High temperatures are associated with substantial reductions in breeding success and offspring quality in an arid-zone bird

T.M.F.N. van de Ven[1], A.E. McKechnie[2,3], S. Er[4] & S.J. Cunningham[1*]

[1]FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, Private Bag X3, University of Cape Town, Rondebosch 7701, South Africa

[2]DST-NRF Centre of Excellence at the FitzPatrick Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

[3]South African Research Chair in Conservation Physiology, South African National Biodiversity Institute, Pretoria, South Africa

[4]Department of Statistical Sciences, University of Cape Town, Rondebosch 7701, South Africa

*corresponding author: susie.j.c@gmail.com; sj.cunningham@uct.ac.za

Abstract

During hot weather, terrestrial animals often seek shaded thermal refugia. However, this can result in missed foraging opportunities, loss of body condition and impaired parental care. We investigated whether such costs could compromise breeding success in a widespread southern African bird: the Southern Yellow-Billed Hornbill *Tockus leucomelas*. We predicted that hornbills might be especially vulnerable to temperature-dependant reductions in parents' foraging capacity due to extreme asymmetry in sex-specific roles during breeding: females are confined within the nest-cavity for most of the nesting period and the burden of provisioning falls solely on the male during this time. We followed 50 hornbill nesting attempts in the Kalahari Desert between 2012 and 2015, collecting data on provisioning rates, adult and nestling body mass, fledging success and size of fledglings. Mean daily maximum air temperatures (T_{max}) during nesting attempts ranged from 33.2°C to 39.1°C. The likelihood of successful fledging fell below 50% at mean T_{max} > 35.1°C; a threshold now regularly exceeded at our study site due to recent climate warming. Additionally, offspring fledging following the hottest nesting attempts were > 50% lighter than those fledging following the coolest. Sublethal costs of keeping cool including loss of body condition, production of poor-quality offspring and breeding failure are likely to become issues of serious conservation concern as climate change progresses; even for currently widespread species. Missed-opportunity costs associated with behavioural thermoregulation and direct sublethal costs of temperature exposure should not be overlooked as a potential threat to populations, especially in environments that are already hot.

Introduction

There is growing evidence that hot weather can directly suppress breeding success in numerous vertebrate taxa (Sinervo et al. 2010; Cunningham et al. 2013; Catry et al. 2015; Woodroffe et al. 2017). Body condition of avian parents and chicks can be affected by daily maximum air temperature (T_{max}) through increases in physiological thermoregulatory costs or decreases in food availability (McCarty and Winkler 1999; Dybala et al. 2013). High air temperatures (T_a) during the breeding season can thus reduce nestling growth rates, subsequently affecting body mass (M_b) of chicks at fledging or post-fledging survival (Green and Cockburn 2001; Greño et al. 2008; Braasch et al. 2009).

Avian responses to increasing temperatures may include breeding earlier in the season (Dunn and Winkler 1999) or selecting cooler nest microsites (Tieleman et al. 2008). However, adjusting reproductive patterns to mitigate the impacts of the thermal environment on reproductive success may incur costs (Dunn and Winkler 2010). For example, in environments that are already hot, further warming can create conditions in which eggs in unattended nests can rapidly reach lethal temperatures (AlRashidi et al. 2010). Increased parental energy expenditure during incubation can limit reproductive investment during chick development (Reid et al. 2000; Coe et al. 2015). Trade-offs between nest attentiveness and behavioural thermoregulation can result in increased risk of nest predation during hot weather (Oswald et al. 2008), but selection of cooler nest microsites may also substantially increase predation risk if predators also seek these areas (Tieleman et al. 2008); and in some cases hot weather while breeding may lead to brood abandonment to ensure adult survival (AlRashidi et al. 2010).

An often-overlooked mechanism that may link high air temperatures to reductions in breeding success is the behavioural changes made by breeding individuals in order to manage their own thermal load. In thermally heterogeneous landscapes, individuals can shelter in thermal refugia

3

during hot periods, reducing their heat load and consequently the physiological costs of maintaining

normothermic body temperatures (e.g. Carroll et al. 2015). Landscape heterogeneity has therefore

been cited as an important factor that may buffer animal populations under climate warming

(Kearney et al. 2009; Sears et al. 2011). However, changes in behaviour for thermoregulation can

carry important costs, especially during breeding, if thermoregulatory behaviours trade-off against

foraging success, for example by forcing animals to forage in less-profitable locations, forage less

efficiently (e.g. due to trade-offs between prey handling and panting), or cease foraging altogether

(du Plessis et al. 2012; Cunningham et al. 2013; van de Ven et al. 2019). Declining offspring

provisioning rates resulting from compromised foraging ability could severely affect nest outcomes

during hot weather, when water demands of offspring for evaporative cooling are high (e.g.

Cunningham et al. 2013; Catry et al. 2015). If trade-offs between behavioural thermoregulation and

foraging are sufficiently severe, such processes could put even common species inhabiting intact and

thermally heterogeneous habitats at risk of decline under ongoing climate warming.

One avian taxon that may be expected to face severe temperature-related trade-offs during

reproduction is the hornbills (Bucerotidae). This is because hornbills are monogamous, pair-breeding

cavity nesters with extreme asymmetry in parental investment: females are confined to the nest for

most of the breeding cycle, during which time males assume sole responsibility for provisioning

(Moreau and Moreau 1941; Kemp 1995). Hornbill pairs are socially monogamous; males and females

form a strong bond during the pre-nesting period, when males present numerous food items to

females (Kemp 1995). The males' capacity to provision is crucial to the females, because soon after

females settle in the nest and seal the entrance they undergo a complete flight feather moult,

rendering them flightless and therefore unlikely to survive outside the nest (Moreau 1937; Kemp

1995). During moult, incubation and nestling rearing, the females and nestlings remain entirely

dependent on the males for food (Stanback et al. 2002). This heavy burden of provisioning on males

4

is likely to make both members of the pair and the breeding attempt vulnerable to any impact of high temperatures on male foraging success (van de Ven et al. 2019).

The capacity of male Southern Yellow-billed Hornbills *(Tockus leucomelas*; hereafter, hornbills) to provision nests likely becomes severely constrained during hot weather by behavioural trade-offs between foraging and thermoregulation (van de Ven et al. 2019). In a concurrent study, increases in panting behaviour and foraging in shaded off-ground microsites led to large decreases in foraging efficiency; in turn leading to reduced diurnal M_b gain at high T_{max} which, combined with approximately constant overnight M_b loss, resulted in nett 24-hr losses approaching 5 % of M_b on each day when T_{max} approached 40 °C (van de Ven et al. 2019). The consequences of hot weather for male foraging success may thus be expected to strongly influence his capacity for nest provisioning.

Southern Yellow-billed Hornbills are widespread in southern Africa, and currently listed as Least Concern by the IUCN (IUCN, 2018). However, much of the species' range encompasses dry savanna and woodland habitats that are warming rapidly under climate change (Kruger and Sekele 2012). Hornbills could therefore be very vulnerable to climate warming if their breeding system predisposes them to experiencing large declines in nest success during hot weather events. We hypothesized that nesting success in Southern Yellow-billed Hornbills is dependent on prevailing environmental temperatures during breeding attempts, on account of behavioural trade-offs faced by males and the consequences thereof for nest provisioning. Because of the temperature-dependence of male foraging efficiency (van de Ven et al. 2019), we predicted that increasing T_a is associated with: 1) decreases in the rate of food delivery to nests, 2) decreases in females' condition, 3) reduced nestling growth rates and reduced fledging quality, and 4) increased probability of nest failure.

Materials and methods

Study site and population

Our study site was the 33-km^2 Kuruman River Reserve (KRR, 26°58' S, 21°49' E), located in the southern Kalahari Desert, South Africa. This area consists mainly of dunefields and dry riverbeds supporting arid savanna (see Clutton-Brock et al. 1999). Mean daily maximum air temperatures (T_{max}) during the austral summer (Dec – Mar) are 34.2 ± 9.7 °C and mean annual rainfall is 202.25 ± 82.4 mm (mean ± SD, data for 1994 – 2017, Van Zylsrus weather station ~30 km from KRR, South African Weather Service). Most rainfall occurs in summer. We collected data from breeding hornbills during the summers (October to March) of 2012-13, 2013-14 and 2014-15. Southern Yellow-billed Hornbills are cavity-nesters that rely on natural tree cavities or sites excavated by other species. Nest-boxes with hinged lids to allow access to nest contents were installed at KRR in 2008 and hornbill pairs now breed in these boxes as well as in natural tree cavities along the dry river bed. We observed 50 nesting attempts, of which 43 involved nest-boxes and seven natural tree cavities.

Temperature

We collected weather data throughout the study period using an onsite weather station (Vantage Pro2, Davis Instruments, U.S.A., placed within six kilometres of the furthest nest box) recording air temperature (T_a, °C), relative humidity (%), wind speed (m s^{-1}), solar radiation (W m^{-2}), and rainfall (mm) at 5-min intervals. We measured nest temperature in 14 occupied nest-boxes and two occupied natural cavities over 219 days across three breeding seasons using Thermochron iButtons (DS1923, Maxim, Sunnyvale, CA, USA, resolution = 0.0625 °C, logging interval 5 min) attached to the underside of nest-box lids or inside the upper part of natural cavities. Prior to deployment, iButtons were calibrated in a circulating water bath against a factory-calibrated NiCr-NiAl thermocouple meter (HH21A, Omega Engineering, Stanford, U.S.A.).

Nest monitoring

At the start of each season, we checked boxes once per week for breeding activity and considered a nesting attempt to have started when a box entrance was sealed and a female confined inside. Nest stage was categorised as "female only", "female with eggs", "female with nestlings" or "nestlings only". During the "female only" and "female with eggs" periods, female body mass (M_b) and tarsus length was measured weekly. Approximately three weeks after egg lay, we began checking boxes daily to determine the hatching date of the first nestling. Thereafter, we visited the boxes twice daily to weigh and measure the nestlings and the female and record the hatching dates of subsequent nestlings. We recorded the dates of female departure from the nest and fledging of each chick. The duration of each nesting attempt was therefore calculated as the number of days between when the nest entrance was sealed until the last chick fledged or the nest failed. It was not possible to check the nesting status of hornbill pairs using natural cavities other than whether these nests successfully fledged one or more chicks.

Morphometric data

Females and nestlings were weighed to 0.01 g on a top-pan electronic balance (MXX-612, Denver Instruments, Germany), and tarsus length measured to 0.1 mm with digital calipers (SDC150, Scangrip, Denmark). Following hatching, M_b and tarsus length were recorded twice daily (< 1 hr after sunrise and < 1 hr before sunset) to quantify both diurnal M_b gain and overnight mass loss. Provisioning male hornbills were weighed using custom-designed digital scales (B0.6U, Axis, Ecotone, Poland) attached to perches that were mounted at nest entrances (n = 14 nest boxes and n = 2 natural cavities; for further details see van de Ven et al. 2019). Diurnal M_b gain was expressed as a percentage change standardized to 12 hr using the formula:

$$Diurnal\ M_b\ gain\ (\%) = \ 100[(w2 - w1)/\ w1]\ /\ [\ \Delta t/12]$$

where w1 = morning M_b, w2 = evening M_b and Δt is the time difference (h) between the morning

and evening weighing times [adapted from du Plessis et al. (2012)]. Overnight M_b loss was calculated

as the M_b loss between sunset and sunrise the following morning, standardised to 12-hour periods

using the formula above.

Nest provisioning

Daily provisioning rates were quantified at nests during the 2014-15 breeding season on a total of

140 days at seven nests, including four nest-boxes and three natural cavities. We placed a motion-

triggered camera (BTC-5, Browning, U.S.A) 2 - 3 m in front of each nest daily between sunrise and

sunset from nestling hatch to fledge. We set the cameras to record for 30 s following each triggering

event. Provisioning data were collected for a mean of 14.1 days per nest (range 3 – 25, variation in

the number of days between nests is due to failures of breeding attempts or our equipment) and a

range of T_{max} and nestling age categories: 0 – 10 days (n = 16 days of observation), 11 – 30 days (n =

50) and > 31 days (n = 33 days). Our provisioning data spanned the periods before and after female

departure from the nest, which occurred when nestlings were 24.3 ± 6.4 days old (n = 33 nests over

three breeding seasons). Provisioning rates were quantified as the number of provisioning events

per day standardized to 12 hr by dividing by the number of hours recorded and multiplying by

twelve. Data from days on which cameras recorded for < 10 hr (typically because of battery failure)

were discarded (n = 45). Nestling age for each nest was taken as the number of days since hatching

of the first nestling, and the number of nestlings in the nest was checked and recorded on each day

of recording. Provisioning rates and biomass provisioned (calculated as the average live mass of at

least five specimens of each prey taxa; van de Ven et al. 2019) to the nest were strongly linearly

correlated (Online Resources Fig. S1); but the relationship had R^2 = 0.57, and we were not always

able to identify prey delivered to nests. We therefore opted to use provisioning rate (i.e., number of

prey items delivered to the nest per day) in all further analyses as we were able to generate a larger

and more reliable dataset for this variable than for biomass provisioned.

Statistical analyses

All statistical analyses were conducted in the R statistical environment using R Studio (RStudio Team,

2016). For most analyses, we used linear modelling and the packages lme4 (Bates et al. 2019),

glmmADMB (Skaug et al. 2016), MuMIn (Barton 2010). General linear mixed models (GLMMs;

provisioning and nest success data) and linear mixed models (LMM; body mass and morphometric

data) were fitted by REML. Normality of model residuals was confirmed visually using Normal Q-Q

plots and binomial and count data models (i.e. provisioning rates) were checked for overdispersion.

We fitted global models including all potentially relevant predictor variables. We compared AICc

values for all nested models within the global models. Competing models within ΔAICc < 2.0 of the

top model were averaged, and model-averaged coefficients are presented. Statistical significance

was taken as $P < 0.05$ and data are presented as mean estimates ± 1 standard error (SE) unless

otherwise stated.

Two potential predictors of nest success, provisioning rate and nest temperature, were strongly

correlated with daily T_{max} (see results below; and Online Resources Table S1; Figs S2-3). Furthermore,

equipment failures meant we had incomplete datasets for nest temperature (n = 14 nests) and

provisioning rates (n = 7 nests) in our first two field seasons. To maximise sample sizes, we therefore

used only T_{max} in LMMs of female and nestling M_b and GLMMs of nest success – this allowed a

complete sample of n = 50 nests. One distinct advantage of using T_{max} is that this variable is used in

climate change projections and our analyses could therefore be used to parameterise models of the

impact of warming trends on our study species.

However, in order to investigate the impact of temperature-dependant changes in male behaviour on breeding outcomes, we were interested in the relative importance of direct effects of temperature on nestling growth versus effects mediated by changes in provisioning rate. We therefore additionally fitted an exploratory path model to a subset of data from our third field season (summer 2014/15) for which we had a complete dataset for provisioning and nest-box temperature (n = four nesting attempts including a total of nine nestlings, measured over 63 nestling-days; methods described in detail below).

Linear models: We analysed provisioning rate data separately for the period during which males were sole provisioners and the period after females left the nest and shared provisioning duties with males. We fitted GLMMs in glmmADMB (Skaug et al., 2016), with negative binomial error structure and variance = $\varphi\mu$. Global models included T_{max}, nestling age, brood size, cumulative rainfall in the two-months prior to nesting and ordinal date (with 1 Sept = "1") as predictors (the latter two variables were included as proxies for potential changes in prey availability in the environment), the log of the length of time the camera was present at the nest (10.03 - 14.88 hrs, mean =12.55 hrs) as an offset variable, and individual identity for male sole provisioning analysis (n = 45 observations on five males); and pair identity for male and female shared provisioning (n = 49 observations on seven pairs) as random terms. To better understand the potential impact of our small sample sizes for provisioning analyses, we additionally explored individual variation in the relationships between T_{max} and provisioning rates by fitting similar GLMs with individual or pair identity as fixed factors.

We used student's t-tests to compare female M_b upon nest entry, at nestling hatch and immediately prior to departing the nest between successful and failed nests (n = 13 females during 17 successful nesting attempts and 11 females during 13 failed nesting attempts). We included all females for which we were able to measure M_b within 5 days of nest entry, 5 days surrounding nestling hatch and 5 days before nest departure.

To test predictions concerning the relationships between T_{max} and diurnal M_b gain of females and nestlings, we fitted LMMs with Gaussian error structure and predictors T_{max}, nestling age, brood size (for both models) and female M_b at nest entry (for the model of female diurnal M_b gain); with individual identity nested within season for females and individual identity nested within brood identity and season (for nestlings) as random terms. Data were obtained from 13 females during 18 nesting attempts (n = 118 M_b data); and 44 nestlings during the same 18 nesting attempts (n = 306 M_b data). Female daily mean M_b and nestling growth curves were also derived from these data and are presented in the Online Resources (Figs S4-5, Tables S3-7), together with the analysis of male daily mean M_b from perch scale data (Fig. S6, Tables S8-9).

The influence of mean daily T_{max} between hatching of the first nestling and fledging of the last nestling per nest on fledgling M_b, tarsus length and age was assessed using LMMs with Gaussian error structure and individual and brood identity as random terms. Sample size was 19 successfully fledged chicks from 17 nests across three breeding seasons. The M_b and tarsus length data used in these analyses were the final measurements collected within 11 days before the nestlings fledged (mean 3.6 days before fledge, range 0-11, note that nestling growth generally reached an asymptote ~ 11 days before fledge, Online Resources Fig. S4).

Potential predictors of nest success (fledging at least one chick) were evaluated using four separate GLMMs with binomial error structure, each including one of the following predictors: (1) mean T_{max} during the nesting period (time between female entry and fledge of the last nestling / nest fail; for this analysis we also included data from twelve additional nests from the 2016/2017 and 2017/18 breeding seasons, during which dates of nest seal and success/failure of nests were recorded (total n = 55 nesting attempts by 19 females over five seasons) and (2) female M_b at nest entry (n = 30 nesting attempts by 19 females); and (3) nestling M_b (of the first hatched nestling in the brood) and (4) nestling age (of the first hatched nestling in the brood) at female departure (n = 23 nesting

attempts by 14 females). Predictor variables were strongly correlated; hence each was fitted

separately. Variation in sample sizes meant AICc values could not be compared between these

models.

Path analysis: To explore the relationships between T_{max}, nest temperature, provisioning rates,

nestling mass gain and nest success we fitted a Piecewise Structural Equation Model (SEM) to data

from the 2014-15 season, including nest and nestling ID as random effects. The analysis was

conducted using packages nlme (Pinheiro et al. 2019), lme4 (Bates et al. 2019), lavaan (Rosseel et al.

2018) and piecewiseSEM (Lefcheck 2016). We hypothesized the following:

H1: T_{max} negatively affects total provisioning rate and positively affects nest temperature.

H2: Total provisioning rate positively affects nestling mass gain.

H3: Nest temperature negatively affects nestling mass gain.

H4: Nestling mass gain positively affects fledging success (measured as successful or not).

Results

Provisioning rates

Three competing models for male provisioning rates were similarly supported (within ΔAICc = 2.0).

These included the predictors T_{max} (all three models), brood size, and nestling age (Online Resources;

Table S1). Model-averaged coefficients reveal male-only provisioning rates declined significantly

with increasing T_{max} (Table 1; Fig. S2) but neither nestling age nor brood size correlated significantly

with male provisioning rate (Table 1).

Table 1: Factors affecting daily provisioning rate by male Southern Yellow-billed hornbills alone *versus* by pairs following female departure from the nest. Model estimates are averaged across three competing models within ΔAICc = 2.0 for male provisioning alone and across five competing models within ΔAICc = 2.0 for male and female provisioning together.

Model	# competing models	Predictor	Estimate	Std. Error	Adjusted SE	Z value	p value
Male provisioning alone	3	**T_{max}**	**-0.04**	**0.01**	**0.02**	**2.70**	**0.007**
		Nestling age	-0.001	0.005	0.005	0.29	0.78
		Brood size	0.03	0.06	0.06	0.40	0.68
Pair provisioning together	5	**T_{max}**	**-0.05**	**0.01**	**0.01**	**-3.97**	**< 0.001**
		Nestling age	**-0.03**	**0.01**	**0.01**	**-5.27**	**< 0.001**
		Brood size	-0.16	0.13	0.13	1.22	0.22
		Rain	-0.01	0.01	0.01	1.81	0.07
		Ordinal date	0.01	0.004	0.004	1.14	0.25

N = 45 days of observations on five males and 49 days of observations on seven pairs. Significant results are highlighted in bold. Rain = cumulative rainfall in the two months prior to nesting.

The significant negative relationship between T_{max} and total provisioning rate remained after females left the nests and assisted males in provisioning nestlings. Five competing models for combined provisioning rates by both sexes were similarly supported, including T_{max} and nestling age (all five models), brood size, ordinal date and rain in the two-months prior to nesting (Table S2). Of these, only T_{max} and nestling age were significantly correlated with provisioning rate (Table 1; Online Resources Fig. S2).

Individual provisioning patterns

A single top model best explained variation in male provisioning rate, when male identity was included as a fixed factor (AICc = 353.9, df = 7, model weight = 0.557). This model included only the variables male identity and T_{max}. There was significant variation between males in individual

provisioning rates; but, controlling for this, provisioning rates declined significantly with T_{max} (-0.04 ± SE 0.01; z = -3.4; p =0.0006). The lack of an interaction term suggests the rate of decline was similar between the five individuals (Online Resources; Table S3; Fig. S3).

Three competing models for provisioning rate by pairs were similarly supported (within ΔAICc = 2.0), when pair identity was included as a fixed factor. These included pair identity, nestling age, T_{max}, and brood size (Online Resources; Table S4). Overall provisioning rates differed significantly between pairs, and there was a non-significant trend towards a decline with T_{max} (-0.04 ± SE 0.03, z = 1.44; p = 0.15; Online Resources; Table S5). The lack of an interaction term in the top model set suggests the rate of change in provisioning with T_{max} was similar across pairs.

Body mass change of adult females

Females that successfully fledged offspring were significantly heavier (239.5 ± SD 27.6 g, n = 15) when they entered the nests than unsuccessful females (216.3 ± SD 22.2 g, n = 17; t = 2.55, p = 0.02), and this difference in mass persisted until the time of nestling hatch (228.0 ± SD 21.4 g, n = 11 and 211.3 ± SD 11.4 g, n = 9 for successful and failed females respectively; t = 2.23 , p = 0.04). However, there was no significant difference in mass at nest exit of successful (191.6 ± SD 26.1 g, n = 15) and unsuccessful females (178.6 ± SD 19.3 g, n = 13; success vs fail; t = 1.30, p = 0.10). Females that failed to fledge any chicks lost a similar % M_b day^{-1} during their shorter nesting periods compared to successful females (successful nests: - 0.89 ± SD 0.66 g.day^{-1}, n = 15; failed nests: - 0.71 ± SD 0.91 g.day^{-1}, n = 13; t = -1.04, p = 0.31).

Female body mass

Diurnal M_b change among breeding females was best explained by a single model including the predictors T_{max} and brood size (AICc = -298.9, df = 6, model weight = 0.650). Female diurnal M_b gain decreased by 0.3 % M_b °C^{-1} with increasing T_{max}, and was positively correlated with brood size (both

results statistically significant; Table 2). Overnight female M_b loss averaged 3.5 ± 0.3 % (n = 101 observations of 13 females), whereas diurnal M_b gain averaged 0.7 ± 0.3 % (n = 118 observations of 13 females). Females therefore lost M_b throughout the period they spent in the nest, but rates of M_b loss were exacerbated by high T_{max}. The threshold T_{max} above which nest-bound females experienced zero diurnal M_b gain was 31.4 °C (Fig. 1A).

Table 2 Factors affecting diurnal M_b change of Southern Yellow-billed Hornbill females and nestlings. Model estimates are averaged across two competing models within ΔAICc = 2.0 for nestling mass change and are from a single best model for female mass change.

Model	# competing models	Predictor	Estimate	Std. Error	Adjusted SE	Z value	p value
Diurnal M_b change: females	1	T_{max}	**-0.27**	**0.09**		**-3.08**	**< 0.01**
		Brood size	**1.08**	**0.39**		**2.79**	**0.02**
Diurnal M_b change: nestlings	2	T_{max}	**-0.93**	**0.17**	**0.17**	**5.55**	**< 0.01**
		Nestling age	**-0.49**	**0.05**	**0.05**	**9.05**	**< 0.01**
		Brood size	-0.87	0.98	0.99	0.88	0.38

N = 118 observations on 18 nesting attempts of 13 females; and 306 observations on 44 nestlings across 16 nesting attempts. Significant results are highlighted in bold.
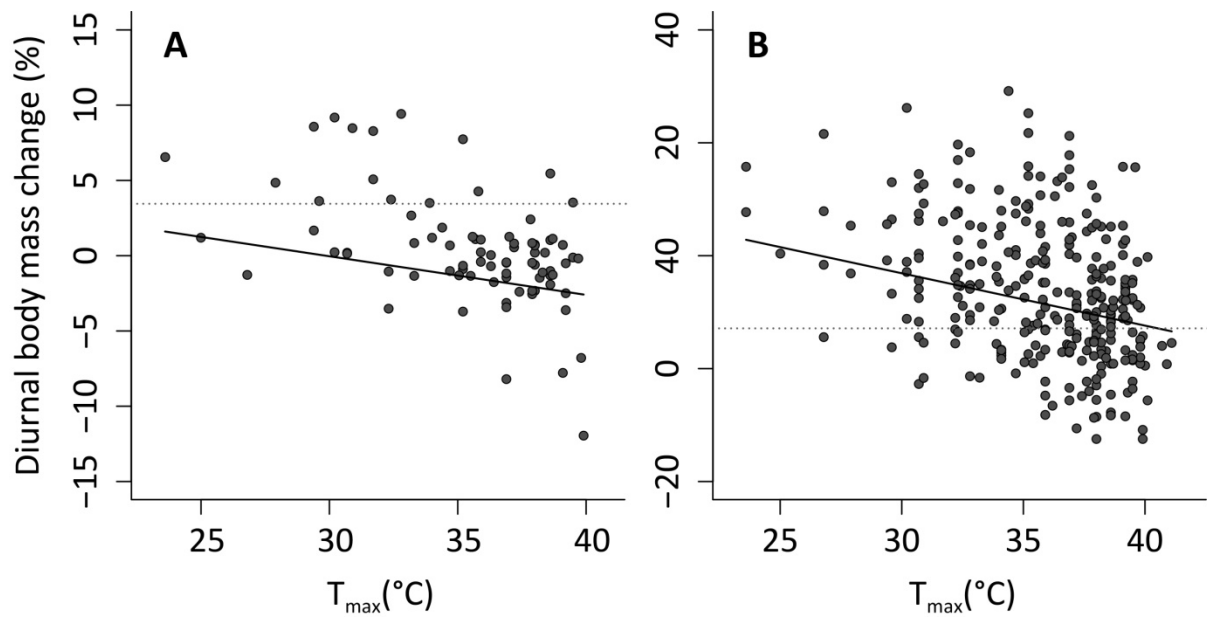
Figure 1: A) Diurnal M_b change (% of morning M_b) of female Southern Yellow-billed Hornbills decreased with increasing T_{max}. The solid line represents the prediction of a GLMM including the T_{max} and brood size; and random term individual identity nested within season. The dotted line represents the average overnight M_b loss of 3.5 %. N = 118 observations on 18 nesting attempts involving 13 females. B) Diurnal M_b change (%) of Southern Yellow-billed Hornbill nestlings as a function of T_{max}. The solid line represents the represents the prediction of a GLMM including T_{max} and nestling age; and individual identity nested within brood identity and season as random terms. The dotted line represents average overnight M_b loss of 7.1 %. N = 306 observations on 44 nestlings from 16 nesting attempts.

Nestling body mass

The best model for nestling diurnal M_b change contained the predictors T_{max}, chick age and brood size, with model weight = 0.596. A competing model within ΔAICc = 2.0 contained only T_{max} and nestling age (Online Resources; Table S12). Nestling diurnal M_b gain decreased by 0.93 % M_b °C^{-1} with increasing T_{max}, and daily fractional M_b gains decreased with nestling age (Table 2). Brood size did not significantly affect M_b gain (Table 2, Fig. 2B). Overnight mass loss by nestlings averaged 7.1 ± 0.5

% (n = 227 observations of 44 nestlings) and nestlings experienced net 24-hr M_b loss when T_{max} exceeded 40.6 °C (Fig. 1B).
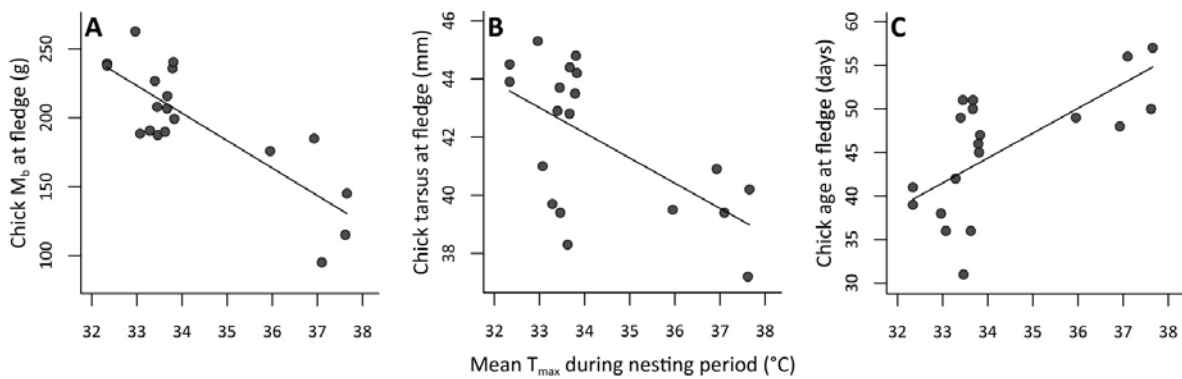

Figure 2: Southern Yellow-billed Hornbill body mass (M_b) (A), tarsus length (B) and age (C) at fledging as a function of mean T_{max} during the nesting period. N = 19 successfully fledged chicks from 17 nesting attempts across three breeding seasons. The solid lines represent the predicted relationships from a model with the fixed factor mean T_{max} during the nestling period (hatch to fledge), and individual identity, brood identity and season as random terms.

Structural development at fledging

Negative effects of T_{max} on nestling M_b gain carried through to fledging: high mean T_{max} across the nesting period correlated with substantial reductions in structural development of nestlings that survived to fledge (n = 19 individuals). For every 1 °C increase in mean T_{max} during the nesting period, fledging M_b (measured within 11 days prior to fledging) decreased by ~20 g (LMM estimate: -19.95 g ± 3.41 g, t = -5.86, p < 0.001; Fig. 2A); tarsus length decreased by ~0.9 mm (LMM estimate: -0.87 mm ± 0.27 mm, t = -3.18, p = 0.006; Fig. 2B); and age at fledge increased by 2.6 days (LMM estimate: 2.61 d ± 0.74 d, t = 3.53, p = 0.003; Fig. 2C).

Of the 19 hornbill chicks that fledged successfully, three were known to be depredated on the day of fledging and remains were found nearby the nest. These chicks experienced T_{max} = 37.5 ± 0.3 °C during the nesting period and fledged with M_b (118.3 ± SD 25.1 g) far below average, as well as

17

reduced tarsus length (38.9 ± SD 1.6 mm). It seems possible they had not reached sufficient structural development at the time of fledge to be able to escape from predators.

Probability of nest success

The probability of successful fledge was strongly negatively related to mean T_{max} during the nesting period (GLMM est. -0.55 ± 0.27, p = 0.04), decreasing below 50 % when mean T_{max} > 35.1 °C (Figure 3). Probability of nest success was also related to female M_b on nest entry (GLMM est. 0.08 ± 0.03, p = 0.01); and nestling mass (GLMM est. 0.03 ± 0.01, p = 0.01) and age (GLMM est. 0.15 ± 0.05, p = 0.01) at female nest departure (Online Resources Fig. S9).
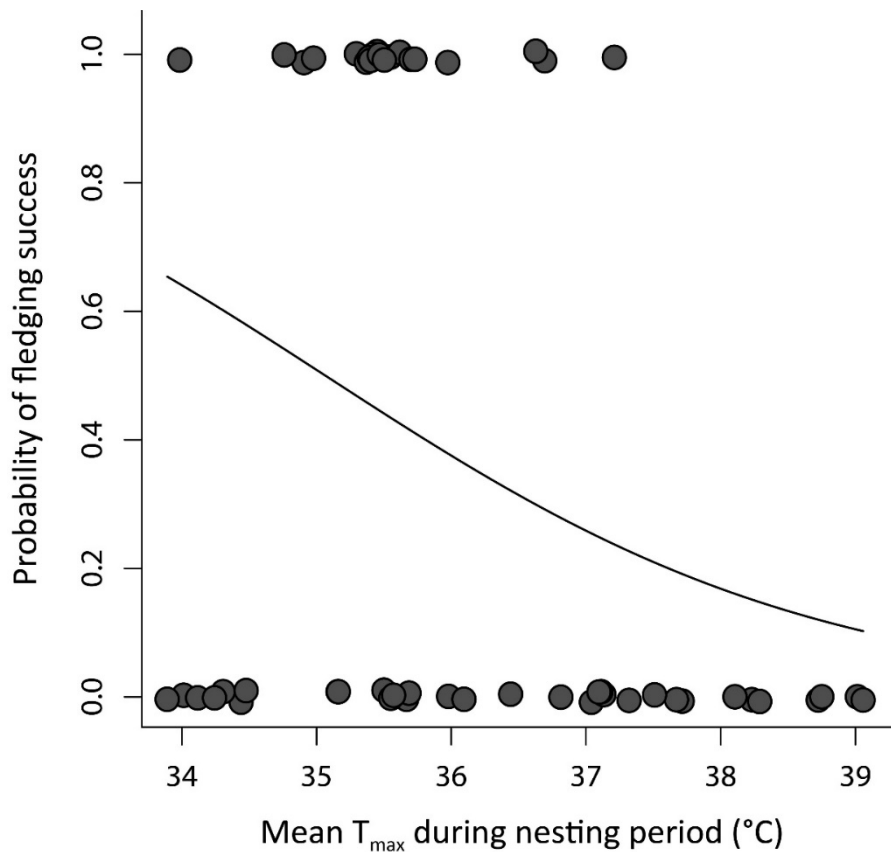
Figure 3: Probability of fledging success in Southern Yellow-billed Hornbills as a function of mean T_{max} during the entire nesting period. N = 55 nesting attempts across five seasons. The solid line represents the prediction from a model with a binomial distribution and season as a random term.

Path model

An exploratory piecewise Structural Equation Model of the relationships between T_{max}, provisioning rate, nest temperature, nestling daily mass gain (measured over 63 nestling-days), and nest success for nine nestlings (four nests) showed that all our hypothesised unidirectional relationships were statistically significant (Figure 4), corroborating the results of our GLMMs and LMMs. T_{max} correlated positively with nest temperature (standardised effect size: 0.912, p-value < 0.0001), and negatively with provisioning rate (standardised effect size: -0.267, p-value < 0.001). Nest temperature correlated negatively and provisioning rate positively with nestling mass gain: (standardised effect sizes: -0.279, p-value = 0.03 and 0.383, p-value = 0.02, respectively). Nestling mass gain was a significant predictor of nest success (unstandardised effect size: 0.132, p-value < 0.01; standardised binomial effects could not be calculated in PiecewiseSEM). The standardised indirect effect of T_{max} on nestling mass gain via provisioning rate was $- 0.103$ ($= - 0.267$ x 0.383); while the standardised indirect effect of T_{max} via via nest temperature was $- 0.255$ ($= 0.912$ x $- 0.279$). The total indirect effect of T_{max} was therefore negative and equal to $- 0.357$ ($= - 0.103 - 0.255$). The impact of T_{max} on nestling growth was more prominent via nest temperature (~71 % of the total indirect effect) than via total provisioning rate (~29 % of the total indirect effect); although both were statistically significant. Overall, the model fit the data adequately ($\chi 2$ = 15.179, p-value = 0.126).

Directed separation tests confirmed all the excluded paths were not statistically significant (T_{max} → nest success; provisioning rate →nest temperature; provisioning rate →nest success; nest temperature →nest success; all p-values > 0.20) except the direct effect of T_{max} on nestling mass gain (unstandardised effect size: 2.153, p = 0.023). However, this direct effect is naturally observed via the nest temperature since the nestlings never leave the nest cavity before fledging; suggesting there might be an additional indirect effect of T_{max} that we were unable to measure (e.g. via female decision-making with regard to partitioning provisioned food to self versus nestlings); or for which

we had insufficient data to include in the model (e.g. via exacerbated rates of female mass loss at high T_{max} causing females to leave nests earlier).
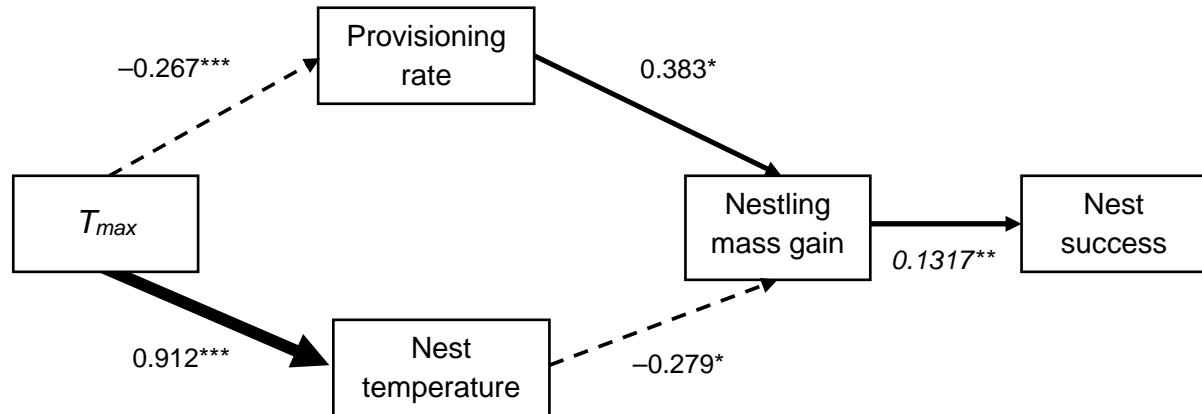

Figure 4: Piecewise SEM model of nest success. Arrows represent the hypothesized unidirectional relationships between observed variables. Estimated parameter values are provided over the arrows representing the paths. All represent standardized effect sizes; except for the relationship between nestling mass gain and nest success (in italics); the standardised binomial effect could not be calculated in *piecewiseSEM* (Leftcheck et al. 2018) and the unstandardised effect is presented. Solid lines indicate positive effects, dashed lines indicate negative effects. Arrow widths relate to the strength of the relationships based on standardised effect sizes. Asterisks indicate the level of significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. N = 63 observation days of 9 nestlings in 4 nests; df = 10; χ^2 : 15.18 (p-value: 0.13); AIC: 47.18.

Discussion

High air temperatures during nesting negatively affected hornbill breeding attempts, correlating with reduced provisioning rates, increased rates of mass loss by breeding females, reduced nestling growth and decreased fledging success. An exploratory path analysis suggested daily nestling mass gain was a positive predictor of fledging success; and that the effect of daily T_{max} on nestling mass gain was mediated most strongly via its influence on nest temperature, but also via its negative

relationship with provisioning rate. Overall, the likelihood of any given nesting attempt resulting in successful fledging of at least one chick was strongly dependant on mean T_{max} during the nesting period, and was below 50% when mean $T_{max} > 35.1$ °C. Breeding success was also linked to nestling age and mass at the time of female departure from the nest, and female mass at nest entry: heavier females that stayed longer in nests were more likely to successfully fledge at least one chick. Nestlings that did fledge after experiencing sustained hot weather in the nest were dramatically lighter than those which fledged during cooler conditions: those fledging after the hottest nesting periods in this study (mean $T_{max} > 37$°C) were ~ 50% lighter than those fledging after the coolest nesting periods (mean $T_{max} < 33$°C). These findings indicate that temperature exerts a strong influence on nesting success, arising largely via direct (presumably physiological) costs of exposure to high nest temperatures but also via behavioural trade-offs faced by breeding males (van de Ven et al. 2019) and the consequences thereof for nest provisioning. During periods of high T_a, low provisioning rates would have left females and nestlings dehydrated as well as facing energy shortfalls. Mismatches between water requirements for evaporative cooling (which will necessarily increase with increasing nest temperature) and water supplied via provisioned food items (which decreased with increasing T_a) could therefore have exacerbated the strong impacts of high nest temperatures on nestling growth via dehydration and the physiological performance costs of hyperthermia (Hochachka and Somero 1984; Angilletta et al. 2010). They could thus increase the likelihood of females abandoning nesting attempts by cannibalising young and then leaving the nest, or leaving the nest early when nestlings are too small to reach food provisioned to them or properly reseal the nest entrance (TMVDV unpub. data).

We documented large effect sizes for negative impacts of high T_{max} on breeding outcomes, despite small sample sizes. Our overall sample was 50 nesting attempts over three breeding seasons, but for many analyses, data were available from only a subset of these. Most notably, we had reliable nest

camera data from only one season (2014/15); from nesting attempts by only seven pairs of birds. This seriously restricted the available sample size for provisioning rate and the exploratory path analyses, so these results should be treated cautiously. We were unable to fit effects of T_{max} mediated via female body mass change and duration of nest tenure into our piecewise SEM because of sample size limitations. However, examination of individual-level effects for provisioning rates suggest the pattern of decline in provisioning with increased T_{max} was very consistent among individuals, especially for males provisioning alone (this period makes up most of the nesting period, including the time when nestlings are growing fastest; Figure S5 and S8). Furthermore, our results are consistent with a growing number of studies suggesting strong temperature-dependence of breeding success and offspring quality during hot periods among birds (Cunningham et al. 2013; Salaberria et al. 2014; Catry et al. 2015; Wiley and Ridley 2016) and mammals (e.g. Woodroffe et al. 2017; Paniw et al 2019; van de Ven et al 2020).

Our concurrent study of the behaviour of breeding male hornbills in this population showed that the thermoregulatory behaviours of shade-seeking and panting (gaping the beak to facilitate respiratory evaporative water loss) both correlated with reduced foraging intake. This effect was particularly strong for panting: foraging efficiency declined by > 90% in males attempting to forage and pant simultaneously (van de Ven et al. 2019); presumably due to mechanical constraints on using the bill for both panting and prey capture (see also du Plessis et al. 2012). Dramatic reductions in male hornbill foraging success associated with behavioural trade-offs between foraging and thermoregulation are therefore likely responsible for the declines in provisioning rate at high T_{max} that we document here.

Hornbill breeding is unusual in that the burden of provisioning falls entirely on a single parent for the majority of the nesting attempt. This extreme asymmetry probably makes this species' breeding attempts particularly sensitive to the behavioural costs of keeping cool incurred by males during hot

22

weather, as well as to heat exposure of females and nestlings in the confined nest environment. In taxa where both members of a pair help provision offspring, or which breed co-operatively, costs may be buffered during hot periods if additional individuals are able to supplement declining provisioning rates, or otherwise share the costs of breeding (e.g. shading nests, AlRashidi et al. 2010). Alternatively, load-lightening by helpers in co-operative breeding groups (Crick 1992) could allow the breeding pair to reduce parental effort during hot periods and thus maintain their own M_b, as is the case in Southern Pied Babblers (Wiley and Ridley 2016). We therefore predict co-operative breeders may show lower effect sizes in terms of costs of breeding for adult individuals (e.g. in birds, Wiley and Ridley 2016) or in terms of lower offspring growth and breeding success during hot weather (e.g. in mammals, van de Ven et al. 2020).

A limitation of our study was that we collected data on M_b and nestling growth from hornbills breeding in nest-boxes, rather than natural cavities. Nest-box temperatures closely tracked outside T_a, and differed substantially from temperatures of two occupied natural cavities at the study site (N = 14 boxes and 2 natural cavities; relationship between nest temperature and air temperature: boxes 0.77 ± 0.01, R2 = 0.89, p < 0.001; natural cavities 0.35 ± 0.03, R2 = 0.50, p < 0.001; Online Resources Fig S4). The higher nest temperatures in nest-boxes, together with the significant direct effect of nest temperature on offspring growth, suggests that the impact of hot weather for birds breeding in boxes should have been more severe than for birds breeding in natural cavities. Forty percent of breeding attempts in nest-boxes during our study successfully fledged one or more chicks (N= 43 breeding attempts); compared with 57% of breeding attempts in natural cavities (N = 7 breeding attempts). However, we were unable to detect a significant difference in success between natural cavities and nest-boxes, likely due to the low number of natural nests we found (n = 7 natural nests; Fisher exact test: 95 % CI = 0.06 – 3.35, odds ratio = 0.50, p = 0.43). Artificial nest-boxes are often provided to cavity-nesting birds to aid in conservation efforts (James et al. 2011;

Pasuwan et al. 2011), but poorly thermally-buffered boxes could expose them to elevated thermal risk (Ardia et al. 2006; Butler et al. 2009). Thermal buffering associated with natural cavities could help mitigate direct effects of nest temperature on nestling growth and improve nest outcomes, suggesting conservation of cavity-bearing older trees is extremely important; though they would presumably not affect the trade-offs determining provisioning rates by males or the consequent temperature-dependence of food (and therefore water) supply to nests.

The southern Kalahari, where we collected data for our study, has warmed rapidly in recent decades (Kruger and Sekele 2012; van Wilgen et al. 2016) and is projected to warm by a further 4 - 5 °C by the end of the century under business-as-usual emissions scenarios (Engelbrecht et al. 2015). Sublethal costs of keeping cool, including loss of body condition (du Plessis et al 2012, van de Ven et al 2019), production of poor-quality offspring and breeding failure (this study, Cunningham et al. 2013, Oswald et al 2008, Salaberria et al 2014, Catry et al. 2015, Wiley & Ridley 2016, Woodroffe et al. 2017, Paniw et al. 2019) are likely to become issues of serious conservation concern globally as climate change progresses, even for species that, like Southern Yellow-billed Hornbills, are currently common and widespread. Low quality individuals produced during hot breeding periods may be vulnerable to carry-over effects with the potential to reduce their lifetime fitness; including poor juvenile survival and poor subsequent breeding success (Metcalfe & Monaghan, 2001; Greño et al., 2008; Catry et al., 2015). For example, in our study, female M_b on nest entry was a significant predictor of nesting success. Small females that suffered hot conditions as nestlings may therefore be unlikely to breed successfully as adults, if they are unable to make up for lost nestling growth after fledging. As climate change advances, we can expect increasing numbers of individuals within arid-zone animal populations to have suffered adverse conditions early in development, potentially leading to weakening of these populations via such carry-over effects on fitness.

In long-lived species like hornbills, the costs of breeding during hot conditions have presumably resulted in strong selection for individuals to skip breeding altogether in unusually hot years. However, this could become maladaptive under strong warming trends, as animals postpone breeding to a 'cool' year that never comes. Indeed, for hornbills at our study site, the threshold temperature above which the likelihood of nest success is reduced below 50% (35.1 °C) is now regularly exceeded and the proportion of nest-boxes used each year has declined steadily since records began in 2008; with some established hornbill pairs electing not to breed in multiple consecutive years (authors' unpublished data). Sublethal costs of high temperatures therefore should not be overlooked as a potential driver of population decline under climate change (Conradie et al. 2019). Operating across multiple species, such costs could cause collapses of animal communities, like that recently documented for desert birds in the Mojave Desert (Iknayan and Beissinger 2018), even before temperatures begin to regularly exceed lethal limits for individuals.

Conflict of interest: The authors declare they have no conflict of interest.

References

AlRashidi M, Kosztolányi A, Küpper C, et al (2010) The influence of a hot environment on parental
cooperation of a ground-nesting shorebird, the Kentish plover *Charadrius alexandrinus*. Front
Zool 7:1.

Angilletta MJ, Cooper BS, Schuler MS, Boyles JG (2010) The evolution of thermal physiology in
endotherms. Front Biosci E2:861–881.

Ardia DR, Pérez JH, Clotfelter ED (2006) Nest box orientation affects internal temperature and nest
site selection by Tree Swallows. J. F. Ornithol. 77:339–344

Barton K (2010) MuMIn: Multi-model inference. R package version 0.13.14.

Bates D, Maechler M, Bolker B (2019) Linear mixed-effects models using "Eigen" and S4. R package
version 1.1.21

Braasch A, Schauroth C, Becker PH (2009) Post-fledging body mass as a determinant of subadult
survival in Common Terns *Sterna hirundo*. J Ornithol 150:401–407.

Butler MW, Whitman BA, Dufty AM (2009) Nest box temperature and hatching success of American
kestrels varies with nest box orientation. Wilson J Ornithol 121:778–782.

Carroll JM, Davis CA, Elmore RD, et al (2015) Thermal patterns constrain diurnal behavior of a
ground-dwelling bird. Ecosphere 6:1–15.

Catry I, Catry T, Patto P, et al (2015) Differential heat tolerance in nestlings suggests sympatric

species may face different climate change risks. Clim Res 66:13–24.

Clutton-Brock TH, Maccoll A, Chadwick P, et al (1999) Reproduction and survival of suricates

(*Suricata suricatta*) in the southern Kalahari. Afr J Ecol 37:69–80.

Coe BH, Beck ML, Chin SY, et al (2015) Local variation in weather conditions influences incubation

behavior and temperature in a passerine bird. J Avian Biol 46:385–394.

Conradie SR, Woodborne SM, Cunningham SJ, McKechnie AE (2019) Chronic, sublethal effects of

high temperatures will cause severe declines in southern African arid-zone birds during the

21st century. Proc Natl Acad Sci U S A 116:14065–14070.

Crick HQP (1992) Load-lightening in cooperatively breeding birds and the cost of reproduction. Ibis

134:56–61

Cunningham SJ, Martin RO, Hojem CL, Hockey PAR (2013) Temperatures in excess of critical

thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: a study of

common fiscals. PLoS One 8:e74613.

du Plessis KL, Martin RO, Hockey PAR, et al (2012) The costs of keeping cool in a warming world:

Implications of high temperatures for foraging, thermoregulation and body condition of an

arid-zone bird. Glob Chang Biol 18:3063–3070.

Dunn PO, Winkler DW (1999) Climate change has affected the breeding date of tree swallows

throughout North America. Proc R Soc B Biol Sci 266:2487–2490.

Dunn PO, Winkler DW (2010) Effects of climate change on timing of breeding and reproductive

success in birds. In: Moller AP, Fiedler W, Berthold P (eds) Effects of Climate Change on Birds.

Oxford University Press, pp 113–126

Dybala KE, Eadie JM, Gardali T, et al (2013) Projecting demographic responses to climate change: Adult and juvenile survival respond differently to direct and indirect effects of weather in a passerine population. Glob Chang Biol 19:2688–2697.

Engelbrecht F, Adegoke J, Bopape M-J, et al (2015) Projections of rapidly rising surface temperatures over Africa under low mitigation. Environ Res Lett 10:85004.

Green DJ, Cockburn A (2001) Post-fledging care, philopatry and recruitment in brown thornbills. J Anim Ecol 70:505–514.

Greño JL, Belda EJ, Barba E (2008) Influence of temperatures during the nestling period on post-fledging survival of great tit *Parus major* in a Mediterranean habitat. J Avian Biol 39:41–49.

Hochachka PW, Somero GN (1984) Biochemical Adaptation. Princeton University Press

Iknayan KJ, Beissinger SR (2018) Collapse of a desert bird community over the past century driven by climate change. Proc Natl Acad Sci U S A. 115:8597–8602.

James D, Bachan A, Kannan R (2011) Installation of artificial nest cavities for the endangered great hornbill: a pilot study in southern India. Raffles Bull Zool 24:73–76

Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proc Natl Acad Sci U S A 106:3835–40.

Kemp AC (1995) The Hornbills : Bucerotiformes. Oxford University Press

Kruger AC, Sekele SS (2012) Trends in extreme temperature indices in South Africa: 1962-2009. Int J Climatol 33:661–676.

Lefcheck JS (2016) piecewiseSEM : Piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods Ecol Evol 7:573–579.

McCarty JP, Winkler DW (1999) Relative importance of environmental variables in determining the growth of nestling tree swallows *Tachycineta bicolor.* Ibis 141:286–296

Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? Trends Ecol Evol 16:254–260.

Moreau RE (1937) The comparative breeding biology of the African hornbills (Bucerotidæ). Proc Zool Soc London 107 A:331–346.

Moreau RE, Moreau WM (1941) Breeding biology of silvery-cheeked hornbill. Auk 58:13–27.

Oswald SA, Bearhop S, Furness RW, et al (2008) Heat stress in a high-latitude seabird: effects of temperature and food supply on bathing and nest attendance of great skuas *Catharacta skua*. J Avian Biol 39:163–169.

Paniw M, Maag N, Cozzi G, et al (2019) Life history responses of meerkats to seasonal changes in extreme environments. Science 363:631–635.

Pasuwan C, Pattanakiat S, Navanugraha C, et al (2011) An assessment on artificial nest construction for hornbills in Budo Sungai Padi National Park, Thailand. Raffles Bull Zool 24:85–93

Pinheiro J, Bates D, DebRoy S, et al (2019) nlme: Linear and Nonlinear Mixed Effects Models

Reid JM, Monaghan P, Ruxton GD (2000) Resource allocation between reproductive phases: The importance of thermal conditions in determining the cost of incubation. Proc R Soc B Biol Sci 267:37–41.

Rosseel Y, Jorgensen T, Oberski D, et al (2018) lavaan: Latant Variable Analysis. R package version 0.6.3

Salaberria C, Celis P, López-Rull I, Gil D (2014) Effects of temperature and nest heat exposure on

nestling growth, dehydration and survival in a Mediterranean hole-nesting passerine. Ibis 156:265–275.

Sears MW, Raskin E, Angilletta MJ (2011) The world is not flat: defining relevant thermal landscapes in the context of climate change. Integr Comp Biol 51:666–75.

Sinervo B, Méndez-de-la-Cruz F, Miles DB, et al (2010) Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894–9.

Skaug H, Fourmier D, Nielson A, et al (2016) glmmADMB: generalized linear mixed models using AD Model Builder. R package version 0.8.3.3.

Stanback M, Richardson DS, Boix-Hinzen C, Mendelsohn J (2002) Genetic monogamy in Monteiro's hornbill, *Tockus monteiri*. Anim Behav 63:787–793.

Tieleman BI, Noordwijk HJVAN, Williams JB (2008) Nest site selection in a hot desert: trade-off between microclimate and predation risk? Condor 110:116–124.

van de Ven TMFN, McKechnie AE, Cunningham SJ (2019) The costs of keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. Oecologia 191:205–215.

van de Ven TMFN, Fuller A, Clutton-Brock TH (2020) Effects of climate change on pup growth and survival in a cooperative mammal, the meerkat. Func Ecol 34: 194–202.

van Wilgen NJ, Goodall V, Holness S, et al (2016) Rising temperatures and changing rainfall patterns in South Africa's national parks. Int J Climatol 36:706–721.

Wiley EM, Ridley AR (2016) The effects of temperature on offspring provisioning in a cooperative breeder. Anim Behav 117:187–195.

Woodroffe R, Groom R, Mcnutt JW (2017) Hot dogs: High ambient temperatures impact

reproductive success in a tropical carnivore. J Anim Ecol 86:1329–1338.