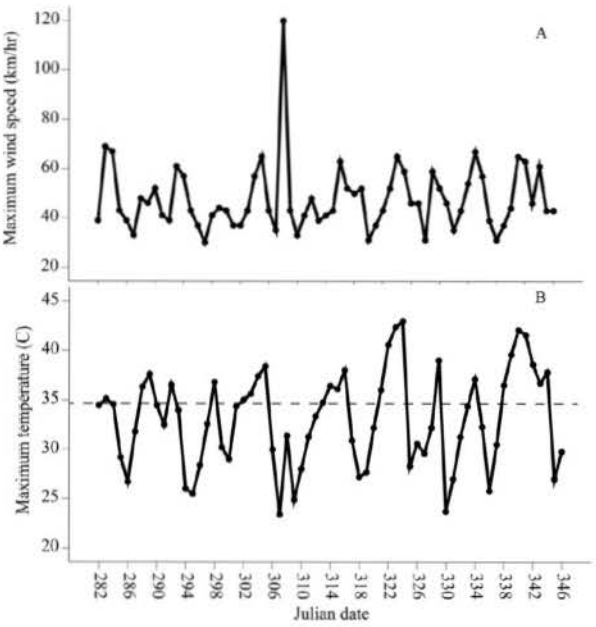

Fig. 1. Maximum daily A) wind speed, and B) temperature during the time this study was conducted. The dashed line represents the threshold temperature for which changes in zebra finch foraging and physiology have previously been described (Funghi et al., 2019).

3. Results

3.1. Weather and nestling CORT levels

The average maximum wind speed over the course of this study was 47.83 ± 13.76 (km/hr; Fig. 1A). The average maximum temperature was 33.10 ± 4.86 (°C). The maximum temperature was 35 °C or greater for 25 of the 65 days (38.46%) during the time period when this study was conducted (Fig. 1B).

Baseline CORT was positively associated with the immediate wind speed when nestlings were sampled ($F_{1,155} = 6.91$, $p = 0.02$, Fig. 2A), but not the sustained wind speed for the ten days preceding sampling ($F_{1,155} = 0.33$, $p = 0.61$). Baseline CORT was not associated with either immediate temperature ($F_{1,155} = 1.05$, $p = 0.12$) nor the sustained temperature ($F_{1,155} = 0.06$, $p = 0.80$ respectively). CORT levels following restraint stress were negatively associated with immediate temperature ($F_{1,146} = 9.73$, $p = 0.02$, Fig. 2B, but not the sustained temperature ($F_{1,146} = 0.35p = 0.51$). There were no associations between restraint-induced CORT levels and immediate nor sustained wind speed ($F_{1,146} = 0.48, 1.16$, $p = 0.60, 0.26$ respectively).

For models examining the effects of immediate weather condition on nestling CORT levels there was no effect of clutch reduction or enlargement, compared to control clutches, on baseline CORT levels ($p = 0.69$, 0.66, d.f. = 2, 155) or restraint-induced CORT levels ($p = 0.57$, 0.98, d.f. = 2, 146). Likewise, models examining the effects of sustained weather on nestlings CORT levels found no effect of clutch manipulation on baseline ($p = 0.73$, 0.82, d.f. = 2, 155) or restraint-induced CORT levels ($p = 0.78$, 0.38, d.f. = 2, 146). Including clutch manipulation in the statistical analyses resulted in models with lower AIC scores and so the term was removed from all final models.

3.2. Body condition

The final model examining variation in body condition in relation to

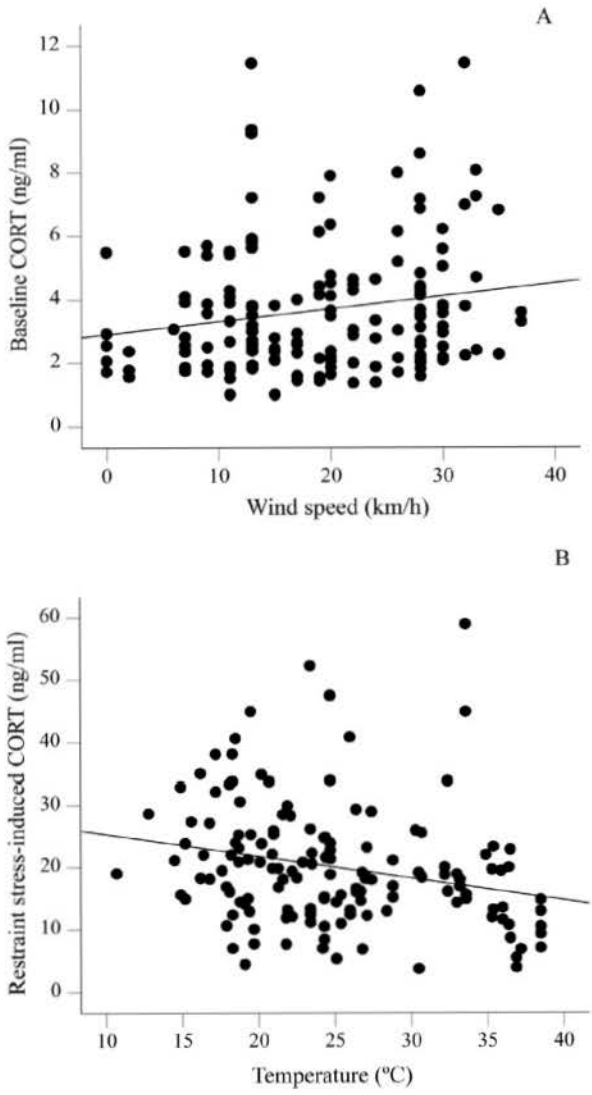

Fig. 2. Nestling CORT levels were associated with weather during the time of sampling: A) baseline CORT levels were higher when sampled under conditions with higher wind speeds, and B) restraint-induced CORT levels were lower when sampled under conditions with high ambient temperatures.

immediate weather conditions included an effect of clutch manipulation ($F_{2,146} = 3.98$, $p = 0.02$, Fig. 2). Nestlings from reduced clutches were in better body condition than nestlings from enlarged clutches ($p = 0.02$; Fig. 3). However, there were no differences in body condition between nestlings from reduced and control clutches ($p = 0.40$) nor control and enlarged clutches ($p = 0.42$; Fig. 3). Body condition was not associated with baseline CORT levels ($F_{1,146} = 0.07$, $p = 0.80$), restraint-induced CORT levels ($F_{1,146} = 3.41$, $p = 0.07$), immediate temperature ($F_{1,146} = 0.63$, $p = 0.43$), or immediate wind speed ($F_{1,146} = 1.00$, $p = 0.32$).

The final model examining variation in body condition in relation to sustained weather conditions included an effect of clutch manipulation ($F_{1,146} = 3.99$, $p = 0.02$). There were no associations between body condition and temperature and wind speed in the ten days preceding sampling ($F_{1,146} = 2.08$, 0.02, $p = 0.15$, 0.89 respectively). Likewise, there were no associations between body condition and baseline CORT levels ($F_{1,146} = 0.01$, $p = 0.90$) or restraint-induced CORT levels ($F_{1,146} = 2.73$, $p = 0.10$)

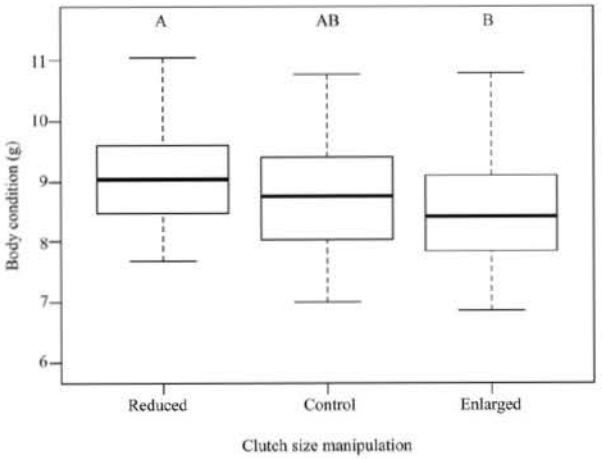

Fig. 3. Average nestling body condition as determined by the scaled mass index from experimentally reduced, control, and experimentally enlarged clutches.

4. Discussion

Our study found that nestling CORT levels reflected current weather conditions. Specifically, baseline CORT levels were positively associated with wind speeds and restraint-induced CORT levels were negatively associated with temperatures when nestlings were sampled. We found no association between weather conditions and body condition, or CORT levels and body condition. However, nestlings from experimentally enlarged clutches were in lower body condition compared to nestlings from experimentally reduced clutches. We found no effects of clutch manipulation on nestling CORT levels, suggesting that the effects of immediate weather conditions on nestling physiology are not indirectly modulated through changes in parental behavior.

We found a negative association between the temperature nestlings experienced at the time of sampling and restraint-induced CORT levels. In birds, prolonged exposure to acute stress is linked to decreased expression of glucocorticoid receptors in regions of the brain associated with negative feedback (Banerjee et al., 2012). In our study, high ambient temperatures may have shortened the amount of time needed for nestlings to reach peak CORT secretion. In this scenario, nestlings would have low levels of CORT after 15 min of restraint stress, because negative feedback mechanisms reduce CORT levels back to baseline levels (Banerjee et al., 2012).

In contrast to the negative association between temperature and restraint-induced CORT levels, we found a positive association between wind speed and baseline CORT. Wind speed could affect nestling CORT levels by disrupting feeding behavior and nest attendance (Rensel et al., 2010). However, we found that weather was not associated with nestling body condition, suggesting that windy conditions did not affect the ability of parents to feed nestlings. It is possible that high wind speeds influence the microclimate in nest boxes by decreasing the relative humidity in the surrounding area. It is also possible that high winds create an artificially noisy environment in nest boxes that contributes to changes in CORT physiology (Crino et al., 2013; Injaian et al., 2018). Future experiments could address these hypotheses by measuring noise in nest boxes and nest microclimate.

In our study, nestlings from experimentally enlarged clutches were in poorer body condition compared to nestlings from smaller clutches. This suggests that, even with supplemental food available in our study, parents are less able or willing to rear large clutches of nestlings. Zebra finches are less likely to forage in hot temperatures (Funghi et al., 2019) and it is possible that the availability of supplemental seed could not offset the metabolic consequences of foraging in hot temperatures. In the absence of the supplemental feeding treatment it is likely that we

would have observed greater differences between enlarged and reduced clutches. Although we found an effect of clutch manipulation on nestling body size, we found no associations between nestling CORT levels and body condition, suggesting there may be no immediate effects of short-term elevation of CORT levels on nestling survival. However, even a single exposure to an acute stressor can have detectable effects on wild nestlings up to ≈50 days post-fledging (Lynn et al., 2010). Future studies could more comprehensively evaluate nestling stress physiology by examining changes in negative feedback in response to weather. Additionally, future studies should track the effects of exposure to extreme weather over multiple life-history stages to determine the long-term fitness consequences for nestlings.

Although we found effects of both temperature and wind speed on CORT, in both cases, this was for the measure taken on the day of sampling rather than the average of these parameters over the ten-day nestling period. These results demonstrate the importance of acute effects of weather on nestling physiology. However, we caution that the apparent lack of chronic effects may be partly due to limitations in our sampling. For logistical reasons, we sampled the nestlings over a total period of 65 days, which represents a relatively small range of the climatic extremes in which zebra finches reproduce. The averaged climate across the ten day developmental period will be less variable than the immediate values taken on just a single day (given the daily variability in climate). From our study, the coefficient of variance for the sustained measures (CV = 0.03, 0.05; temperature, wind) was much lower than that for the immediate measures (CV = 0.27, 0.49; temperature, wind) in our sample. An earlier study from the same location, found that nestlings were smaller when they developed during hotter periods, and this analysis focused on a larger number of nestlings (n ≈ 900) reared over a seven month period, that included both cooler and hotter periods, than the current study (Andrew et al., 2017). These earlier findings, on overall body size (but not body condition) are consistent with the idea that nestling growth is limited in sub-optimal weather conditions.

Global climate change has led to an increased incidence of extreme and unpredictable weather both generally and during periods when animals might not normally expect to encounter such conditions (McKechnie et al., 2012). The ecoregions of Australia are considered to be some of the most vulnerable to global climate change (Loarie et al., 2009; Williams et al., 2007). Past studies have focused on the effects of elevated temperature on nestlings in temperate areas (Bize et al., 2010; Dawson et al., 2005; Fairhurst et al., 2012), but no study to date has examined how weather conditions affect nestling physiology in arid environments, and yet such information is important in building a picture of resilience to a changing climate (Urban et al., 2016). Understanding how developing birds respond to extreme weather conditions is of great relevance for predicting how they will cope with rapidly changing global conditions.

5. Conclusions

Our data suggest that nestlings are susceptible to extreme weather conditions via changes in CORT secretion. In a world with rapidly changing climatic conditions, it is imperative to assess the effects of weather on developing animals. Future studies should investigate the sustained effects of weather conditions on developing animals and whether or not such effects are adaptations to the forecasted environment or developmental constraints.

Authors contributions

O.C, S.D., and S.G designed this study. S.D. and H.B. conducted the field research. O.C. conducted the hormone assays and wrote the manuscript with S.G. and K.B. All authors agree to be held accountable for the content of this paper and approve the final version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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