The costs of keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird

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Behavioral thermoregulation can carry fitness costs & may not buffer animals against climate change. This has implications for conservation & selective pressures faced by animals in hot places.

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Abstract

Avian responses to high environmental temperatures include retreating to cooler microsites and/or increasing rates of evaporative heat dissipation via panting, both of which may affect foraging success. We hypothesized that behavioural trade-offs constrain the maintenance of avian body condition in hot environments, and tested predictions arising from this hypothesis for male Southern Yellow-billed Hornbills (*Tockus leucomelas*) breeding in the Kalahari Desert. Operative temperatures experienced by the hornbills varied by up to 13 °C among four microsite categories used by foraging males. Lower prey capture rates while panting and reductions associated with the occupancy of off-ground microsites, resulted in sharp declines in foraging efficiency during hot weather. Consequently, male body mass (M_b) gain between sunrise and sunset decreased with increasing daily maximum air temperature (T_{max}), from ~ 5 % when $T_{max} < 25$ °C to zero when $T_{max} = 38.4$ °C. Overnight M_b loss averaged ~ 4.5 % irrespective of T_{max}, creating a situation where nett 24-hr M_b loss approached 5 % on extremely hot days. These findings support the notion that temperature is a major determinant of body condition for arid-zone birds. Moreover, the strong temperature-dependence of foraging success and body condition among male hornbills provisioning nests raises the possibility that male behavioural trade-offs translate into equally strong effects of hot weather on female condition and nest success. Our results also reveal how rapid anthropogenic climate change is likely to substantially decrease the probability of arid-zone birds like hornbills being able to successfully provision nests while maintaining their own condition.

Introduction

Behaviours such as retreating to thermally-buffered microsites and reducing activity levels mitigate thermoregulatory costs in hot environments, in particular water and energy requirements for evaporative cooling among diurnal species (Carroll et al. 2015; Martin et al. 2015; Scheffers et al. 2014), and have been suggested to buffer fitness impacts of high temperatures (Carroll et al. 2015; Kearney et al. 2009; Sears et al. 2011). However, these behavioural responses to high environmental temperatures may themselves impact fitness, as even small changes in activity patterns can induce trade-offs affecting foraging, reproduction and territoriality (Sinervo et al. 2010; Visser 2008; Wuethrich 2000). In the context of avian reproduction, high air temperatures (T_as) can drive trade-offs between thermoregulation and incubation effort (AlRashidi et al. 2010), nest site location (Tieleman et al. 2008) and provisioning effort (Cunningham et al. 2013; Wiley and Ridley 2016; Winkler et al. 2002).

Two widespread avian responses to hot weather which have potential to drive consequential behavioural trade-offs are: panting, the forced ventilation of the respiratory tract to increase rates of evaporative heat dissipation (Dawson 1982); and changes in microsite use such as a switch from sunlit to shaded foraging locations (e.g., Clark 1987). Panting resulted in significantly decreased foraging efficiency during hot weather in a desert-dwelling population of Southern Pied Babblers (*Turdoides bicolor*, du Plessis et al. 2012). In breeding Common Fiscals (*Lanius collaris*), prey capture rates were halved when birds switched from sunlit to shaded foraging perches (Cunningham et al. 2015). In general, however, few studies have focused on the association between thermoregulatory behaviour and foraging efficiency, and how the interplay between these factors is affected by T_a (but see Bacigalupe et al. 2003; Cunningham et al. 2015; Hetem et al. 2012; Mason et al. 2017).

Behavioural responses to high environmental temperatures are constrained by the thermal landscapes in which organisms operate, with the heterogeneity of thermal landscapes

and the range of microclimates potentially available to organisms strongly related to topography and vegetation structure (Rosenberg et al. 1983; Sears et al. 2011; Suggitt et al. 2011). The value of a particular microsite as a thermal refuge is affected by factors such as exposure to solar radiation and height above the ground (Camacho et al. 2015; Seymour and Dean 2010; Wolf and Walsberg 1996). Operative temperature [T_e; an integrated measure of temperature incorporating radiative, convective and conductive heat fluxes (Bakken 1976; Robinson et al. 1976)] can vary by as much as 15 − 20 °C between sunlit and shaded sites for small species, such that even small changes in a birds' location in the landscape can have large consequences for physiological (energy and especially water) costs of thermoregulation (Carroll et al. 2015; Wolf and Walsberg 1996). As a consequence, many small desert birds spend the hottest part of the day resting in the coolest microsites they can find, such as tree crevices (Wolf and Walsberg 1996) and, more rarely, burrows dug by other animals (Williams et al. 1999; A.R. Bourne *pers. comm.*).

Changes in behaviour with increasing temperature and the associated selective use of microsites within thermal landscapes might therefore drive many aspects of the behavioural ecology of arid-zone birds. Linking microsite use, panting behaviour, time-activity budgets and foraging success in response to the thermal landscape can reveal the costs and benefits of using thermal refugia in physiologically challenging environments for endotherms as well as ectotherms (Bennett et al. 1984; Oswald and Arnold 2012; van Beest et al. 2012). Therefore, understanding fine-scale landscape use by animals provides information on current microsite quality and both behavioural and physiological consequences of changes in microsite use, and can be used to model sensitivity of species to climate change (Angilletta et al. 2010; Hovick et al. 2014; Sears et al. 2011; Suggitt et al. 2011).

We hypothesized that temperature-dependent behavioural trade-offs involving foraging and thermoregulation constrain the maintenance of avian body condition in hot environments. To test this hypothesis, we investigated the temperature-dependence of

behavioural decisions and microsite use in breeding male Southern Yellow-Billed Hornbills (*Tockus leucomelas*), a species widespread in southern Africa. Hornbills (Bucerotidae) are thought to be particularly vulnerable to hot weather while breeding on account of their unusual breeding system whereby the female seals herself in the nest cavity as a protective mechanism against predators (Kemp and Woodcock 1995; Moreau and Moreau 1941; Witmer 1993). During incubation and part of the nestling period females are confined to the nest and males are solely responsible for the provision of food to the females and chicks (Klaassen et al. 2003). This extreme asymmetry in breeding effort makes male hornbills an excellent model for testing hypotheses concerning mechanistic links between temperature and body condition.

We tested four predictions arising from our hypothesized mechanistic link between temperature, behaviour and body condition, using repeated measurements of body mass as a proxy for short-term variation in condition among breeding adult male Southern Yellow-billed Hornbills (hereafter, hornbills). First, we predicted that high air temperatures (T_a) are associated with reductions in foraging effort, which we tested by quantifying time allocation to foraging as a function of T_a. Second, we predicted that male hornbills spend more time in cooler microsites during periods of high T_a, and tested this prediction by quantifying T_e in various microsite categories and the time spent by males in each as a function of T_a. Third, we predicted that increased time spent in cooler microsites and/or engaged in panting during hot weather results in reduced foraging efficiency (i.e., food intake per unit time foraging), which we quantified as prey capture rates. Finally, we predicted these temperature-dependent shifts in behaviour are associated with progressive body mass loss during hot weather.

Materials and methods

Study site and population

Our study population consisted of breeding male Southern Yellow-billed Hornbills in the 33-km^2 Kuruman River Reserve (KRR) in the southern Kalahari Desert, South Africa (26°58' S, 21°49' E). Habitats at KRR include dunefield and dry riverbeds supporting typical sparsely-treed Kalahari arid savanna vegetation (described by (Clutton-Brock et al. 1999). Mean annual rainfall in the area is 186.2 ± SD 87.5 mm, falling mostly during the austral summer (Dec − Mar), and mean daily summer maximum air temperatures (T_{max}) are 34.2 ± 9.7 °C (mean ± SD, data for 1995 − 2015, Van Zylsrus weather station ~30 km from KRR, South African Weather Service). A weather station placed at the study site (Vantage Pro2, Davis Instruments, Hayward, U.S.A.) recorded air temperature (T_a; °C), wind speed (m s^{-1}), rainfall (mm) and solar radiation (W m^{-2}) and dewpoint (°C) at 10-min intervals throughout the study period.

Our study took place over three austral summers (October to March) between 2012 and 2015, during the hornbills' breeding season. During breeding, male hornbills are central place foragers (in proximity to the location of the nest) and thus easy to locate for observation. Hornbills in this study population are generally single-brooded, lay clutches of 3-5 eggs and show strong hatching asynchrony and brood reduction (T.M.F.N. van de Ven *unpubl. data*). All data for this study were collected from breeding males whose female partners and / or offspring were sealed within nests.

Operative temperature

We quantified variation in the hornbills' thermal landscape using black globe thermometers (hereafter, 'blackbulbs') each comprising two copper half-spheres (60 mm diameter, approximating mean adult male hornbill thoracic depth) enclosing a Thermochron iButton^{TM} (DS1923, Maxim, Sunnyvale, CA, USA), sealed together with cyanoacrylate adhesive and spray-painted matt black (Bakken 1980; Carroll et al. 2015). These were deployed at the start of the study and logged temperature at 5-min intervals during all three study seasons. Three

replicate blackbulbs were placed at each height (ground, 0-1 m, 1-3 m, > 3m) and exposure category (exposed to the sun, dappled, and fully shaded) in microsites representative of locations used by birds during focal observations. Blackbulb temperatures were compared to T_e measured using two hornbill taxidermic models each made of a hollow copper spheroid and copper sheeting shaped to resemble the hornbill body shape, enclosing an iButton and covered with a hornbill skin (following Wathes and Clark 1981; additional details in Online Resources). We positioned three blackbulb replicas together with the two taxidermic models (facing north) at locations representative of our original 12 microsite categories over a period of 2 - 3 days per microsite category. During this time, iButtons within taxidermic models and blackbulbs and the onsite weather station were all programmed to log temperature at 1-min intervals. In order to standardise field conditions, comparisons were made over a range of air temperatures between 20 and 40 °C on clear days only (solar radiation > 600 $W.m^{-2}$, n = 27) and at a low wind speed (< 5 $m.s^{-1}$), since low solar radiation (< 600 $W.m^{-2}$) and high wind speeds (> 5 $m.s^{-1}$) were rare during the study period (1.5 % and 4.7% of days, respectively).

We fitted linear regressions of taxidermic model T_e as a function of blackbulb data (Online Resources, Fig. S2) and found that blackbulb temperature accounted for > 95 % of variation in taxidermic model T_e in all microsites. Taxidermic model T_e were estimated from blackbulb data collected throughout the study period using these regression equations (see Fig S2). These calibrated T_e data were used in all analyses of microsite temperatures.

Based on the observed variation in T_e among the 12 initial microsite categories and the sample sizes in our behavioural data set, we opted to include four broad microsite categories in our analyses: on-ground shade, off-ground shade, on-ground sun, off-ground sun.

Behavioural observations

Over the course of the three breeding seasons during our study, we obtained 204 behavioural observations from 12 male hornbills engaged in 17 breeding attempts. Behavioural data were

collected during ~30-min (31.1 ± 4.4 min; range 21.2 – 48.5 min) continuous focal observation sessions (hereafter 'focals'), conducted at a randomly selected time within each of three diurnal periods: morning (sunrise – 10h59; n = 82 focals on 13 males), midday (11h00 – 14h59; n = 64 focals on 11 males) and afternoon (15h00 – sunset; n = 58 focals on 10 males). If we lost sight of a bird for longer than 5 min during a focal, the focal was abandoned and a new focal commenced once the bird was relocated. Focal data were recorded using a digital voice recorder (ICR-FP550, SANYO Electric Co., Osaka, Japan) and transcribed with a PDA (Trimble Juno 3D, Trimble Navigation Limited, Westminster, U.S.A.) into a custom-built database using Cybertracker software (CyberTracker 3.372).

During focals, the microsite occupied by the hornbill was recorded continuously, categorised by location of perch (ground or off-ground) and exposure to the sun (exposed or shaded). In addition, we recorded time allocation to foraging and other mutually exclusive behaviour categories: moving between or within microsites, provisioning a nest, territorial (calling from an exposed perch, chasing conspecific males or other birds), preening or resting. Foraging involved searching behaviour during which the hornbills hopped around while scanning for potential food items, and the outcomes of foraging attempts were recorded (number of prey items captured, size and type of prey when visible). We also recorded the presence or absence and duration of panting over the entire focal period. Panting was identified by characteristic beak gaping and co-occurred with many of the behaviour categories listed above, including foraging. Focal T_a was calculated from the weather station data as the mean for the hour during which focal took place.

Body mass

The M_b of the hornbills was monitored using perch scales (mounted at nest entrances (n = 14 nest boxes and n = 2 natural cavities). Each perch scale was powered by a 12 V lead-acid battery and consisted of a small (10 cm) twig attached to a load cell which was mounted

horizontally (confirmed using a spirit level) on the side of the nest box or tree trunk (natural cavities), using a metal bracket to ensure the load cell did not touch the nest box / tree trunk (Online Resources, Fig. S4). The load cell was connected to a digital scale (B0.6U, Axis, Ecotone, Poland) which recorded M_b, date and time on an external USB flash drive. The branch affixed to the load cell was positioned so as to provide an obvious perch from which to provision the female. Morning and evening M_b were taken respectively as the earliest (within half an hour before to half an hour after sunrise: mean 5h43, range: 5h36 − 5h53) and latest (within half an hour before to half an hour after sunset: mean 19h26, range 19h19 − 19h30, calculated from the local latitude and sun declination) M_b values recorded each day. Video footage from a camera placed at each nest was used to establish bird identity (via colour ring combinations) and to ensure the bird correctly used the perch scale, i.e., both feet on the perch, and not touching any other parts of the nest box or the load cell itself. Total diurnal M_b gain (ΔM_b) was calculated as a percentage of the morning M_b and corrected for time elapsed between the morning and the evening measurement following du Plessis et al. (2012):

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

where w1 is morning M_b at time t1, w2 is evening M_b at time t2 and the intervening periods is Δt (equation from du Plessis et al. 2012). Due to factors including battery failures and incorrect perch use, the sample sizes for M_b were lower than those for observational data: a final M_b sample size of 73 from seven males during 10 breeding attempts.

Statistical analyses

All statistical analyses were carried out in the R statistical environment using R Studio interface with the core packages and *lme4* (Bates et al. 2014). General linear mixed models (GLMM) and linear mixed models (LMM) were fitted to behaviour and M_b data, and linear models to temperature data, by REML and normality of model residuals was confirmed visually using Normal Q-Q plots. The predicter variables 'time of day' and 'T_a' were strongly

correlated in our focal behavioural observation datasets and therefore could not be included within the same models; as were variables 'T_a' and 'dewpoint' (a measure of moisture content of the air) from the weather station. The T_a at any given hour varied by up to 18°C among days over the course of the study. Comparison of AICc values confirmed that models including 'T_a' better predicted variation in behavioural response variables than models including 'time of day' or 'dewpoint'; we therefore included 'T_a' in behavioural models (further details below). Models fitted to behaviour and M_b data all included the predictor variables T_a (behaviour analyses) or T_{max} (M_b analysis), chick age (counted from the hatch date of the oldest chick; set to 0 before chicks hatched), and the number of dependant birds in the nest (including female and chicks). The model for M_b additionally included Julian date to control for any effects due to time elapsed since the beginning of the breeding season.

Statistical significance was taken as $P < 0.05$ and data are presented as mean estimates $\pm$ 1 standard error (SE) unless otherwise stated. When stating our sample sizes, we use 'n' to denote the number of observations, and 'N' to denote the number of individual birds.

Relationship between environmental temperature and air temperature

Calibrated blackbulb temperatures (T_e) were averaged across the replicate blackbulbs within each of the four microsite categories: on-ground shade, off-ground shade, on-ground sun, off-ground sun. A separate linear model with Gaussian error distribution was fitted to data for each microsite category to describe the relationship between T_e and concurrently-recorded weather station T_a.

Relationship between air temperature and foraging effort, panting, and microsite use

Models for foraging effort, time spent panting and microsite use per focal were fitted using GLMMs with a binomial error distribution. Foraging effort was modelled as a combined vector of 'total time spent foraging (mins)' versus 'total time engaged in other behaviours

(mins)'; time spent panting was modelled as a combined vector of 'total time panting (mins)' versus 'total time not panting (mins)'; and microsite use was modelled as a combined vector of 'total time spent in microsite (mins)' versus 'total time not in microsite (min)'. Models included the offset "focal length" to allow for the fact that the length of focals varied (from 21.2 – 48.5 min, see above), random terms "Bird ID" and "Season" (i.e. austral summer breeding season: 2012/13; 2013/14 or 2014/15) and predictor variables 'T_a' (calculated as mean focal T_a); 'chick age' (in days counted from the hatch date of the oldest chick, set to '0' for the incubation period), and 'number of dependents' (number of birds sealed in the nest cavity including both nestlings and the female). Sample size was 191 focals from 19 breeding attempts by 17 males.

Relationship between air temperature and foraging success

Foraging success, measured as the total number of prey caught per focal, was modelled using a GLMM with Poisson error distribution. The model included the focal length as an offset; random terms 'Bird ID' and 'Season' ; and predictor variables 'T_a' (calculated as mean focal T_a); 'chick age', and 'number of dependents'. Sample size was 191 focals from 19 breeding attempts by 17 males.

Foraging efficiency as a function of panting behaviour and microsite use

The average biomass of individual prey items captured by hornbills during this study was not related to T_a (linear model of biomass per item as a function of T_a: t = -0.11, df = 4, p = 0.912, details on estimation of prey biomass provided in Online Resources). We therefore quantified foraging efficiency as number of prey captures per minute foraging as a measure of foraging efficiency, as this approach was not dependent on detailed observations of prey size and type. The number of prey captures per minute varied greatly when foraging bout duration was < 2.5 min, but stabilised when bout duration > 2.5 minutes in length (Online Resources).

Consequently, we excluded data from foraging bouts shorter than 2.5 min from analyses of foraging efficiency.

We assessed the effects of panting behaviour and microsite use on foraging efficiency using paired non-parametric Wilcoxon signed rank tests; i.e. one paired test for foraging efficiency while panting versus not panting; six paired tests to assess differences in foraging efficiency between each of the four microsite categories. We applied a Bonferroni correction for multiple tests to the microsite analyses, accepting p = 0.008 (i.e. p = 0.05/6) as our threshold for statistical significance. Datasets were prepared by selecting only observations in which birds were observed foraging both while panting and while not panting within the same focal (for panting analysis; N = 10); or were observed foraging within all four microsite categories within the same focal (for microsite use analysis; N = 8). This allowed us to test the effect of panting/not panting and microsite use on foraging efficiency while controlling for temperature and prey availability (which likely did not vary meaningfully within focal periods; see du Plessis et al 2012). If more than one focal was available for a single individual, as occurred on just two occasions, the mean value was used.

Body mass

Diurnal M_b change of the hornbills was analysed using a LMM with a Gaussian error structure. The global model included the predictor variables T_{max} (calculated as maximum daily T_a from the weather station), 'chick age', and 'number of dependents', and 'Julian date', and random terms "Bird ID" and "Season".

Results

Thermal landscape

Calibrated microsite T_e always exceeded T_a as measured by the weather station during the daytime (6h00 to 19h00; Figure 1a). In all four microsites, T_e increased significantly with T_a

(all p < 0.001); but the rate of increase was fastest in sun-exposed locations (Table 1). The difference in T_e between microsites therefore increased as T_a increased (Figure 1b), such that at 40.2°C (the highest T_a we recorded during this study), temperatures on the ground in sun-exposed locations were 13°C higher than those in the shade (55.6°C vs 42.5°C respectively; Fig 1b).

Focal observations: foraging effort, foraging success and time spent panting

As T_a increased, hornbills maintained foraging effort (time spent foraging per focal did not vary significantly with T_a; Z = 1.09, df = 7, p = 0.274), controlling for chick age and the number of dependants in the nest (Table 2). However, with increasing T_a the amount of time birds spent panting per focal increased (Z = 36.69, df = 7, p < 0.001) and their foraging success (number of prey items caught per focal; Z = 3.92, df = 7, p < 0.001) declined (Table 2).

Focal observations: microsite use

Male hornbills spent an increasing amount of time per focal observation in shaded microsites both on the ground (Z = 8.74, df = 7, p < 0.001) and in trees (Z = 10.11, df = 7, p < 0.001), as T_a increased (Table 3). The time spent in sun-exposed microsites off the ground declined with T_a (Z = 16.73, df = 7, p < 0.001), but there was no relationship between T_a and the time spent in sun-exposed microsites on the ground (Z = 1.24, df = 7, p = 0.214; Table 3).

Impacts of panting on foraging efficiency

Within the same focal (therefore presumably under the same T_a and prey availability conditions) male hornbills caught on average 0.89 ± SD 1.26 prey items per minute foraging when not panting; but only 0.04 ± SD 0.06 prey items per minute foraging when panting (paired Wilcoxon signed rank test, effect size = 0.82, Z = 2.61, p = 0.009). Two individuals

had unusually high prey capture rates when not panting (> 1.5 x interquartile range). Re-running the analysis with these individuals removed still returned significantly lower foraging efficiency for the remaining eight birds when panting versus when not panting (paired Wilcoxon signed rank test, effect size = 0.72, Z = 2.28, p = 0.022).

Implications of microsite choice for foraging efficiency

Within the same focal, male hornbills caught the highest number of prey items per minute when foraging on the ground, regardless of microsite exposure to the sun (Figure 2). Differences in foraging efficiency between sun-exposed off-ground vs shaded on-ground (Z = 2.66, p = 0.0078); and shaded off-ground vs shaded on-ground microsites (Z = 2.66, p = 0.0078) were statistically significant after applying a Bonferroni correction for multiple comparisons (threshold p = 0.008; Online Resources Table S2).

Male body mass

Diurnal M_b change (mass gain over 12 hours as a percentage of M_b at sunrise) in breeding male hornbills was negatively correlated with T_{max} (LMM estimate: -0.29 ± 0.10, t = -2.89, df = 8, p = 0.010), controlling for chick age, number of dependant birds in the nest and Julian date. Chick age, number of dependents and Julian date did not significantly predict variation in diurnal change in mass (t = - 1.12, df = 8, p = 0.148; and t = -0.40, df = 8, p = 0.351; t = 0.88, df = 8, p = 0.204; respectively). The threshold temperature above which breeding males did not gain any mass over a 12hr day was 38.4 °C; controlling for chick age, number of dependents and Julian date (Figure 3). We were able to estimate an average overnight mass loss of 4.5 ± 0.9 % from a small sample of birds for which we had reliable consecutive dusk and dawn mass data (n = 19 observations from 8 males); suggesting breeding males lost negligible amounts of mass over 24 hr cycles when T_{max} in the mid-20°Cs, but that the magnitude of 24-hr mass loss increased as T_{max} increased.

Discussion

Our data support the hypothesis that desert-dwelling hornbills' ability to maintain body condition is constrained by temperature-mediated behavioural trade-offs. Although time allocation to foraging (foraging effort) did not decrease with increasing T_a as we predicted, hornbills did show the expected increases in occupancy of cooler microsites during hotter weather. As predicted, foraging efficiency (prey captures per unit time foraging) was negatively affected by both panting and increasing time spent in cooler microsites, especially those off the ground; resulting in lower numbers of prey captured overall per focal observation at high T_a despite no change in foraging effort. Behaviours associated with thermoregulation (i.e. microsite use and increases in panting) therefore appear to trade-off against foraging. The overall effect of these temperature-dependent behavioural trade-offs and associated reductions in foraging efficiency was that hornbills' diurnal M_b gain was negatively related T_{max}. Combined with the average overnight M_b loss of 4.5 %, the temperature-dependence of diurnal M_b gain resulted in the hornbills losing M_b more rapidly per 24-hr period during hot weather compared to cooler conditions.

Although sample sizes in our study were relatively small (19 breeding attempts by 17 individual males for most analyses), large effect sizes were evident for many of the interactions between T_a, behaviour and M_b – most notably the reduction in foraging efficiency associated with panting behaviour. Moreover, the quantitative and qualitative similarities between temperature effects on behaviour, foraging and/or M_b in the present study and those that emerged using similar sample sizes for other species (e.g. Cunningham et al. 2015; du Plessis et al. 2012) support the notion that our sample size here was adequate. Thus, we consider it unlikely that our conclusions would have differed had our sample sizes been larger.

The hornbills in our study were breeding, and in addition to obtaining their own energy and water they were provisioning females and nestlings sealed within nests. The present study thus took place during a period of overall M_b loss for the males; they typically lost $10 - 12$ % of initial M_b over the course of the nestling period. The average overnight M_b loss for males was ~4.5 %, and so males were able to completely compensate during the day for overnight losses only when T_{max} = ~25 °C (Figure 3). Days with T_{max} > 38.4 °C were associated with diurnal M_b loss, and hence nett 24-hr loss of > 4.5 %. Hornbills at our study site, like many arid-zone birds, do not drink and must fulfil both water and energy requirements from food. Hornbills significantly increased time spent panting with increasing T_a. Therefore, an important determinant of changes in male M_b between sunrise and sunset would have been water losses via evaporative cooling, which would have increased as a fraction of M_b on hotter days. When T_e exceeds body temperature, evaporative cooling is the only mechanism whereby organisms can dissipate heat (Dawson 1954), and during extremely hot weather hourly avian evaporative water losses can comprise substantial fractions of M_b and potentially lead to lethal dehydration (Albright et al. 2017; McKechnie and Wolf 2010). Male hornbills occupying exposed microsites on hot days are likely to experience operative temperatures in the region of 50 °C and rates of evaporative water loss of ~ 8 g H_2O hr^{-1} (B. van Jaarsveld and A.E. McKechnie *unpubl. data*); emphasising the need to consider both water and dry mass losses to explain the mass change we observed in our study birds. Dehydration occurring via rapid evaporative losses, exacerbated by reduced capacity to replace water due to compromised foraging ability, could be highly consequential for male hornbills' ability to thermoregulate at high T_a and thus their risk of exposure to lethal body temperatures.

The magnitude of temperature effects on daily M_b fluctuations and consequences thereof for the overall trajectory of the males' M_b during breeding attempts would have been strongly influenced by the males' provisioning decisions, for which three broad possibilities

exist. One is that males prioritized their own energy and water intake over those of dependent females and nestlings, and the fraction of biomass obtained while foraging that was provisioned to nests decreased with increasing T_a. A second scenario that the fraction of biomass provisioned to nests remained constant (and hence food intake of both males and females/nestlings were equally affected by high T_a). Either of these scenarios would involve negative consequences of high T_a for females and nestlings particularly if, as per the first scenario, males compensated for reduced foraging success by increasing the fraction of captured prey items they consumed themselves. A third scenario is that the males sacrificed their own condition by increasing the fraction of biomass provisioned to nests during hotter weather. However, hornbills in general are relatively long-lived and iteroparous (Kemp and Woodcock 1995), and life-history theory (Lack 1948; Lack 1954; Trivers 1972; Trivers 1974) would predict that the abandonment of breeding attempts would be a much more likely outcome than males sacrificing their own condition and probability of survival. During the present study, all nest abandonments were instigated by females (T.M.F.N. van de Ven, *unpubl. data*), but we cannot rule out the possibility of this being a response to reduced male provisioning rates.

Our data reveal some of the limits to the potential for behavioural flexibility to buffer birds from the effects of high environmental temperatures, and suggest that some behavioural decisions that are thought to primarily reflect perceived predation risk may in fact arise from thermal considerations. In hornbill territories, T_e at the hottest time of day varied by as much as ~13 °C between exposed on-ground and shaded off-ground microsites, highlighting that studies considering only T_a without quantifying thermal landscapes in terms of temperatures actually experienced by the birds (i.e., T_e) can severely underestimate the effects of variation in thermal load on animals (Camacho et al. 2015). In addition, our data reveal how the avoidance of exposure to high heat loads may, in some systems, provide as powerful an

explanation for why birds avoid foraging in exposed areas as the more-frequently invoked arguments for higher predation risk (Cresswell 2008).

Thermoregulatory behaviours related to microsite selection and heat dissipation behaviours such as panting can incur substantial fitness costs related to missed opportunities (Sinervo et al. 2010; Cunningham et al. 2015; du Plessis et al. 2012; Edwards et al. 2015). In terms of hornbill microsite selection in the present study; prey capture rates were highest in microsites on the ground, but the birds spent increasing amounts of time in shaded off-ground microsites with increasing T_a (occupancy of shaded site on the ground also increased with T_a but remained low compared to off-ground locations). These shaded, off-ground sites were sub-optimal locations for foraging. Our data thus reiterate that thermoregulatory behaviour in response to hot weather has the potential to severely limit foraging opportunities (van Beest et al. 2012) and the cost of high temperatures often involve reductions in foraging success and activity levels (Abadi et al. 2017; Cerdá et al. 1998; Edwards et al. 2015; Nowicki et al. 2012; Owen-Smith 1998).

We suggest that negative effects of hot weather on foraging behaviour and consequently M_b could be a general feature of avian behaviour in environments where evaporative cooling and other heat dissipation behaviours are a routine aspect of diurnal activity (e.g. Cunningham et al. 2015; du Plessis et al. 2012; Edwards et al. 2015). This argument is strengthened by the phylogenetic distance between hornbills (Bucerotiformes) and Southern Pied Babblers (Passeriformes), which to the best of our knowledge are the only two species in which negative correlations between environmental temperature and nett 24-hr variation in M_b have been shown in free-living adult birds (suburban Australian Magpies *Cracticus tibicen dorsalis* show similar trade-offs between thermoregulation and foraging which appear to affect mass over longer timescales; Edwards et al. 2015). In addition to changes in microsite use, reductions in foraging efficiency in both hornbills and Southern Pied Babblers appear strongly associated with mechanical constraints of panting and foraging

simultaneously. Therefore, these temperature effects may *a priori* be expected to be more pronounced among taxa in which increases in respiratory evaporation (facilitated by panting or gular flutter, both involving gaping of the bill) is the major avenue of evaporative heat dissipation. Some taxa, most notably Columbiformes, rely to a much greater extent on cutaneous evaporation and can increase rates of evaporative heat dissipation without panting (Marder and Gavrieli-Levin 1986; McKechnie and Wolf 2004; Smith and Suthers 1969; Webster et al. 1985). Columbiformes and other taxa in which cutaneous evaporation predominates are thus likely buffered from the decreases in foraging efficiency associated with panting evident in hornbills and babblers, and which we would expect for any birds for which respiratory evaporation is the major pathway of evaporative heat loss.

The large reductions in foraging efficiency and diurnal M_b gain associated with high T_a we report here suggest that rapid anthropogenic climate change could have severe negative repercussions for this hornbill population. The southern Kalahari has warmed rapidly in recent decades (Engelbrecht et al. 2015; Kruger and Sekele 2013; van Wilgen et al. 2016) and, in the absence of meaningful global emissions reductions, T_{max} is projected to increase by 4-5 °C by the end of the 21st Century (Engelbrecht et al. 2015; Conradie et al in review). Our findings here suggest that warming of this magnitude will force male hornbills to spend larger fractions of their time panting and using shaded microsites, thereby leading to large reductions in male foraging efficiency and capacity to maintain M_b during breeding. Our data also reveal some of the ways in which thermal landscapes and species' foraging modes might interact to determine vulnerability to warming (Hall et al. 2016). For instance, species for which foraging returns are higher in sun-lit microsites may be affected by trade-offs between foraging and thermoregulation to a greater degree compared to species that forage within tree canopies (Martin et al. 2015). Such interactions may also have important implications for the conservation of threatened taxa in hot environments. Finally, our data reveal some of the

functional limits to increased resilience to warming via behavioural thermoregulation (Huey et al. 2012).

In conclusion, our data support the hypothesis that the capacity of birds to maintain body condition in hot environments is constrained by behavioural trade-offs between foraging and thermoregulation. Similar reductions in foraging efficiency and capacity to maintain M_b during hot weather to those evident in Southern Yellow-billed Hornbills likely affect many other arid-zone species (e.g., Cunningham et al. 2015; du Plessis et al. 2012; Edwards et al. 2015), and potentially have major implications for the persistence of species under warmer future conditions. The direct links between temperature, microsites and body condition operating in our study system provide a sobering example of the potential for climate change to render habitats unsuitable for birds as a direct consequence of higher temperatures, even in the absence of more obvious anthropogenic impacts such as land-use changes.

material are those of the authors and do not necessarily reflect the views of the National Research Foundation.

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Table 1 Operative temperature (T_e; °C) as a function of T_a (°C) for each of the microsites;

degrees of freedom, estimates of effect sizes, standard error, t and p values and 95% CI.

Microsite	df	Estimate	Std. Error	t value	p value	95% CI
Ground sun	3	1.40	0.014	103.51	<0.001	1.37 – 1.43
Off-ground sun	3	1.38	0.009	150.44	<0.001	1.36 - 1.40
Off-ground shade	3	1.17	0.004	262.11	<0.001	1.16 – 1.18
Ground shade	3	0.98	0.004	257.90	<0.001	0.98 – 0.99

Table 2 Time spent foraging, time spent panting, and number of prey captures per focal as a function of T_a (°C), the number of dependent birds in the nest (female and chicks) and chick age; by breeding male Southern Yellow-billed Hornbills; degrees of freedom, estimates of effect sizes, standard error, z and p values and 95% CI. Significant predictor variables are highlighted in bold; n = 191 focal observations from 19 breeding attempts by 17 males.

Model	Error Dist.	Predictors	df	Estimate	Std. Error	z value	p value	95 % CI		
		T_a		-0.01	0.01	1.09	0.274	-0.04	-	0.01
Time spent foraging	Binomial	**Number of dependants**	7	0.27	0.10	2.78	0.006	0.08	-	0.46
		Chick age		0.02	0.01	1.94	0.053	0.00	-	0.03
		T_a		0.43	0.01	36.69	< 0.001	0.41	-	0.46
Time spent panting	Binomial	**Number of dependants**	7	0.46	0.08	5.87	< 0.001	0.31	-	0.61
		Chick age		0.01	0.01	1.51	0.131	0.00	-	0.03
		T_a		-0.02	0.01	3.92	< 0.001	-0.03	-	-0.01
Foraging success	Poisson	Number of dependants	7	-0.01	0.06	0.16	0.870	-0.12	-	0.10
		Chick age		0.02	0.01	3.73	< 0.001	0.01	-	0.03

Table 3 Time spent foraging in each of four different microsites per focal as a function of T_a (°C), the number of dependent birds in the nest (female and chicks) and chick age; by breeding male Southern Yellow-billed Hornbills; estimates of effect sizes, standard error, absolute z values and p values and 95% CI. Significant predictor variables are highlighted in bold; n = 191 focal observations from 19 breeding attempts by 17 males. Models are fitted with binomial error distribution.

Model	Predictor variables	df	Estimate	Std. Error	z value	p value	95 % CI		
Off-ground shade	**T_a**		0.05	0.00	10.11	< 0.001	0.04	-	0.05
	Number of dependants	7	0.23	0.05	4.60	0.000	0.13	-	0.32
	Chick age		0.01	0.00	1.16	0.246	0.00	-	0.01
Ground shade	**T_a**		0.07	0.01	8.74	< 0.001	0.06	-	0.09
	Number of dependants	7	-0.11	0.08	-1.29	0.198	-.27	-	0.06
	Chick age		0.00	0.01	0.59	0.554	-0.01	-	0.02
Off-ground sun	**T_a**		-0.10	0.01	16.73	< 0.001	-0.11	-	-0.09
	Number of dependants	7	-0.48	0.06	7.48	< 0.001	-0.61	-	-0.36
	Chick age		-0.01	0.01	2.91	0.004	-0.02	-	0.00
Ground sun	T_a		-0.01	0.01	1.24	0.214	-0.02	-	0.01
	Number of dependants	7	0.09	0.08	1.09	0.276	-0.07	-	0.25
	Chick age		0.02	0.01	3.43	< 0.001	0.01	-	0.04

Figure legends

Figure 1. Raw data for air temperature (T_a; derived from the weather station) and operative temperature (T_e; per microsite category) as a function of time of day (in hours; A); and operative temperature as a function of air temperature (T_e data are averages of replicate blackbulbs in each microsite; B). Error bars represent one standard error. Data were derived from three summer seasons of T_a and T_e recordings. Figure is available in colour online.

Figure 2. Prey captures per minute foraging by male Southern Yellow-billed Hornbills per microsite category (off-ground shade, ground shade, off-ground sun and ground sun), during the same focal (therefore under conditions of comparable temperatures and prey abundance). The letters above each box plot represent Bonferroni-corrected significant differences ($p <$ 0.008) in foraging efficiency per microsite. Data were collected from eight individual birds.

Figure 3. Diurnal M_b change (%) of male Southern Yellow-billed Hornbills as a function of daily maximum temperature (T_{max}). Mass was measured at dawn and dusk using perch scales mounted at nest boxes. The line represents the prediction from the model that includes the predictor variables T_{max}, chick age, number of dependant birds in the nest, Julian date and individual ID nested within season as a random effect. The dotted line represents mass change of 0 %. Data were derived from 73 days of diurnal M_b change recordings during 10 nesting attempts of 7 males.
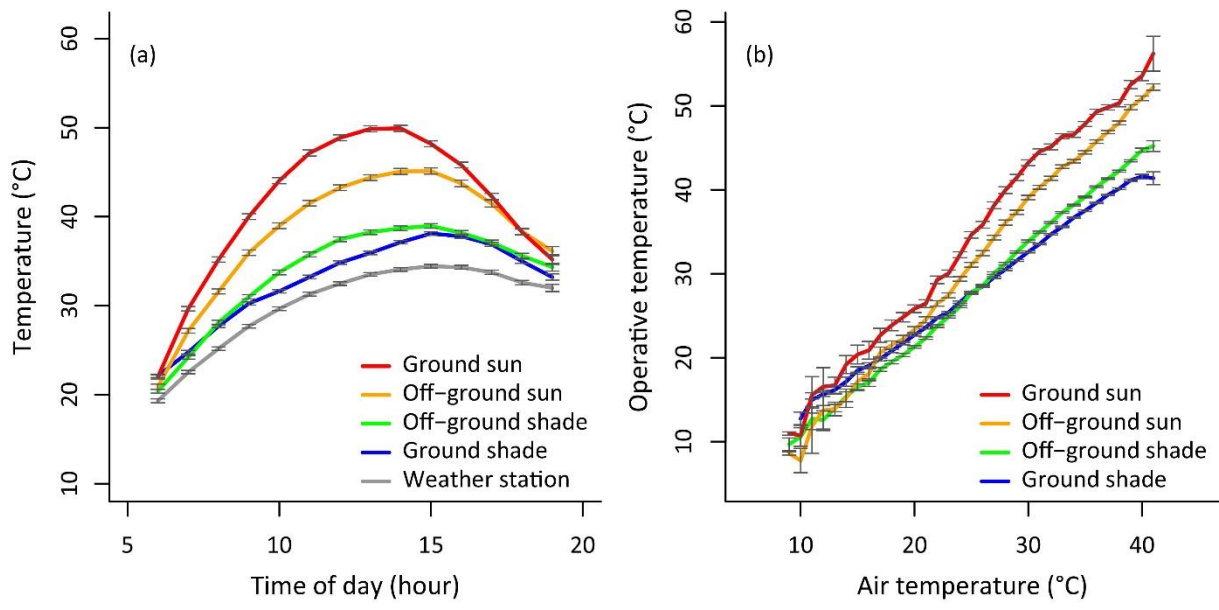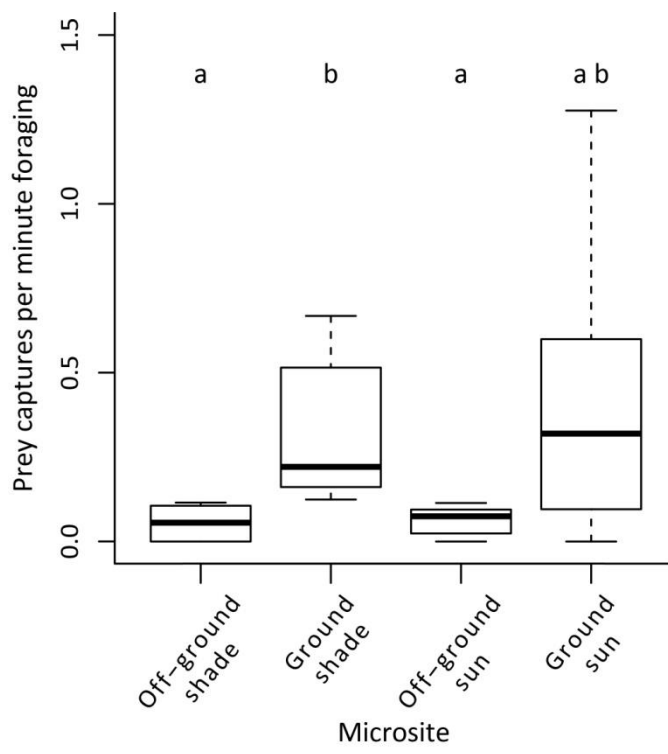
Figure 1.

Figure 2

Figure 3