

Non-evaporative heat dissipation across the beaks and casques of large forest hornbills

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ABSTRACT

Heat loss across the beak is an important thermoregulatory mechanism among birds, particularly in large-beaked taxa such as toucans (Ramphastidae) and hornbills (Bucerotidae). The number of species investigated remains limited, as does our understanding of how the functional significance of this pathway varies with environmental variables such as humidity, with little previous research on species inhabiting humid environments. We used infrared thermography to test the hypothesis that large (600–1300 g) Afrotropical forest hornbills use their beaks and casques as thermal radiators. We collected data over air temperatures (T_{air}) of 15–34 °C for wild-caught trumpeter hornbills (*Bycanistes bucinator*) and captive-bred silvery-cheeked hornbills (*Bycanistes brevis*) and black-casqued hornbills (*Ceratogymna atrata*). Surface temperatures of the beaks and casques (T_{beak}) tracked T_{air} below 24–25 °C, but at higher T_{air} , the $T_{\text{beak}} - T_{\text{air}}$ gradient increased to maximum values of 10–12 °C. Maximum rates of beak heat loss were 2.5–3.8 W, equivalent to 31–83 % of estimated resting metabolic heat production. Facial skin showed also evidence for active regulation of heat loss. We also analysed the scaling of the inflection T_{air} above which the $T_{\text{beak}} - T_{\text{air}}$ gradient increases ($T_{\text{inflection}}$) by combining our data with published and three unpublished values. We found that $T_{\text{inflection}}$ decreases with increasing body mass (M_b), with the relationship best described by the linear regression model $T_{\text{inflection}} = -9.134\log_{10}M_b + 50.83$, with M_b in g.

1. Introduction

Avian beaks function as controllable heat radiators, with regulation of heat across the outer surfaces of the beak confirmed in representatives of six orders (see Tattersall et al., 2009, 2018; Greenberg et al., 2012; van de Ven et al., 2016; Playà-Montmany et al., 2021; McQueen et al., 2023). These range from large-beaked taxa such as toucans, hornbills and ground-hornbills (Tattersall et al., 2009; van de Ven et al., 2016; Janse van Vuuren et al., 2020) to smaller-beaked including Darwin's finches and song sparrows (Tattersall et al., 2018; Greenberg et al., 2012). Species spanning body masses of 12–8500 g can dissipate 2–400 % of resting metabolic heat production via their beaks, with heat loss maximized when environmental temperature (T_e) is 5–10 °C below T_b (Tattersall et al., 2017). However, sources of interspecific variation in heat exchange capacity remain unclear, and likely include body mass (M_b , Ryeland et al., 2017), beak surface area (Symonds and Tattersall, 2010) and possibly climate-correlated adaptive variation (Danner and

Greenberg, 2015; Monge et al., 2023). Although regulation of heat losses across the avian beak is less pronounced compared to that across birds' legs (McQueen et al., 2023), non-evaporative heat loss via the beak is an important component of thermoregulation at moderate T_e within ~20 °C below normothermic body temperature (T_b) (Janse van Vuuren et al., 2020; Tattersall et al., 2017).

In arid environments, maximizing non-evaporative heat dissipation may *a priori* be expected to confer benefits in term of water conservation by reducing reliance on evaporative cooling (Greenberg et al., 2012; Tattersall and Cadena, 2010). However, non-evaporative heat loss across the beak is also likely adaptive in environments where high humidity constrains evaporative cooling (Buzan and Huber, 2020; Freeman et al., 2024), as suggested by several authors (Luther and Greenberg, 2014; Tattersall et al., 2017; van de Ven et al., 2016). Birds occupying humid lowlands have evolved a greater capacity for pronounced hyperthermia compared to their arid-zone counterparts (Freeman et al., 2022; Weathers, 1997), suggesting these species can

Abbreviations: T_b , body temperature; T_{air} , air temperature; T_{facial} , eye skin surface temperature; T_{wattle} , wattle skin surface temperature; T_{beak} , beak surface temperature; T_s , surface temperature; Q_{rad} , radiative heat loss; Q_{conv} , convective heat loss; Q_{total} , total heat loss.

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maintain a positive $T_b - T_{air}$ gradient and dissipate heat non-evaporatively at higher T_e .

Several variables related to avian heat tolerance and evaporative cooling scale with M_b (Gerson et al., 2019; McKechnie et al., 2021), but the scaling of non-evaporative heat dissipation via the beak has received little attention so far. For instance, the lower limit of thermoneutrality decreases with increasing M_b (Riek and Geiser 2013), making it likely that the inflection T_e above which blood is redistributed to the beak to accelerate non-evaporative heat loss also scales negatively (Tattersall et al., 2017). Negative scaling of the environmental temperature at which beak heat dissipation commences would result in larger birds using this avenue of heat loss over a wider T_e range than small birds.

Here, we quantified heat transfer across the beaks and casques of three Afrotropical forest hornbill species, ranging in M_b from 600 g to 1300 g. All three possess large beaks and casques, which are also sites for regulated heat loss (Eastick et al., 2019). We hypothesized these structures function as controllable heat radiators in forest hornbills, similarly to those of their arid-zone and savanna counterparts (i.e., Janse van Vuuren et al., 2020; van de Ven et al., 2016). We tested the prediction that, in shaded microsites (i.e., in the absence of solar heat loads), surface temperatures of the beak and casque track T_{air} under cool conditions, but increase above T_{air} to facilitate heat loss above some threshold T_{air} . We also examined the scaling of heat dissipation via the beak, and combined our data for three hornbill species with data from several published sources and one unpublished source to test the prediction that the inflection T_{air} above which blood is shunted to the beak and casque, evident as increases in the gradient between surface temperature and T_{air} , scales negatively with M_b .

2. Methods

2.1. Study site and species

We obtained data from trumpeter hornbills (*Bycanistes bucinator*, male = 13, female = 10) inhabiting lowland coastal forests of KwaZulu-Natal province, South Africa, in the towns of St Lucia, Richard's Bay and Mtunzini (28.3726° S, 32.4142° E – 28.9597° S, 31.7501° E). Individuals were caught using mist nets (Nylon 100-mm mesh, Denier/ply 210/4, 5 shelves, 3 m height, Avinet, Dryden, USA) and transported in large cotton pillowcases to our nearby field station. Trumpeter hornbills were housed in a 2 m × 2 m × 2 m aviary constructed under a tree and covered with 80% shade-netting, minimising wind and solar-radiation effects. Birds had *ad libitum* access to water and soft fruit, mainly pawpaw. Birds were kept in captivity for 3–5 days and released at the site of capture thereafter.

In addition, we obtained data for captive silvery-cheeked hornbills (*Bycanistes brevis*, male = 5, female = 7) and black-casqued hornbills (*Ceratogymna atrata*, male = 5, female = 7) housed in private collections in Durban and Vanderbijlpark, South Africa. We also obtained data from two captive-bred trumpeter hornbills, in addition to the wild-caught individuals. Captive birds were housed in large, well-shaded and sheltered aviaries. We obtained thermal images throughout the day between sunrise and sunset (06h00–18h00) in the austral spring/summer and winter of 2022 and 2023 in their respective outdoor enclosures. Air temperatures (T_{air}) ranged from 18 to 34 °C and 15–33 °C for wild and captive trumpeter hornbills, respectively, 15–33 °C for silvery-cheeked hornbills and 15–32 °C for black-casqued hornbills (see Appendix A.2, Table A.2). A total of 935 thermal images were obtained.

2.2. Air and surface temperature measurements

Using a handheld thermal imaging camera (FLIR model T600-series, FLIR Systems, Wilsonville, Oregon, USA), we obtained images of individual hornbills from a distance of 0.5–3 m. The thermal imaging camera was calibrated by the supplier and again before measurements were taken by comparing the temperature of water in a circulating water

bath (Julabo F34-ME, Julabo, Allentown, Pennsylvania, USA) measured with a mercury-in-glass thermometer with NIST-traceable accuracy against values measured by the camera.

Potentially confounding effects of solar radiation and activity were minimized by including images in subsequent analyses only if 1) the hornbill spent ≥ 3 min in complete shade prior to imaging, 2) birds were calm and inactive, 3) wind speed was $< 1 \text{ m s}^{-1}$, and 4) the dew point was above air temperature (T_{air}) to ensure that there was no condensation on the beak. Relative humidity (RH), dew point, T_{air} and wind speed were measured using a handheld weather meter (Kestrel 3500 Delta T, Nielsen-Kellerman, Boothwyn, USA). The T_{air} and RH values were used to set the camera's parameters, with reflected temperature assumed to equal T_{air} and emissivity assumed to be 0.97, following Tattersall (2016). Surface temperatures were measured for the beak and casque, bare skin around the eye (T_{facial}) and wattles (T_{wattle}).

2.3. Data analysis

Average surface temperature measurements of the beak and skin regions were extracted from thermal images using ThermaCam software (ThermaCAM Researcher Pro 2.9, FLIR Systems Inc, Wilsonville). The polygon and line functions were used to specify the region where surface temperature was measured. Mean temperatures across each area of interest were extracted. Using a generalised linear model and a post hoc multiple comparison test (Tukey HSD), we tested whether surface temperatures of the distal, proximal, upper, lower and casque sections of the beak differed significantly, and found no significant difference across the different sections of the beak for all species (see Appendix A.2, Table A.1).

2.4. Estimates of heat exchange

Morphological measurements for each species were obtained from preserved specimens held in the Ditsong Museum, Pretoria, South Africa and the Natural History Museum at Tring, UK. We also obtained additional measurements for the wild-caught trumpeter hornbills at our study site to compare with the museum specimens and found no differences in the measurements. We were unable to obtain morphological measurements for the other species held in private collections. Surface areas of the beak (upper, lower and casque combined) and facial skin were measured (Appendix A.2, Table A.3). Briefly, 10 individuals (trumpeter hornbills) or 10 museum specimens per species were photographed from directly above while flat against a blank background with a ruler used as a scale bar. These images were then processed in ImageJ (version 1.53, National Institute of Health, USA) image analysis software, where surface areas were selected with the polygon tool, measured and duplicated to account for both sides of the beak. These values were validated with physical measurements taken of the beak and casque length, width and height from the specimens. The same was repeated for the eye skin and wattle measurements.

Estimates of heat exchange were calculated following previous studies (Eastick et al., 2019; Janse van Vuuren et al., 2020; Tattersall et al., 2009, 2018; van de Ven et al., 2016). Heat exchange (Q) estimates were calculated as the sum of the radiative (Q_{rad}) and convective (Q_{conv}) heat exchange using T_{beak} , T_{facial} or $T_{wattle,skin}$, T_{air} , wind speed and humidity. Total heat exchange (Q_{total}) was estimated for each area of interest by multiplying the estimated surface-area specific Q by the surface area (see Appendix A.1: Methods). Furthermore, to assess the role of the casque and beak in overall heat flux, we fitted a linear mixed-effect model of heat exchange across the beak as a function of T_{air} . We then used the slope estimates as an indicator of the proportion of heat exchanged by the appendage of each species and fitted linear mixed-effects models with T_{beak} , T_{facial} or $T_{wattle,skin}$ as the response variable and T_{air} , humidity, wind speed and $T_{air} \times$ humidity as predictors, with bird identity as a random fixed effect. Lastly, to estimate the contributions of the beak to total heat exchange, we compared model

estimates for total beak heat exchange per T_{air} increment to resting metabolic rate (RMR). For trumpeter hornbills, diurnal thermoneutral RMR was measured using flow-through respirometry (B. Coulson, M. T. Freeman, S. R. Conradie and A. E. McKechnie, unpublished data) and used to estimate heat loss as a percentage of RMR. Empirical RMR data for the other two species were not available, so we first calculated allometrically-predicted basal metabolic rate (BMR) using Londoño et al.'s (2015) equation for non-passerines excluding Apodiformes ($\text{BMR} (W) = 0.021M_b^{0.724}$). To estimate the equivalent diurnal thermoneutral RMR, we used equations 4 and 5 of Aschoff and Pohl (1970) to estimate the allometrically-predicted amplitude of circadian rhythms of RMR; for both species, diurnal thermoneutral RMR represents 123.5% of BMR. These estimated values were used to express heat loss across the beak as a percentage of active-phase thermoneutral RMR for silvery-cheeked and black-casqued hornbills.

2.5. Scaling of beak heat loss

To investigate the scaling of overall heat flux and inflection T_{air} for the redistribution of blood to the beak, we collated data from other thermal imaging studies of beaks as thermal radiators, including only data that were a) collected and analysed in a similar manner as the present study to ensure comparability and b) permitted the identification of the inflection T_{air} (i.e., $T_{\text{inflection}}$) above which T_{beak} increased above T_{air} . We included data for nine species: four hornbills (three in present study plus *Tockus leucomelas* - van de Ven et al., 2016), a ground-hornbill (*Bucorvus leadbeateri* - Janse van Vuuren et al., 2020), a toucan (Tattersall et al., 2009)] and three African vultures – *Gyps africanus*, *Gyps coprotheres* and *Torgos tracheliotos* (J. Wessels, unpubl. data, see Appendix A.2 – Vulture dataset).

2.6. Statistical analyses

Statistical analyses were performed using the R interface (v4.2.2) and RStudio (RStudio, inc.). We conducted model selection using the “model.sel” function (Barton, 2019). We calculated absolute humidity from RH and T_{air} using equations provided by Campbell and Norman (1998). Our standardised model included T_{air} , wind speed, absolute humidity, sex, body mass and the $T_{\text{air}} \times$ humidity interaction. We made use of Akaike weights and the Akaike information criterion values corrected for small sample sizes (AICc) for model selection (Burnham and Anderson, 2002). To account for pseudo-replication, we a) included individual identity as a random factor in all models and b) used only a single thermal image per 1 °C increment T_{air} per individual bird. Significance was assessed at $\alpha < 0.05$ and all values are presented as mean \pm SD. We tested whether significant heteroscedasticity was present between variables using the lme4 package. No heteroscedasticity was detected among residuals and linear models were fitted.

We modelled the mean surface T_{beak} , T_{facial} and T_{wattle} against the predictor variables such as T_{air} , wind speed, humidity, sex, body mass and the $T_{\text{air}} \times$ humidity interaction with bird identity as a random effect in all models. We again made use of “model.sel”, and selected the model with the highest explanatory power as above. For each response variable (T_{beak} , T_{air} and T_{wattle}) we found that wind speed, body mass and sex were not included in the best models for all species and excluded from further analyses. Using the “segmented.lme” function (segmented package; Muggeo, 2016), we identified the respective inflection points at which surface temperatures deviated from T_{air} , with each individual bird ID included as a random effect, for each species and each region (i.e., beak and facial skin). To quantify how the T_{beak} , T_{facial} or $T_{\text{wattle_skin}}$ varied with T_{air} above and below the point of inflection, we analysed the response variable using linear mixed-effect models in the R package nlme, where slopes of T_{beak} , T_{facial} or $T_{\text{wattle_skin}}$ and the difference between the respective surface temperatures and T_{air} were estimated as functions of T_{air} .

For the interspecific scaling analysis, we fitted a linear mixed effect

model where the responses of T_{air} inflection point (i.e., the T_{air} at which the surface of the beak heated up) were modelled against the predictor variables \log_{10} -transformed body mass, the interaction of $T_{\text{inflection}}$ and body mass with order as a fixed effect, using the nlme package (Pinheiro et al., 2015). The model with the highest explanatory power was selected as described above using the “model.sel” function.

3. Results

Thermal images revealed active regulation of beak and casque surface temperatures in all three hornbill species. At $T_{\text{air}} < 20$ °C, T_{beak} (i.e., pooled casque and beak data) closely tracked T_{air} . Commencing at $T_{\text{air}} \sim 24$ – 25 °C, however, $T_{\text{beak}} - T_{\text{air}}$ gradients increased (Figs. 1 and 2). The increases in surface temperatures were, in some instances, highly variable across the surface of the beak and particularly the casque, giving rise to distinctive branch-like patterns that presumably reflect the arrangement of underlying vasculature (e.g., Fig. 1. – images in 2nd and 3rd rows of centre column). At $T_{\text{air}} > 30$ °C, hornbills reduced activity and commenced heat dissipation behaviours including panting and wing-drooping. In one instance, a trumpeter hornbill was observed secreting nasal fluid from the nares at $T_{\text{air}} = 34$ °C (Appendix A.1, Fig. A1.).

3.1. Beak surface temperatures

The T_{beak} data for all three species were best described by models involving a single inflection point ($p < 0.001$ for number of selected break-points). Segmented linear mixed-effect models detected inflections (95% CI) in T_{beak} at $T_{\text{air}} = 23.3$ – 25.4 °C, $T_{\text{air}} = 23.5$ – 24.6 °C and $T_{\text{air}} = 24.2$ – 26.8 °C for trumpeter, silvery-cheeked and black-casqued hornbills, respectively (Fig. 2A–C).

Below $T_{\text{air}} = 24.2 \pm 0.7$ °C, trumpeter hornbill T_{beak} remained within ~ 1 °C of T_{air} and did not differ significantly from T_{air} ($df = 65$, $t = 22.056$, $p = 0.059$). Above $T_{\text{air}} = 24.2 \pm 0.7$ °C, trumpeter hornbill T_{beak} increased at 2.05 °C $T_{\text{beak}} \text{ } ^\circ\text{C } T_{\text{air}}^{-1}$ to maximum of 44 °C at $T_{\text{air}} = 34$ °C, differing significantly from T_{air} ($df = 132$, $t = 23.710$, $p < 0.001$) (Fig. 2A and D). Similarly, T_{beak} of silvery-cheeked and black-casqued hornbills tracked T_{air} below $T_{\text{air}} = 24.5 \pm 0.4$ °C ($df = 69.638$, $t = 23.42$, $p = 0.072$) and $T_{\text{air}} = 25.1 \pm 1.2$ °C ($df = 24$, $t = 6.684$, $p = 0.051$), respectively. At T_{air} above these inflection points, T_{beak} increased rapidly with increasing T_{air} , with slopes of 2.06 °C $T_{\text{beak}} \text{ } ^\circ\text{C } T_{\text{air}}^{-1}$ ($df = 38.43$, $t = 5.309$, $p < 0.001$) and 1.45 °C $T_{\text{beak}} \text{ } ^\circ\text{C } T_{\text{air}}^{-1}$ ($df = 35.67$, $t = 5.366$, $p < 0.001$; Fig. 2B and C and 2D–E), respectively, in silvery-cheeked and black-casqued hornbills. Humidity, T_{air} and the $T_{\text{air}} \times$ humidity interaction (but not wind speed or sex) were significant predictors of T_{beak} above T_{air} inflection points for all three species., (Appendix A.2, Table A.5). The gradients for $T_{\text{beak}} - T_{\text{air}}$ above the inflection point increased linearly with T_{air} to maxima of 1.37 °C $T_{\text{beak}} \text{ } ^\circ\text{C } T_{\text{air}}^{-1}$, 1.71 °C $T_{\text{beak}} \text{ } ^\circ\text{C } T_{\text{air}}^{-1}$ and 1.47 °C $T_{\text{beak}} \text{ } ^\circ\text{C } T_{\text{air}}^{-1}$ for trumpeter, silvery-cheeked and black-casqued hornbills, respectively (Fig. 2D–F).

3.2. Skin surface temperature

In all three species, T_{facial} remained 5–10 °C higher than T_{air} . Segmented linear mixed-effect models revealed that no inflection points were detected for T_{facial} among trumpeter hornbills ($P = 0.8822$), and the slope of T_{facial} was 0.54 °C $T_{\text{facial}} \text{ } ^\circ\text{C } T_{\text{air}}^{-1}$ (Fig. 3A). For silvery-cheeked hornbills, one inflection point was detected ($P < 0.001$) for T_{facial} at $T_{\text{air}} = 24.3 \pm 0.37$ °C, with slopes above and below the inflection T_{air} for T_{facial} of 1.67 °C and 0.27 °C $T_{\text{facial}} \text{ } ^\circ\text{C } T_{\text{air}}^{-1}$ (Fig. 3B). For black-casqued hornbills, T_{facial} and T_{wattle} differed significantly ($df = 110.4$, $t = 7.983$, $P < 0.001$) and were analysed separately. At $T_{\text{air}} < 25$ °C, T_{facial} increased rapidly at 1.15 °C $T_{\text{facial}} \text{ } ^\circ\text{C } T_{\text{air}}^{-1}$ but stabilised (slope = 0.04 °C $T_{\text{facial}} \text{ } ^\circ\text{C } T_{\text{air}}^{-1}$) at $T_{\text{air}} > 25$ °C. In contrast, T_{wattle} of black-casqued hornbills remained constant at $T_{\text{air}} < 18$ °C (slope = 0.004 °C $T_{\text{wattle}} \text{ } ^\circ\text{C } T_{\text{air}}^{-1}$), but increased rapidly at $T_{\text{air}} \geq 18$ °C at 1.26 °C $T_{\text{wattle}} \text{ } ^\circ\text{C } T_{\text{air}}^{-1}$ (Fig. 3C).

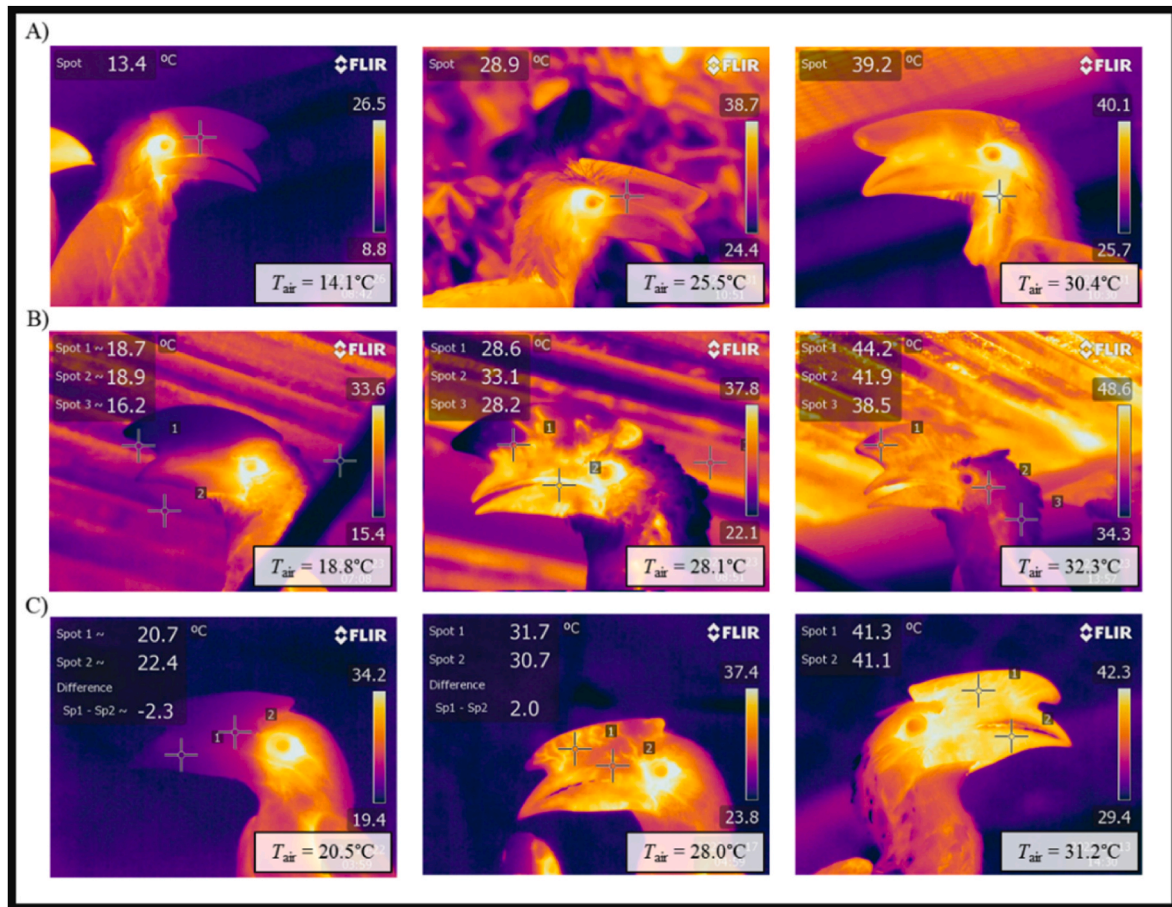


Fig. 1. Thermal images of (row A) black-casqued hornbills (*Ceratogymna atrata*), (row B) silvery-cheeked hornbills (*Bycanistes brevis*) and (row C) trumpeter hornbills (*Bycanistes bucinator*) illustrating the beak and facial skin surface temperatures in response to a range of air temperatures (T_{air}). The beak functions as a thermal radiator from higher T_{air} (middle and right columns) but not at lower T_{air} (left column).

Significant predictors of T_{facial} in all species included T_{air} , humidity and the T_{air} x humidity interaction (Appendix A.2. Table A.5.) however, the only significant predictor of T_{wattle} , in black-casqued hornbills, and T_{facial} , for trumpeter hornbills, was T_{air} .

3.3. Estimated heat exchange

The means of maximum heat loss rates across the beak were 3.482 ± 1.12 W (equivalent to 83 % of estimated active-phase thermoneutral RMR) at $T_{air} = 34$ °C in trumpeter hornbills, 4.750 ± 2.04 W (38 %) at $T_{air} = 31$ °C in silvery-cheeked hornbills 4.500 ± 2.36 W (31 %) at $T_{air} = 32$ °C in black-casqued hornbills (Fig. 4, Appendix A.2, Table A.6). Slopes of heat loss above inflection T_{air} values were 0.370 W °C T_{air}^{-1} , 0.266 W °C T_{air}^{-1} and 0.260 W °C T_{air}^{-1} for trumpeter, silvery-cheeked and black-casqued hornbills, and did not differ significantly among species (Fig. 4A–C, Appendix A.2, Table A.7 and A.8). Maximum heat dissipation from the facial skin significantly decreased with increasing T_{air} and was 0.574 ± 0.09 W for trumpeter hornbills, 0.345 ± 0.02 W for silvery-cheeked hornbills and 0.446 ± 0.04 W for black-casqued hornbills (Fig. 4D–F).

Surface-area specific heat loss across the beak at 31 °C (i.e., the highest common T_{air} with data for >1 individual per sex per species) was not significantly different between males and females for any of the study species ($p > 0.05$ - see Appendix A.2, Table A.9 and A.10). Similarly, inflection points did not differ significantly between males and females (CI: 95% - Appendix A.2, Table A.9 and A.10), nor did slopes of heat loss above inflection points between males and females of trumpeter hornbills ($t = 0.361$, $df = 22$, $p = 0.719$), silvery-cheeked hornbills

($t = 0.252$, $df = 10$, $p = 0.801$) or black-casqued hornbills ($t = 0.372$, $df = 10$, $p = 0.711$).

3.4. Scaling of inflection air temperature for beak surface temperature

The $T_{inflection}$ above which beak surface temperature increased scaled negatively with M_b , decreasing from 30.5 °C in the 200-g southern yellow-billed hornbill to 14.4 °C in the 8500-g Cape vulture. The relationship was best described by the regression model $T_{inflection} = -9.134 \log_{10} M_b + 50.83$ ($r^2 = 0.881$, $t = -4.930$, $df = 7$, $p = 0.002$; Fig. 5). Linear mixed-effects models revealed that $T_{inflection}$ was significantly predicted by M_b ($F_{2,7} = 9.466$, $p < 0.05$) but not beak surface area ($F_{2,7} = 0.013$, $P = 0.914$) nor the interaction of M_b and beak surface area ($F_{2,7} = 0.062$, $p = 0.815$).

4. Discussion

The patterns of beak and casque surface temperatures we documented in three Afrotropical forest hornbills support our first prediction and confirm these structures function as controllable thermal radiators, with blood flow to these regions facilitating non-evaporative heat loss at $T_{air} > 24$ –25 °C. These findings are consistent with previous studies of large-beaked non-passerines (Tattersall et al., 2009; van de Ven et al., 2016; Janse van Vuuren et al., 2020). Our data also suggest regulation of facial and wattle skin surface temperatures. The interspecific scaling analysis supported our prediction that the T_{air} inflection above which the beak is used to regulate T_b scales negatively with body mass among birds for which data are available. We discuss these observed patterns in

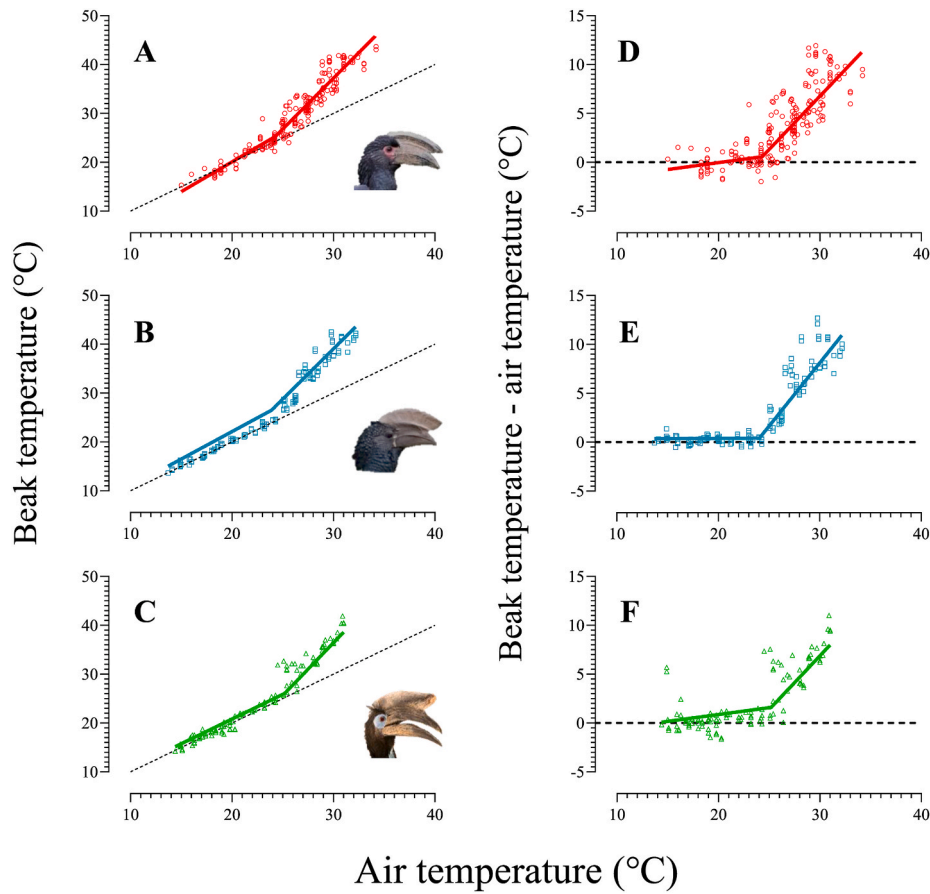


Fig. 2. Beak surface temperature (T_{beak}) as a function of air temperature (T_{air}) (A–C) and the difference between beak surface temperature and air temperature ($T_{\text{beak}} - T_{\text{air}}$) as a function of T_{air} (D–F) in trumpeter hornbills (*Bycanistes bucinator*, panels A and D) in red circles, silvery-cheeked hornbills (*Bycanistes brevis*, panels B and E) in blue squares and black-casqued hornbills (*Ceratogymna atrata*, panels C and F) in green triangles. The lines of equality (i.e., $T_{\text{beak}} = T_{\text{air}}$) are indicated using dashed lines.

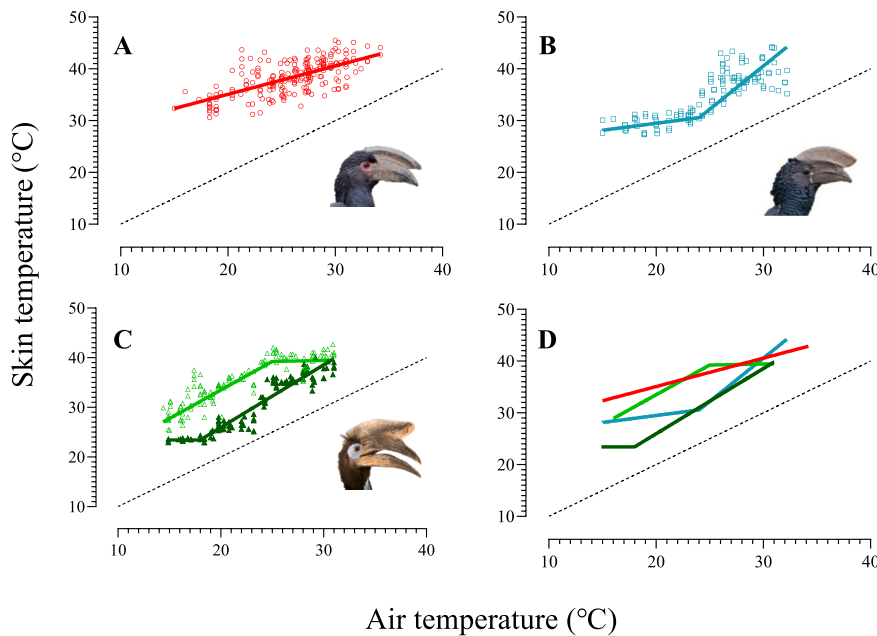


Fig. 3. Surface temperatures of facial skin (T_{facial}) in (A) Trumpeter hornbills (*Bycanistes bucinator*), (B) Silvery-cheeked hornbills (*Bycanistes brevis*) and T_{facial} and wattle skin (T_{wattle}) in Black-casqued hornbills (*Ceratogymna atrata*) (C) as a function of air temperature (T_{air}). In panel C, light green triangles indicate T_{facial} and while dark green represents T_{wattle} . The dashed line shows the line of equality where $T_{\text{facial}} = T_{\text{air}}$. Panel (D) Represents the segmented linear regression model slopes for the relationship of T_{skin} and T_{air} for each species.

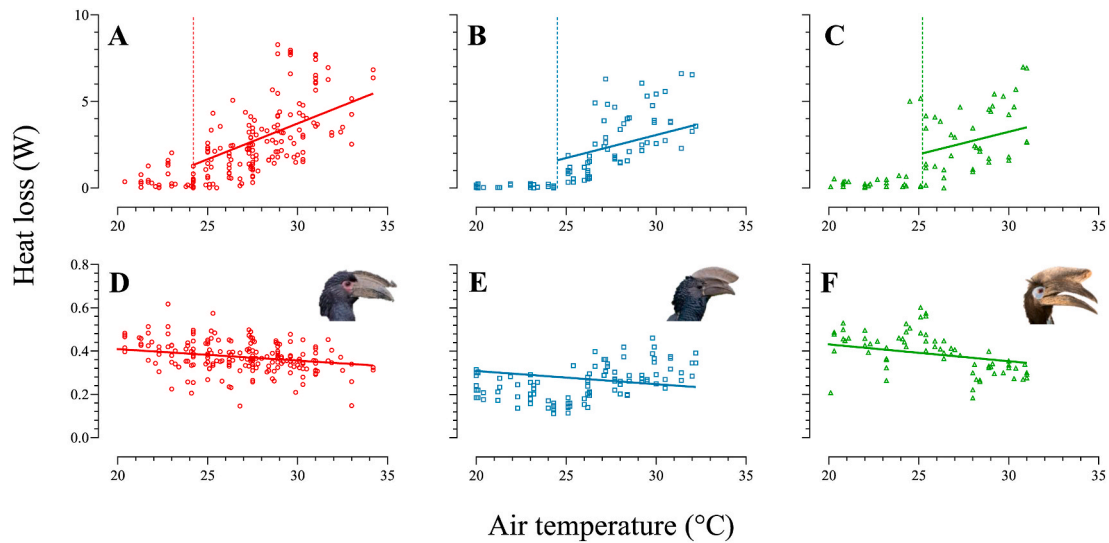


Fig. 4. Heat dissipation (W) as a function of air temperature (T_{air}) across the beak (top row, A-C) and facial skin (bottom row, D-F) of (A + D) trumpeter hornbills (*Bycanistes bucinator*) in red circles, (B + E) silvery-cheeked hornbills (*Bycanistes brevis*) in blue squares and (C + F) black-casqued hornbills (*Ceratogymna atrata*) in light green triangles. The vertical dashed line indicates each species' respective inflection point.

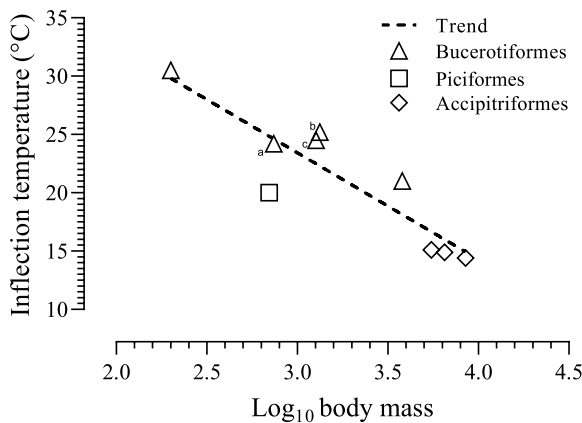


Fig. 5. The relationships between \log_{10} body mass (g) and inflection air temperature ($T_{inflection}$, the air temperature above which vasodilation of the bill occurs) of nine species. Avian orders are indicated as follows: Bucerotiformes (hornbills and ground hornbills) - triangles, Piciformes (*Toco toucans*) - squares and Accipitriformes (vultures) - diamonds. The three species from this study, *Bycanistes bucinator*, *Ceratogymna atrata* and *Bycanistes brevis*, are indicated using a, b and c, respectively. (See Appendix A.2., Table A.11).

the subsequent sections.

Patterns of increases in $T_{beak} - T_{air}$ gradients above inflection T_{air} values in our study species differed from those documented in other bucerotiform species. In southern ground-hornbills and southern yellow-billed hornbills, T_{beak} increased abruptly by $\sim 6^\circ\text{C}$ in the former and $\sim 3^\circ\text{C}$ in the latter when T_{air} exceeded the $T_{inflection}$ values of 22°C and 30°C , respectively (Janse van Vuuren et al., 2020; van de Ven et al., 2016). Similarly abrupt increases in $T_{beak} - T_{air}$ were absent in the two *Bycanistes* spp. we investigated here, with $T_{beak} - T_{air}$ increasing linearly. Several black-casqued hornbills increased $T_{beak} - T_{air}$ immediately above $T_{inflection}$, but showed approximately linear increases in $T_{beak} - T_{air}$ with increasing T_{air} thereafter. In toco toucans, patterns of increases in $T_{beak} - T_{air}$ differed along the length of the beak, with a rapid, $\sim 4^\circ\text{C}$ increase in $T_{beak} - T_{air}$ at the proximal region of the beak, but a more gradual increase at the distal end (Fig. 2C and D of Tattersall et al., 2009). The

functional significance of this variation among species remains unclear, but we speculate it involves factors such as surface area, rhamphotheca thickness and interspecific variation in the structure of beak microvasculature.

Non-evaporative heat dissipation via thermal radiators is thought to be particularly important for birds occupying water-limited environments (Greenberg et al., 2012), but our study reveals that hornbills associated with humid lowlands can dissipate a considerable amount of heat through their beaks (31–83 % of estimated active-phase thermoneutral RMR). These findings support the view that beak heat loss is important in birds occupying a wide range of habitats. In the case of our study species and other occupants of humid lowlands, evaporative cooling during hot weather can be severely constrained by humidity. In trumpeter hornbills, for example, wet bulb temperatures of $\sim 32^\circ\text{C}$ impede evaporative cooling to the extent that the species can dissipate only 36 % of metabolic heat production (B. Coulson, unpublished data).

An additional factor enhancing the adaptive value of non-evaporative heat dissipation among birds inhabiting hot, humid regions concerns their significantly greater hyperthermia tolerance, characterised by higher maximum T_b during acute heat exposure compared to their counterparts from other habitats (Weathers 1997; Freeman et al., 2022, 2024). Trumpeter hornbills tolerate T_b as high as 46.6°C under humid conditions (B. Coulson, unpublished data), and this pronounced hyperthermia increases the range of T_{air} over which a positive $T_{beak} - T_{air}$ gradient can be maintained to facilitate non-evaporative heat dissipation. The observation that some hornbills in our study maintained $T_{beak} - T_{air}$ gradients of $\sim 12^\circ\text{C}$ at $T_{air} = 30^\circ\text{C}$ (Fig. 2) lends support to the notion that hyperthermia is likely an important aspect of heat dissipation via the avian beak, particular in humid environments where it may mitigate diminished scope for evaporative dissipation of heat loads (Weathers, 1997; Freeman et al., 2024). In very hot, arid environments where T_{air} regularly exceeds T_b and birds spend more time in exposed microsites with high solar heat loads, large, highly vascularized beaks may incur costs during very hot weather on account of heat uptake when environmental temperatures exceed T_b (van de Ven et al., 2016). An unanswered question concerns whether birds, when faced with environmental temperatures exceeding T_b , can reduce heat gain via the beak by reducing blood flow to this structure.

Regulated heat dissipation in all three study species involved their casques, consistent with findings for Southern cassowaries (*Casuari casuarius*) in which heat loss across the casque reached 2.04 W at $T_{air} =$

35 °C (Eastick et al., 2019). Among hornbills, large-casqued genera such *Ceratogymna*, *Bycanistes*, *Buceros*, *Anthracooceros* and *Rhabdotornhinus* are all forest-dwelling, whereas many species of the smaller-casqued *Tockus* and *Lophoceros* occupy drier areas. Although arguments for the evolution of casques in hornbills often focus on intraspecific signalling (Mayr, 2018), including sound projection (Alexander et al., 1994), our study raises the possibility that thermal considerations may also have been involved in hornbill casque evolution.

Patterns of T_{facial} suggest that blood regulation differed among our three study species. The linear pattern and lack of any inflections in T_{facial} of trumpeter hornbills suggest no active regulation of blood flow to these unfeathered regions, whereas the presence of inflections for T_{facial} in silvery-cheeked and black-casqued hornbills suggest fine-scale changes in blood flow to subcutaneous capillary beds in these regions. The differences in patterns between these species, however, suggest differing relationships between T_{air} and vascular adjustments. In addition, the inflection evident in T_{wattle} in black-casqued also indicates changes in blood flow to this region. Surface temperatures of facial and gular skin in southern ground-hornbills followed patterns more similar to that of black-casqued than trumpeter or silvery-cheeked hornbills (Janse van Vuuren et al., 2020).

The negative scaling with body mass of the inflection T_{air} , indicating the threshold for vascular recruitment supported our second prediction and reveals the large variation among birds in the environmental temperature at which blood flow to the beak commences (Appendix A.2, Table A.9.). These decreases in inflection T_{air} with increasing M_b are consistent with both theoretical predictions and empirical evidence for the M_b -dependence of the lower critical limit of thermoneutrality among endotherms (e.g., Riek and Geiser, 2013). It is striking that toco toucans show the largest absolute residual, with an inflection T_{air} equivalent to 4.84 °C lower than the allometrically predicted value (Fig. 5), although our analysis is limited by the small number of species (nine) and orders (three) represented.

5. Conclusion

Our data show that Afrotropical forest hornbills have evolved non-evaporative mechanisms for heat loss as effective and energetically inexpensive thermoregulatory processes relative to other avenues of heat regulation such as panting (Chaves et al., 2023). This is important as these species occur in lowland habitats characterised by humid heat, shown to impede the efficiency of evaporative cooling (Weathers, 1997; Freeman et al., 2024; Coulson et al., in prep). Bird species investigated to date have shown the capacity to dissipate heat across their beaks. Our data, and those from other studies, draw attention to the variation in threshold temperatures of the beak depending on a bird's body size. This variation among species underscores the importance of empirical data and may have implications for parametrizing biophysical models, such as NicheMapR (Kearney et al., 2021) that may improve the accuracy of these models going forward. Future research encompassing the validation of biophysical models that include the effects of thermal radiators may improve the precision of these models when predicting species vulnerability to environmental change.

CRedit authorship contribution statement

Bianca Coulson: Writing – original draft, Investigation, Formal analysis, Conceptualization. **Marc T. Freeman:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Juanita Wesels:** Investigation. **Andrew E. McKechnie:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Ethics

This work was approved by the Animal Ethics Committee of the University of Pretoria (protocol NAS063/2022) and the Research and

Scientific Ethics Committee of the South African National Biodiversity Institute (SANBI NZG/RES P2022/16). Trumpeter hornbills were captured under permit OP 3026/2022 from KwaZulu Natal province's Ezemvelo KZN Wildlife.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2024.103993>.

Data availability

The data collected in this study are available at <https://data.mendeley.com/datasets/7dsxgffjby/1>.

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