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Article

Higher temperatures are associated with reduced nestling body condition in a range-restricted mountain bird

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Demonstrated negative effects of increased temperatures on avian reproductive success suggest a mechanism by which climate change may impact species persistence. High temperatures can result in reduced parental care and reduced nestling condition in passerines with dependent young, resulting in lowered fledging success and population recruitment. We examined provisioning rate and nestling condition in a South African mountain endemic, the Cape rockjumper *Chaetops frenatus*, whose population declines correlate with warming habitat. Our aim was to determine whether rockjumper reproductive success could be affected by high air temperatures. We set up video cameras on nests at three nestling age classes ($\leq$ 7 days old; 8–12 days old; $\geq$ 13 days old) for 8 hours on 37 separate days. We successfully collected full-day footage on 25 of the 37 days (four days with predation, eight with equipment failure). Nestlings were weighed at the beginning and end of each film day, barring the four days with mid-day predation ($n = 65$ nestling measures from 33 of the 37 days). Average mass gain across all nestlings per nest was positively correlated with provisioning rate (0.78 g provisions^{-1} hr^{-1}, CI: 0.26–1.30), and provisioning rate decreased at increasing temperatures (-0.08 provisions hr^{-1} °C^{-1}, CI: -0.15 to -0.01). Daily change in mass of individual nestlings was negatively correlated with air temperatures above a significant temperature threshold (22.4°C; -0.30 g °C^{-1}, CI: -0.40 to -0.19). This suggests nestling energy requirements were not being met on higher temperature days – perhaps because nestling energy and water demands for thermoregulation are elevated and provisioning rate is not correspondingly maintained or increased. These results suggest that higher temperatures negatively affect nestling mass gain. While in our study this did not directly affect fledging rates, it may affect post-fledging survival.

Keywords: mountain species, nestling condition, provisioning rate, range-restricted species, temperature

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Introduction

Increasing air temperatures (T_{air}) due to climate change are correlated with decreased abundance of multiple bird species both inter-annually (Jiguet et al. 2006) and over several decades (Iknayan and Beissinger 2018). Changes in temperature can affect avian demographics by altering reproductive phenology, fecundity and fledging success (Bradley et al. 1997, Steenhof et al. 1999, Bolger et al. 2005, Borgman and Wolf 2016, Conrey et al. 2016, Martin et al. 2017). Stochastic weather events (e.g. heat waves, drought) often result in reduced fledging success (reviewed by Moreno and Møller 2011), and the chronic sublethal costs of increasing temperatures and heat exposure may lead to declines in avian populations (Conradie et al. 2019). These sublethal costs can include the additive and interactive effects of daily adult body mass (M_b) loss (du Plessis et al. 2012), interannual adult M_b loss (Lee et al. 2020) and reduced nestling growth rates (Catry et al. 2015, van de Ven et al. 2020).

Passerines produce altricial young which require extensive parental care to raise successfully to independence. Reduced nestling condition (e.g. M_b) can result directly from higher T_{air} (e.g. from increased physiological costs of nestlings; van de Ven et al. 2020), or from decreased provisioning rates by adults at higher T_{air} (Luck 2001, Cunningham et al. 2013, Barras et al. 2021). Reduced nestling condition can result in reduced recruitment (reduced fledging success and post-fledge survival), lifetime fitness and longevity as an adult (Magrath 1991, Thompson et al. 1993, Greno et al. 2008, Schwagmeyer and Mock 2008, Bourne et al. 2020). Decreased nestling condition resulting at higher T_{air}, leading to decreased fledgling condition and fledging success, may thus be a key mechanism by which climate warming is responsible for declining populations in many avian species.

We examined the breeding biology of the Cape rockjumper *Chaetops frenatus* (hereafter 'rockjumper'), endemic to the semi-arid mountain fynbos of south-west South Africa. Rockjumpers live in small groups of 2–4 adult birds (although occasionally groups of five); rockjumpers occupy territories of 10–20 ha (Holmes et al. 2002), although territories may be larger in the eastern part of their distribution (Lee et al. 2017). Groups consist of a single breeding pair, with 1–2 additional helpers (usually male), often offspring from the previous year (Holmes et al. 2002, Oswald et al. 2020). Holmes et al. (2002) observed male and female rockjumpers, including helpers, sharing in parental duties including incubation and brooding. As mountain specialists, rockjumpers are especially vulnerable to changes in climate due to disproportionate habitat loss and unique ecology within a narrow thermal range (Midgley et al. 2002, Parmesan 2006, Sinervo et al. 2010, Reif and Flousek 2012, Scridel et al. 2018). Previous studies showed rockjumpers have overall decreased nest success associated with higher temperatures from increased snake predation (Oswald et al. 2020), and have experienced population declines correlated to areas of their habitat with the greatest warming trends (Milne et al. 2015).

Along with overall decreases in nest success at higher temperatures, our aim was to examine whether the reported temperature-related decrease in populations of rockjumpers (Milne et al. 2015) could also be explained by changes in breeding behaviour associated with higher temperatures. We monitored rockjumper nests over two breeding seasons to assess whether increasing temperatures negatively affected rockjumper breeding behaviour. We predicted parental care (provisioning rate, brooding) and nestling mass gain would be negatively correlated with higher air temperatures.

Methods

Study site and species

This study took place at Blue Hill Nature Reserve (33.59′S; 23.41′E; 1000–1530 m a.s.l.), in the Western Cape Province, South Africa (Oswald et al. 2019 for more complete details on study site). Data were collected over two breeding seasons (September–November 2017 and August–December 2018). Air temperature (°C) was recorded every 30 min by an on-site weather station (Vantage Vue, Davis Instruments Corp., California USA) set 1.5 m above the ground, 200–4000 m from rockjumper territories.

Nest initiation may begin as early as July (mid-winter), and some territories have nestlings into January (early summer), with nest attempts occurring continually from September to November – up to five nest attempts were observed within a single territory. Each territory contains a single breeding pair. Average daily maximum T_{air} ('daily T_{max}') in 2017 and 2018 combined (mean ± SD) for August was 14.97 ± 4.42°C and for December was 27.5 ± 4.6°C. Absolute maximum and minimum daily T_{air} were 36.6°C and −2.1°C, occurring in October and August respectively. These T_{air}s may underrepresent operative temperatures at nests with occasional sun, but the majority of nests were built in shaded microsites that have similar temperatures to those recorded by the weather station (Oswald et al. 2019).

Holmes et al. (2002) recorded only 2-egg clutches, but in our study we found rockjumper clutch size to vary: four nests had a single egg (possibly due to partial predation) and 10 nests had 3-egg clutches. The average incubation and nestling periods are both ~20 days, with a total development period of ~40 days before fledging (Holmes et al. 2002). While Holmes et al. (2002) observed no evidence of rockjumpers having multiple nest attempts within a single breeding season, during behavioural observations in 2016 we observed one territory with fledglings as well as an active nest with a nestling. We thus continued to search for nests in territories even after we had recorded a successful or failed nest attempt. Observations suggested individual territories held the same breeding pair throughout the season, and our nest attempts and territory designations were based on the breeding female's identity. We located 59 nests from 14 territories throughout this study with 22 failing before the nestling period. We collected data from 37 nests (25 with 'full-day' data; Oswald et al. 2021).

For details of capture, monitoring and ethical considerations refer Oswald et al. (2018b, 2019, 2021).

Filming setup

We filmed individual nests from ~9:00 to 17:00 SAST, three days per nest where possible, once within each of three different nestling age classes (early: ≤ 7 days old; mid: 8–12 days old; late: ≥ 13 days old). We used age class because we could only determine age of nestlings to within 3–4 days based on our 4–5 day nest check intervals. We estimated age based on a previously collected set of nestling photographs from nests with known hatch dates. Initially, in 2017, nests were recorded with a Panasonic XS-100 video camera ($n = 4$ cameras), but frequent equipment failure (below) led us to switch in November 2017 to Panasonic HC-V385 ($n = 3$; Panasonic Corporation, Osaka, Japan).

In total, we filmed 19 individual nests on 37 days and collected full-day data for 13 nests on 25 days (Oswald et al. 2021). Four nests were depredated on film days and we experienced equipment failure on an additional eight film days ('part-day' data; Oswald et al. 2021).

Nestling mass gain

Nestling mass data was collected from all full-day nests and from part-day nests regardless of equipment failure, barring the four days with mid-day predation ($n = 65$ individual nestling measures). On film days, we weighed nestlings on a portable electronic scale immediately before and after filming to determine change in body mass ('ΔM_b'). Diurnal ΔM_b was standardised to an 8 h (480 min) time period for both daily mass gain and percent daily mass gain, calculated using a modified formula from du Plessis et al. (2012) (Table 1).

Nestlings were marked individually by clipping different toenails. Colour-rings were originally used, but parents were observed pecking at rings in video footage. After filming the oldest age class, any surviving nestlings were weighed and ringed with one aluminum ring and three uniquely identifying colour rings. After nestlings were ringed, that territory was not visited until researchers retrieved trail and infrared cameras on day 22–25.

Table 1. Cape rockjumper nestling mass data collected in the morning (~9:00) and evening (~17:00) of days that nests were filmed to record provisioning behaviour, over two breeding seasons (2017 and 2018).

Year	Nestling age class	Morning M_b	ΔM_b	Nests
2017	Early	14.1 ± 3.4	2.1 ± 1.9	3 (5)
	Mid	27.0 ± 5.50	0.8 ± 0.6	3 (6)
	Late	37.2 ± 2.9	3.2 ± 1.7	3 (5)
2018	Early	12.2 ± 4.3	1.3 ± 1.0	11 (25)
	Mid	24.2 ± 3.3	2.3 ± 1.5	7 (13)
	Late	33.3 ± 4.9	2.0 ± 2.1	6 (11)

Data were collected from three separate nestling age classes (early: ≤ 7 days old; mid: 8–12 days old; late: ≥ 13 days old) and include: morning body mass ('M_b'; g; collected before 9:00 on the filming day), change in M_b ('ΔM_b'; from ~9:00 to 17:00) and number of nests (number of individual nestling measures in parentheses).

Video data extraction

We analyzed 279 h of video. We extracted data for each nest visit including: whether the adult was panting (bill held open ≥ 2 sec: '0' = absence, '1' = presence), occurrence of provisioning (adult placing food in nestlings' bills: '0' = absence, '1' = presence) and total time (from entry to exit of nest by the adults). Initially we tried to separate brooding from shading (i.e. maintaining the body above the nestlings and/or holding wings askew to provide protection from solar heat; Clauser and McRae 2017) but in over 30% of cases we could not determine the difference between the two. However, based on previous studies, for the youngest nestlings we presumed time spent in the nest by parents was most likely time spent brooding (Johnson and Best 1982, Sanz and Tinbergen 1999). We did not include individual nestling identification as we could not identify which nestling was being provided with parental care. Similarly, while we observed nestlings of all age classes panting on some occasions, in general we could not properly identify occurrence of this behaviour for most visits.

Data analysis

All analyses were performed in the R statistical environment ver. 3.5.3 (<www.r-project.org>) using RStudio ver. 1.2.5033 (RStudioTeam 2018). Packages used included *lme4* (Bates et al. 2015), *multcomp* (Hothorn et al. 2008), *MuMIn* (Barton 2019), *lmerTest* (Kuznetsova et al. 2017), *segmented* (Muggeo 2017), *ciTools* (Haman and Avery 2020) and *ggplot2* (Wickham 2016). Data are presented as mean ± SD, model estimates are presented together with 95% confidence intervals (CI). Significance was inferred when 95% CI did not contain zero.

For ΔM_b and % ΔM_b of individual nestlings we used data from all nests where we collected morning and evening M_b (Table 1; Oswald et al. 2021 for raw data). While this meant we could not directly correlate individual nestling M_b with provisioning rate, it did allow for a more precise analysis of how individual nestling M_b was related to our other predictor variables (daily T_{max}, brood size, adult group size and age class). To examine how nestling M_b may be directly related to provisioning rate, we used our full-day dataset and calculated average ΔM_b gain across all nestlings per nest ('average ΔM_b per nest'; below). Initial data visualization led us to suspect non-linear relationships for ΔM_b and % ΔM_b with daily T_{max} (i.e. the data appeared to have an inflection point above which the patterns differed) so we first ran broken-stick analyses on linear models (LMs) with daily T_{max} as predictor to check for significant inflection points. We found significant inflection points for ΔM_b at 22.4°C ($p < 0.01$) and % ΔM_b at 23.9°C ($p = 0.030$), so analyses of ΔM_b and % ΔM_b were performed on data above these inflection points.

For average ΔM_b per nest, provisioning and panting, we used the full-day dataset (nests with full days of footage, n = 25 days at 13 nests; Oswald et al. 2021 for raw data), while for brooding we used only data from the early age class of nestlings (n = 12 of 25 days). We calculated provisioning as an hourly rate (provisions per hour).

We applied an information theoretic approach (Burnham et al. 2011) to compare a list of competing models created using the *dredge* function from the *MuMIn* package – this approach allowed for us to consider an exploratory method to our hypothesis testing. To accommodate for differences in time between weighing and filming, we included the fixed effect of log-transformed time between weighing (ΔM_b, % ΔM_b) or log-transformed video length (provisioning, panting, brooding). We used AICc (Akaike's information criterion adjusted for small sample size) and discuss all competing models within 2 AICc of the top model (Oswald et al. 2021 for competing model outputs and model coefficients). Parameters are discussed based on their occurrence in the set of top models. As we did not have specific predictions regarding how levels within factors might affect the response variable, we used post hoc Tukey's tests to assess where significant difference lay on multi-level factors (i.e. age class, brood size, adult group size) present in our top models.

Nestlings: change in mass

To explore factors affecting individual nestling change in M_b (ΔM_b, % ΔM_b) above the inflection points, we fitted linear mixed-effects models (LMMs) with potential predictor variables of daily T_{max}, brood size, adult group size and age class with territory as a random effect. To explore how average ΔM_b per nest was related to provisioning (we did not have provisioning rates for individual nestlings, so could only analyse this with respect to averages for the entire brood), we fitted a LMM with potential predictor variables daily T_{max}, provisioning rate, brood size, group size and age class.

Adults: provisioning

To explore factors affecting provisioning, we fitted a LMM with potential predictor variables of daily T_{max}, brood size, adult group size and age class with territory as a random effect.

Adults: panting

To explore factors affecting adult panting, we fitted a Generalized LM (GLM), with potential predictor variables of daily T_{max}, brood size, adult group size and age class and a binomial error distribution.

Adults: brooding

We log-transformed time spent brooding younger nestlings to achieve a more normal distribution as the data were strongly right-skewed. To explore factors affecting the time adults spent brooding, we then fitted a LMM to the log-transformed data with potential predictor variables of daily T_{max}, adult group size and brood size, with territory as a random effect.

Adults: group composition

We included part-day data in analysis of how group composition (i.e. addition of a helper) effects parental care in cooperative groups to increase our number of 3-adult territories, and removed the one nest with the single breeding female where the breeding male disappeared between film days (n = 32 days, seven with three adults from three territories, 25 with two adults; Oswald et al. 2021 for raw data). As all helpers in our study were male, to explore factors affecting male provisioning, we fitted LMMs to the proportion of male provisions and the proportion of time males spent brooding younger nestlings with the predictor variable of adult group size (i.e. 2-adult or 3-adult) with territory as a random effect. As we were only able to differentiate between the breeding and helper male at one territory, we calculated male proportion of provisioning and brooding. While this would not allow for analysis of the degree of help a helper gave to the breeding male/female, it would allow us to determine if a helper resulted in load lightening among all adults.

Results

Nestlings: change in mass

For absolute individual ΔM_b (g), above the inflection point (22.4°C) there was only one top model within 2 AICc (Oswald et al. 2021). Individual nestling daily ΔM_b was best explained by daily T_{max}: mass gain declined as temperature increased (coefficient estimate = −0.30, 95% CI: −0.40 to −0.18; Oswald et al. 2021; Fig. 1A). For individual nestling % ΔM_b, above the inflection point (23.9°C) there was one model within 2 AICc (Oswald et al. 2021). Nestling % ΔM_b was also best explained by daily T_{max}: percent mass gain declined as temperature increased (coefficient estimate = −1.65, 95% CI: −2.65 to −0.57; Fig. 1B). The number of adults in the territory, age of the nestlings and brood size, were included in the top model but had responses that were not significant (Oswald et al. 2021).

For average ΔM_b per nest (g) there were two competing models within 2 AICc (Oswald et al. 2021). Average ΔM_b per nest was best explained by provisioning rate (included in both models) and brood size (included in the second model; Oswald et al. 2021). Greater average ΔM_b of all nestlings per nest was associated with higher rates of provisioning (coefficient estimate = 0.78, 95% CI: 0.26–1.30; Fig. 2A). While the top model did indicate lower mass gain associated with 3-nestling broods (coefficient estimate = −1.40, 95% CI = −4.30 to −0.59; Oswald et al. 2021), post hoc Tukey's test found no difference among age classes (2 nestlings–1 nestling: coefficient estimate = −0.72, 95% CI = −3.19 to 1.75; 3 nestlings–1 nestling: coefficient estimate = −2.32, 95% CI = −5.69 to 1.04; 3 nestlings–2 nestlings: coefficient estimate = −1.60, 95% CI = −4.03 to 0.83).

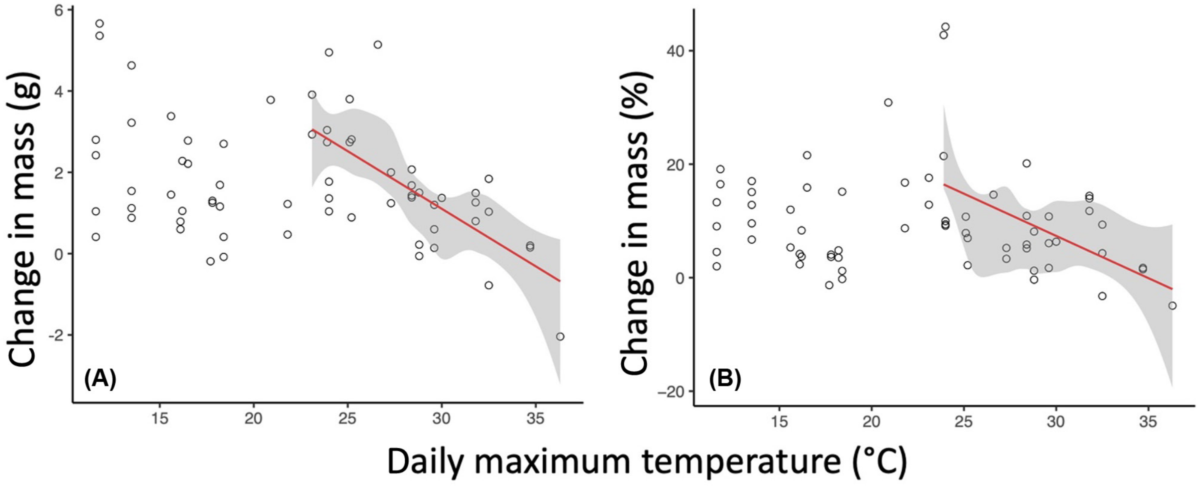

Figure 1. Individual nestling change in body mass (‘M_b’; (A) daily M_b change in grams, and (B) daily M_b change as percent of morning mass) across daily maximum temperature for nestling rockjumpers observed from 9:00 to 17:00 SAST from 33 days of data collected from 15 nests of rockjumpers (n = 65 total nestling measures). Each datapoint represents an individual nestling. Model fit is LMM with linear regression and shaded 95% confidence intervals for slope above the significant inflection point ((A) 22.4°C, n = 35 nestling measures; (B) 23.9°C, n = 33 nestling measures).

Adults: provisioning

There were two competing models within Δ2 AICc explaining provisioning rates (Oswald et al. 2021). Hourly provisioning rate was best explained by temperature (included in both models) and brood size (included in the top model; Oswald et al. 2021). Provisioning rate was best explained by temperature, and decreased at increasing daily T_{max} (coefficient estimate = −0.02, 95% CI: −0.04 to 0.00; Fig. 2B, Oswald et al. 2021). Provisioning rate also differed among brood sizes (Oswald et al. 2021): the largest broods had a greater provisioning rate compared to the smallest broods (3 nestlings–1 nestling: coefficient estimate = 0.60, 95% CI = 0.00–1.20) although there were no differences among other brood sizes (2 nestlings–1 nestling: coefficient estimate = 0.32, 95% CI = −0.14 to 0.79; 3 nestlings–2 nestlings: coefficient estimate = 0.28, 95% CI = −0.19 to 0.75).

Adults: panting

There were two competing models within 2 AICc explaining probability of adults panting, including daily maximum temperature (in both models), and brood size (in the second model; Oswald et al. 2021). Panting was best explained by daily T_{max}, with panting more likely to be observed on days with higher maximum temperatures (top model coefficient

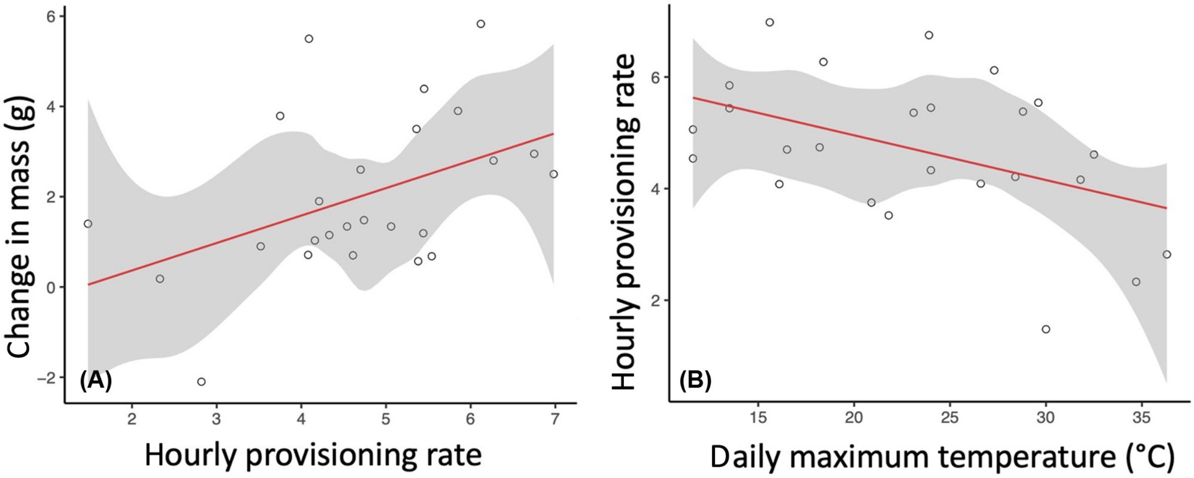

Figure 2. (A) Average ΔM_b across all nestlings per nest (g) as a function of hourly provisioning rate, and (B) hourly provisioning rate as a function of daily maximum temperature (°C). Data were collected from 25 days of filmed observations (cameras placed from 9:00 to 17:00 SAST) at 13 nests of rockjumpers. Model fits are LMM with linear regressions (red line) and shaded 95% confidence interval. Each datapoint represents an individual nest.

estimate = 0.21, 95% CI: 0.07–0.41; Oswald et al. 2021; Fig. 3). Brood size had a minimal effect on the probability of panting and was not significant (Oswald et al. 2021).

Adults: brooding

There were three competing models explaining the amount of time (log-transformed min) adults spent brooding younger nestlings, which included the null model (top model), adult group size (present in the second competing model) and daily maximum temperature (present in the third competing model; Oswald et al. 2021). While adult group size was in the second competing model, the response was minimal and not significant (Oswald et al. 2021). In our third competing model, adults spent less time brooding on days with higher maximum temperatures (coefficient estimate = −0.14, 95% CI: −0.23 to −0.05; Oswald et al. 2021).

Adults: effect of group composition

The overall proportion of provisioning events carried out by males was not significantly different for nests with only a single adult male compared to nests with two adult males (coefficient estimate = 0.09, 95% CI: −0.04 to 0.23; 1-male: male proportion provisioning = 0.50 ± 0.16; 2-males: male proportion provisioning = 0.59 ± 0.16; Fig. 4A). There was also no significant difference in the proportion of time males spent brooding younger nestlings at nests with one versus two adult males (coefficient estimate = −0.18, 95% CI: −0.40 to 0.04; 1-male: male proportion nest attendance = 0.35 ± 0.24; 2-males: male proportion brooding: 0.33 ± 0.24; Fig. 4B).

Discussion

We found that on days with higher temperatures adult provisioning rates decreased (95% CI marginally included zero at two significant digits, the upper bound was −0.002), which likely led to our observed reduction in nestling mass gain. This suggests on warmer days adults may not be able to provide sufficient food for their nestlings to maintain nestling mass gain. However, the rate of decrease in individual nestling mass above a temperature threshold suggests there may be additional factors leading to lower mass gain at high temperatures. Additional factors on warmer days may include: 1) adults delivering smaller prey items above specific temperatures (Barras et al. 2021); 2) nestlings losing greater water mass via evaporative cooling (Oswald et al. 2018a) or; 3) nestlings prioritising energy resources towards other areas of growth such as feather development during hot weather (Murphy 1985). Any factor that results in a decrease in nestling mass gain could result in a decrease in fledgling mass and recruitment and have implications for fledging success (Magrath 1991, Schwagmeyer and Mock 2008) and post-fledging survival (Greno et al. 2008).

Combined effects of temperature, provisioning and mass gain

In most bird species, nestlings need to gain mass throughout the nestling period to develop and fledge successfully, and there is evidence from across disparate bird taxa that heavier nestlings (both early in the nestling period and at the time of fledging) are more likely to fledge and survive to breed themselves (Magrath 1991, Thompson and Flux 1991, Greno et al. 2008, Schwagmeyer and Mock 2008, Bourne et al. 2020, van de Ven et al. 2020). While hourly provisioning rate decreased steadily as temperatures increased (Fig. 2A) and average ΔM_b across all nestlings per nest was positively correlated with provisioning rate (Fig. 2B), rockjumper nestlings showed reduction in mass gain only at temperatures above specific thresholds (Fig. 1). In line with Barras et al.'s (2021) finding that both provisioning rate and prey biomass of provisions decreased at higher air temperatures, it may be that while provisioning rate decreased steadily with temperature, prey biomass (not recorded here) only decreased below certain temperature thresholds.

Our individual nestling mass thresholds are relatively low compared to temperature thresholds for detrimental effects on nestlings previously recorded for other southern African passerines. For example, the southern fiscal *Lanius collaris*, and southern pied babbler *Turdoides bicolor*, both had detrimental effects > 30°C (Cunningham et al. 2013, Bourne et al. 2020), although our results were higher than those recorded for a Mediterranean-climate passerine the spotless starling *Sturnus unicolor* (~15°C; Salaberria et al. 2014). Cunningham et al. (2013) and Bourne at al. (2020) respectively showed specific consequences for fledging at temperatures above the threshold identified for southern fiscals (i.e. delayed fledging with associated increased predation risk) and southern pied babblers (i.e. shorter survival times and reduced probability of fledging).

Adults may be decreasing provisioning visits at increased temperatures to reduce predation risk by minimizing activity near the nest (Conway and Martin 2000, Martin et al. 2000). Rockjumper snake predation also increases beginning at relatively low temperatures (minimum temperature of snake predation = 14.2°C, mean = 23.4°C; Oswald et al. 2020). That rockjumpers may decrease provisioning rate to reduce predation risk is an idea supported by relatively low provisioning rates: rockjumpers had an hourly provisioning rate of 4.7 (for all nestlings 4–16-days old) compared to 8.0 for 3–13-day old nestlings observed by Barras et al. (2021), and 6.0 for 6–14-day old nestlings observed by Cunningham et al. (2013).

While we did find greater provisioning at nests with three nestlings when compared to nests with one nestling, the lack of any significant relationship between provisioning and age class in our dataset is puzzling. Provisioning rates are generally higher for older nestlings (Grundel 1987, Filliater and Breitwisch 1997, Falconer et al. 2008, Barba et al. 2009), as older nestlings require more energy and water due to increased metabolic rates (Olson 1992). Adults can increase

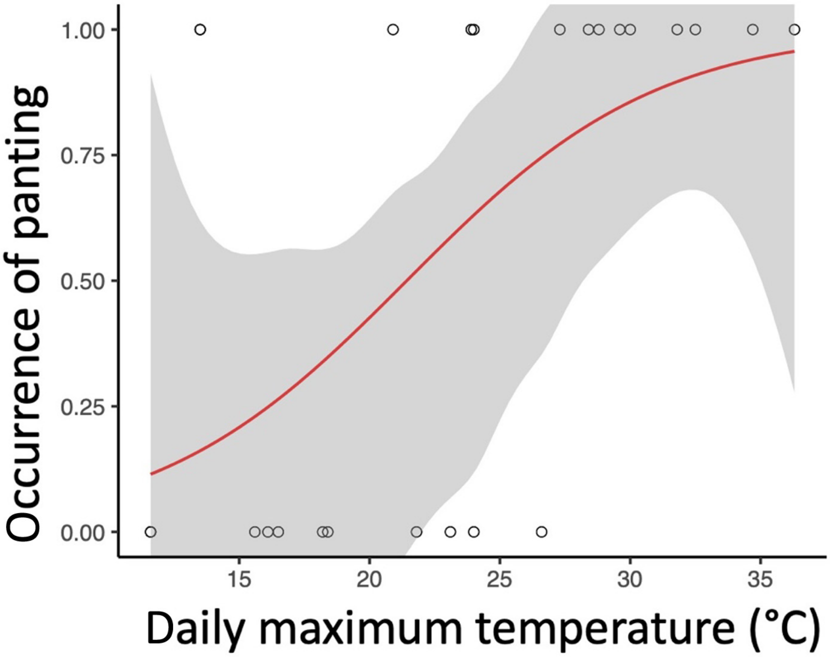

Figure 3. Probability of occurrence of adult panting across daily maximum temperature (°C) observed from 9:00 to 17:00 SAST from 25 days of observations at 13 nests of rockjumpers. Each datapoint represents an individual nest. Model fit is GLMM with binomial error structure, logistic regression and shaded 95% confidence intervals.

both provisioning volume (Grundel 1987) and prey type (Radford 2008) to maintain mass gain for older, heavier nestlings. It may be that we did not find a relationship between age class and provisioning rate because none of our oldest broods had three nestlings – while in general, we had fewer nests survive throughout the nestling period (n = 13 early age class, n = 7 mid age class, n = 5 late age class), in all cases of 3-nestling broods only two nestlings remained by day 13 (late age class), likely due to partial predation.

The post-fledging survival and fitness implications of our results remain unclear for several reasons: 1) because predation was the only cause of nest failure during this study (Oswald et al. 2020), and; 2) because we do not have sufficient data on post-fledging survival. Further, our results are tempered by the fact that our oldest nestlings (13–16 days old) would still have experienced 3–5 days more in the nest before fledging. It is possible, then, that rockjumpers could provide compensatory increases in provisioning if exposed to cooler days during the remainder of the nesting period. Our results are also tempered by relatively few days > 30°C (n = 4), and we can only assume more hot days would strengthen our pattern.

Figure 4. Proportion of (A) provisioning events by males [one male (n = 25 days) or two males (n = 7 days), respectively], and (B) brooding by males [data includes only observations of the youngest nestlings at nests with only one male (n = 13 days) or two males (n = 2 days). The midline indicates the median, mean values are indicated by 'x' and outliers (dots) indicate values > 1.5 times the interquartile range.

Panting and brooding

We found adults panted at daily T_{max} as low as 13.5°C (Fig. 3), although adults panted on all days with daily $T_{max} > 26.8°C$. This is in keeping with previous studies demonstrating that rockjumpers have relatively low thermal thresholds for evaporative heat dissipation (Milne et al. 2015, Oswald et al. 2018b). We also found that adults spent less time brooding nestlings as temperatures increased. The inclusion of the null model as our top model suggests there is variation amongst territories in the amount of time adults spend brooding that is not related to our predictor variables.

Group composition

Cooperative breeding can provide benefits to individual adults, as more individuals sharing the workload can buffer the effects of environmental stressors ('load-lightening', Ridley and Raihani 2007, Meade et al. 2010, Johnstone 2011, Wiley and Ridley 2016). Surprisingly, the presence of a helper (in all cases, male) did not correlate with increased overall parental care in this study. This is in line with several other studies in which helpers share parental care with no increase in the total amount of care nestlings receive (Ridley and Raihani 2007, Savage et al. 2015, Wiley and Ridley 2016). Koenig and Walters (2011) refer to this strategy as 'compensatory feeding' as opposed to 'additive feeding'. The addition of a helper male in our study only resulted in decreased provisioning by the breeding male, as the overall proportion of care provided by males altogether was indistinguishable between 2- and 3-adult groups (Fig. 4). Similarly, Meade et al. (2010) examined breeding behaviour for the cooperative breeding long-tailed tit *Aegithalos caudatus*, and found helper males only decreased the overall provisioning load of breeding males. While we were only able to distinguish between individual males in one territory, the helper (offspring from the previous year) provided 29.5% of provisions and the breeding male provided 24.8% of provisions, while the breeding female provided 45.7% of all provisions. The breeding male also experienced load-lightening in brooding from the addition of a helper male. To the best of our knowledge, no studies have examined time spent brooding of cooperative breeders for species where both sexes brood (as with rockjumpers), as in long-tailed tits only the females brood (Meade et al. 2010).

Conclusions

We demonstrated that adult rockjumpers may be unable to provision at a rate or quality that maintains mass gain for nestlings on days with warmer air temperatures. We suggest the most likely reason for the decrease in nestling mass gain at higher temperatures was a combination of increased nestling physiological demands and decreased prey quality with no corresponding compensation from adults (i.e. via an increase in provisioning rate or prey quality). Adults may themselves face high individual heat stress risk if they attempt to mitigate negative impacts to nestlings by increasing provisioning rates; as with our temperature thresholds for reductions in nestling mass gain, rockjumper adults began panting at a relatively low temperature compared to other South African passerines (du Plessis et al. 2012, Smit et al. 2013, 2016).

The apparent inability of adult rockjumpers to mitigate the costs of high air temperature on nestling growth did not necessarily manifest as reduced fledging success as the only reason for failed fledging at our study site was nest predation (Oswald et al. 2020). While we were unable to examine post-fledge success, smaller fledglings generally have lower survival across species (Magrath 1991, Thompson and Flux 1991, Greno et al. 2008, Schwagmeyer and Mock 2008). Any factor which limits nestling mass gain may therefore lead to lower quality fledglings. As rockjumper fledglings also have relatively low thermal thresholds for physiological thermoregulatory responses (i.e. low panting thresholds; Oswald et al. 2018a), high temperatures may lead to overall decreased population recruitment. Of the 25 film days during this study, just over half had a daily maximum temperature of greater than 22.4°C (the threshold for declining nestling mass gain, $n = 14$ of 25 days). As global temperatures continue to increase, the number of days with maximum temperature greater than 22.4°C in rockjumper habitats will increase, potentially compromising rockjumper nestling growth. Predictive distribution modelling combining vulnerability based on temperature thresholds which could reduce breeding success (reduced nestling mass gain, increased nest predation) show rockjumper nests will be increasingly vulnerable in the future (unpubl.). We may begin to see decreased fledging success, post-fledging survival and overall reduced lifetime fitness in this species – perhaps explaining the rockjumper population declines in warming habitat (Milne et al. 2015).

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Krista Oswald: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead). **Ben Smit**: Conceptualization (equal); Data curation (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (equal); Supervision (lead); Writing – review and editing (equal). **Alan Lee**: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Resources (equal); Supervision (equal); Writing – review and editing (equal). **Ceili Ping**: Data curation (equal); Investigation (equal); Writing – review and editing (supporting). **Cameryn Brock**: Data curation (equal); Investigation (equal); Writing – review and editing (supporting). **Susan Cunningham**: Conceptualization (lead); Funding acquisition (supporting); Investigation (supporting); Methodology (lead); Supervision (equal); Writing – review and editing (equal).

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Data accessibility statement

Data available from the the Dryad Digital Repository: <http://doi.org/10.5061/dryad.gtht76hkk> (Oswald et al. 2021).

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