

The beak and unfeathered skin as heat radiators in the Southern Ground-hornbill

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Abstract

The avian beak is increasingly recognised as an important organ for thermoregulation, particularly in disproportionately large-beaked taxa such as toucans and hornbills. We used infrared thermography to test the prediction that Southern Ground-hornbills (*Bucorvus leadbeateri*) physiologically regulate the surface temperature of their beak (T_{beak}), as well as that of their facial (T_{facial}) and gular skin (T_{gular}) in such a way that these surfaces provide avenues for non-evaporative heat dissipation in warm weather. Our data, collected over air temperatures (T_a) ranging from 11 °C to 36 °C, supported these predictions. At $T_a < 20$ °C, T_{beak} tracked T_a , but rapidly increased to values 6-12 °C above T_a at $T_a = 20-22$ °C. The $T_{\text{beak}}-T_a$ gradient was maintained at approximately 7 °C between $T_a = 22$ °C and 28 °C, before decreasing linearly with $T_a > 28$ °C. We also found evidence for active regulation of T_{facial} and T_{gular} , with both surfaces regulated at approximately constant increments above T_a up to inflection T_a values of 22 °C and 29 °C, respectively. The presence of inflection T_a values corresponding with abrupt changes in physiological regulation of these surface areas suggests a high degree of physiological control. Estimates of heat exchange suggest that SGH may be able to dissipate up to 75 % of basal metabolic rate via these surfaces, confirming the beak and areas of unfeather skin play an important thermoregulatory role in these large, distinctive and threatened birds.

Keywords: thermal radiator, Bucorvidae, heat dissipation, thermoregulation

Introduction

Highly vascularized, uninsulated regions from which heat dissipation is modulated via vascular networks play an important role in thermoregulation in many taxa, including birds (Hagan and Heath 1980, Tattersall et al. 2009, Tattersall et al. 2018). By providing avenues for non-evaporative heat dissipation, these thermal radiators lower the need for evaporative water loss in warm environments (Tattersall et al. 2009, Tattersall et al. 2017, Tattersall et al. 2018, van de Ven et al. 2016). A growing body of literature reveals the avian beak to be an important and versatile thermoregulatory organ, analogous in function to thermal windows such as elephant ears (Weissenböck et al. 2010) and bat wings (Reichard et al. 2010). Moreover, correlations between beak size and thermal environments exist at both interspecific and intraspecific levels, supporting the notion that bill size has evolved in response to selection favouring heat loss in warm environments and heat conservation in cool environments (Luther and Greenberg 2014, Campbell-Tennant et al. 2015, Danner and Greenberg 2015).

That the avian beak functions as an adjustable thermal radiator was first demonstrated for Toco Toucans (*Ramphastos toco*; Tattersall et al. 2009). These authors found that this species uses its enormous beak to dissipate up to 100 % of total metabolic heat production. To dissipate heat, vascular networks within the dermis, between the bony and horny part of the beak, dilate to increase peripheral blood flow, increasing beak surface temperature and creating a thermal gradient between the beak surface and the cooler external environment (Tattersall et al. 2009). The avian beak's capacity to function as an adjustable thermal radiator has subsequently been demonstrated for other species (Tattersall et al. 2018, Tattersall et al. 2017, van de Ven et al. 2016). The Old World Hornbills (Bucerotidae) show considerable morphological convergence with toucans by having disproportionately large beaks, and van de Ven et al. (2016) demonstrated that in Southern Yellow-Billed Hornbills (*Tockus leucomelas*) an average of 8% of total non-evaporative heat dissipation occurs via the beak. A similarly adjustable capacity to radiate heat has recently been demonstrated for the casque of cassowaries (Eastick et al. 2019), suggesting that adjustable heat radiators are more widespread among birds than previously thought.

The ground-hornbills (Bucorvidae) consist of two species endemic to Africa. Southern Ground-Hornbills (hereafter, SGHs) are large, turkey-sized birds with black body plumage and disproportionately large beaks that occupy savanna and woodland habitats in southern Africa, where they regularly encounter air temperatures (T_a)

approaching or exceeding avian normothermic body temperature (T_b) (Kemp and Kemp 1980). The species forages on the ground, often in the sun, which likely results in SGH experiencing high operative temperatures (Bakken 1976, Robinson et al. 1976) while foraging (Kemp and Kemp 1980). The beak of the SGH is a large, curved and hardened structure, resembling the beaks of toucans and other hornbills (Kemp 2005). In addition, SGH have large patches of bare facial and gular skin (Figure 1), the thermoregulatory role of which has not been explored despite several authors arguing that brightly coloured, unfeathered regions of the head and neck can act as important sites of heat loss (Buchholz 1996, Crowe and Withers 1979). Arguments for an active thermoregulatory role of unfeathered regions of the skin would be supported if blood flow to these regions is regulated in such a way as to maximise heat dissipation under warm conditions.

We hypothesized that the beak and facial and gular skin of the SGH play an important role in thermoregulation, and quantified changes in beak surface temperature across a range of T_a using infrared thermography. We predicted that, in shaded microsites, beak surface temperature (T_{beak}) tracks T_a at low and moderate values, but that the $T_{\text{beak}}-T_a$ gradient rapidly increases at some T_a threshold, thereafter gradually decreasing as T_a approaches normothermic T_b . We also predicted that gradients between surface temperature of the facial (T_{facial}) and gular (T_{gular}) skin of SGH and T_a vary in a manner indicative of active regulation of these regions.

Materials and Methods

Study sites

Data were collected from eight female SGH at two locations, the National Zoological Garden of South Africa in Pretoria (S 25° 44', E 28° 12') and the Mabula Ground Hornbill Project's facility (in partnership with Mpumalanga Tourism and Parks Agency) at Loskop Dam Nature Reserve (S 25° 24', E 29° 21'). Individuals were housed in large flight aviaries (50-100 m²), where they were provided with a diet of day-old chicks, rodents, chicken heads and boiled eggs. Data were collected during the austral summer in December 2018 and January 2019, and winter in July 2019. Images were taken between 05:00 and 18:00, covering a T_a range of 11 – 36 °C. Our approach of obtaining images from unrestrained birds experiencing natural thermal conditions follows that of (Eastick et al. 2019), precluding the experimental manipulation of T_a but

obviating the need to restrain individuals within temperature-controlled chambers (e.g., Tattersall et al. 2009, van de Ven et al. 2016).

Experimental design and data analysis

Measurements of beak and facial skin surface temperatures were taken using thermal imagery. Individuals were photographed with a handheld thermal imaging camera (FLIR Model T600-series, FLIR Systems, Wilsonville, Oregon, USA) from a distance of 0.5 – 4 m. Images were taken only after individuals spent a minimum of 3 min in the shade. Prior to starting the study, we checked the camera's calibration by comparing the surface temperature of water in a circulating water bath against a mercury-in-glass thermometer with NIST-traceable accuracy. Camera parameters set for each image included air temperature (T_a), reflected temperature and relative humidity, with an emissivity of 0.96 assumed. Measurements of T_a and relative humidity were obtained using a hand-held weather meter (Kestrel 3500 Delta T, Nielsen-Kellerman, Boothwyn, USA), with the air temperature sensor checked against a mercury-in-glass thermometer with NIST-traceable accuracy and the humidity sensor against a dewpoint generator (DG-4, Sable Systems, Las Vegas NV, USA)..

Average surface temperature was measured for three regions, the beak, facial skin and gular skin (Figure 1) by analysing thermal images with ThermaCAM software (ThermaCAM Researcher Pro 2.9, FLIR Systems Inc, Wilsonville). The polygon function of this software allows for accurate measurements of the body part or area under investigation and was used for all areas under study. All statistical analyses were performed in R 3.5.2 (R Development Core Team 2011). We also used the *segmented* package (Muggeo 2009) to fit segmented models and identify inflections. Linear mixed-effects models were fitted using the *nlme* package (Pinheiro et al. 2009). To analyse the effect of air temperature (T_a), $T_{\text{beak}} - T_a$ was used as the response variable, with T_a , absolute humidity (kPa) and the T_a X humidity interaction term as predictors and bird identity as a random factor. To quantify how T_{beak} varied with T_a above and below the threshold T_a , we fitted separate linear mixed-effects models for the data above and below the threshold T_a . AICc values provided by the *dredge* function of the *MuMin* package (Bartoń 2013) were used to select best-fits models for $T_{\text{beak}} - T_a$ above and below the threshold T_a respectively. The same approach was used to analyse relationships between T_a and surface temperatures of facial and gular skin data.

To estimate the contribution of heat exchange across the beak, facial and gular skin to overall heat balance of SHG, we calculated total heat exchange (Q_t) for each region as the sum of radiative (Q_r) and convective (Q_c) heat exchange, following Tattersall et al. (2009). Briefly, $Q_r = \varepsilon\sigma A(T_s^4 - T_a^4)$, where ε is combined emissivity, σ is the Stephan-Boltzmann constant, A is surface area in m^2 and T_s and T_a are surface and ambient temperatures (which we assumed to equal air temperature) in $^{\circ}K$, and $Q_c = h_c A(T_s - T_a)$, where h_c is the convective heat transfer coefficient for each region (see Tattersall et al. 2009 for details of calculations). We measured surface areas of the beak, facial skin and gular skin, as well as characteristic dimension required for estimates of h_c , in two SGH specimens at the Ditsong National Museum of Natural History, Pretoria, and used the average value for these two birds for all subsequent calculations. Because the birds in this study were not held in a controlled thermal environment within a chamber during data collection, our estimates of Q_r and Q_c are not as reliable of those of previous workers (e.g. Tattersall et al. 2009, van de Ven et al. 2016). Because of the complex radiative environments experienced in outdoor conditions, we likely overestimate Q_r , whereas any air movement likely causes Q_c to be underestimated (Campbell and Norman 1998).

Results

Analysis of the surface temperatures of the beak, facial skin and gular skin provided evidence that SGH can regulate heat exchange across all three of these areas. In the case of the beak, T_{beak} remained within 1-2 $^{\circ}C$ of T_a when $T_a < 20^{\circ}C$, but then increased rapidly between $T_a = 20^{\circ}C$ and $T_a = 22^{\circ}C$ to values ranging between 5 $^{\circ}C$ and $> 10^{\circ}C$ above T_a (Figures 1,2). At $T_a > 20^{\circ}C$, an inflection occurred at $T_a = 28.01 \pm 0.77$ (SE) $^{\circ}C$, with the relationship between $T_{\text{beak}} - T_a$ and T_a differing above and below this inflection. Below the inflection ($22^{\circ}C < T_a < 28.01^{\circ}C$), the best model for $T_{\text{beak}} - T_a$ was the null model (Table 1), revealing $T_{\text{beak}} - T_a$ to be independent of T_a and humidity. Above the inflection, however, $T_{\text{beak}} - T_a$ was significantly and negatively related to T_a (Table 1, $F_{1,48} = 54.304$, $P < 0.001$), declining at a rate of 0.54 $^{\circ}C$ per 1 $^{\circ}C$ increase in T_a (Figure 1). Estimated Q_t across the beak increased from 0.1 – 0.4 W at $T_a < 20^{\circ}C$ to a maximum of 3.1 W at $T_a = 26^{\circ}C$, before decreasing at higher T_a as $T_{\text{beak}} - T_a$ decreased.

For facial skin, the relationship between T_{facial} and T_a also showed an inflection point, at $T_a = 21.96 \pm 0.55$ (SE) $^{\circ}C$ (Figure 1). Below this inflection, the null model emerged as the best, with $T_{\text{facial}} - T_a$ independent of T_a and humidity (Table 1). Above the

inflection, $T_{\text{facial}}-T_a$ decreased significantly with increasing T_a (Table 1, $F_{1,140} = 377.849$, $P < 0.001$) at a rate of $0.43\text{ }^{\circ}\text{C}$ per $1\text{ }^{\circ}\text{C}$ increase in T_a (Figure 1). Estimated Q_t for facial skin averaged 0.83 W at $T_a < 26\text{ }^{\circ}\text{C}$. Gular skin showed an inflection at a higher $T_a = 29.64 \pm 0.46$ (SE) $^{\circ}\text{C}$. As was the case for T_{facial} , below the inflection the null model provided the best explanation for determinants of T_{gular} (Table 1), whereas at $T_a > 29.64\text{ }^{\circ}\text{C}$ $T_{\text{gular}}-T_a$ was significantly and negatively related to T_a (Table 1, $F_{1,54} = 192.635$, $P < 0.001$), decreasing steeply at $0.74\text{ }^{\circ}\text{C}$ per $1\text{ }^{\circ}\text{C}$ increase in T_a . Estimated Q_t for gular skin averaged 2.27 W at $T_a < 26\text{ }^{\circ}\text{C}$. Total Q_r for the beak, facial skin and gular skin increased from $3.0\text{-}3.5\text{ W}$ at the lowest T_a values to a maximum of 6.2 W at $T_a = 26\text{ }^{\circ}\text{C}$. before decreasing to 2.2 W at $T_a = 35\text{ }^{\circ}\text{C}$.

High T_a was also associated with reductions in activity, panting, shade-seeking, wing-dropping and perching off the ground. At $T_a > 35\text{ }^{\circ}\text{C}$, some individuals were observed to secrete fluid from their nostrils, which appeared to augment evaporative cooling from parts of the bill surface (Figure 3). Some individuals were also observed rubbing their beaks on feathers, apparently in order to spread the secretion across the beak surface.

Discussion

Our data confirm that the beak of the Southern Ground-hornbill functions as a controllable heat radiator, with enhanced heat loss from the bill commencing at $T_a = 20\text{-}22\text{ }^{\circ}\text{C}$. At higher T_a , the presence of an inflection point suggests precise control of T_{beak} , with an approximately constant $T_{\text{beak}}-T_a$ gradient regulated between $T_a = 23$ and $28\text{ }^{\circ}\text{C}$ before this gradient decreases at higher T_a . Our data also suggest active regulation of the surface temperatures of the facial and gular skin, with the $T_{\text{facial}}-T_a$ and $T_{\text{gular}}-T_a$ gradients maintained at approximately constant levels at $T_a < 22\text{ }^{\circ}\text{C}$ and $T_a < 28\text{ }^{\circ}\text{C}$, respectively.

Patterns of T_{beak} we observed in SGH confirm that this species, like Toco Toucans (Tattersall et al. 2009), Southern Yellow-billed Hornbills (van de Ven et al. 2016) and four species of Darwin's finches (Tattersall et al. 2018) use the bill as a controllable heat radiator via adjustments of blood flow to the beak vasculature. Besides supporting the notion that heat loss via this avenue is more important among birds than previously thought, our data also reiterate interspecific variation in patterns of T_{beak} regulation: rapid increases in T_{beak} at $T_a = 20\text{-}22\text{ }^{\circ}\text{C}$ in SGH occurred at similar T_a values as maximum $T_{\text{beak}}-T_a$ gradients in Toco Toucans (Tattersall et al. 2009), but at much

lower values than in Southern Yellow-billed Hornbills ($T_a = 30-31$ °C; (van de Ven et al. 2016). The marked difference between SGH and Southern Yellow-billed Hornbills likely reflects the much smaller size of the latter species (200-250 g), but it is noteworthy that Toco Toucans and SGH also differ substantially in body mass (~700 g versus 3,300-4,200 g; (Kemp 2005). *A priori*, non-evaporative heat loss from the avian beak and other unfeathered surfaces may be expected commence at lower T_a in larger species, on account of the constraints imposed on heat loss by smaller surface area-volume ratios.

One novel observation to emerge from our T_{beak} data concerns differences in the relationships between $T_{\text{beak}}-T_a$ and T_a above and below $T_a = \sim 28$ °C. The constant $T_{\text{beak}}-T_a$ gradient at $T_a = 23-28$ °C suggests precise control of beak blood flow and hence T_{beak} over this T_a range. This pattern is broadly similar to relationships between the T_{beak} and T_a in adult Toco Toucans, and the distal (but not proximal) section of beaks of juveniles (Figure 2C-F of (Tattersall et al. 2009). The relationship between $T_{\text{beak}}-T_a$ and $T_a > 30$ °C in Southern Yellow-billed Hornbills was modelled with a single linear model, but visual inspection does suggest that an inflection point could exist at $T_a = \sim 36$ °C for the surface temperature of the entire beak (lower left panel, Figure 5 of (van de Ven et al. 2016). Collectively, these patterns suggest that some species regulate T_{beak} in more complex ways than previously documented. Another variable whose importance in heat exchange across the avian beak remains uninvestigated is facultative hyperthermia at high T_a , which is widespread among birds (Gerson et al. 2019); increases in T_b (and hence the temperature of blood supplied to the beak) could potentially allow birds to maintain $T_{\text{beak}}-T_a$ gradients under hotter conditions than if T_b remains at normothermic levels.

The maintenance of approximately constant $T_{\text{facial}}-T_a$ and $T_{\text{gular}}-T_a$ below respective T_a inflections suggest that blood flow to the facial and gular skin is under fine control, almost certainly involving fine-scale changes in blood flow to subcutaneous capillary beds. In domestic fowls, blood flow in unfeathered skin increases to much greater extent than in feathered skin during heat exposure (~20-fold versus ~ 5-fold, respectively (Wolfenson 1983), underscoring the potential thermoregulatory importance of areas of bare skin. The strong negative correlations in SGH between $T_{\text{beak}}-T_a$, $T_{\text{facial}}-T_a$ and $T_{\text{gular}}-T_a$ and T_a above the respective inflection points correspond, we suspect, with maximum blood flow to these regions; the regression models for all three parameters as functions of T_a have x-intercepts at $T_a = 40-43$ °C, typical of avian body temperature

(Dawson and Whittow 2000). However, the ~ 8 °C difference between the inflection T_a values for T_{facial} and T_{gular} suggest differences in the regulation of blood flow to these areas.

Humidity did not emerge as a significant predictor of heat loss from the beak, facial skin or gular skin during our study, but this result may reflect the relatively narrow range of humidity values (48.0 ± 10.8 % at $T_a > 30$ °C). Given the potential importance of non-evaporative cooling pathways under humid conditions (Powers 1992, van Dyk et al. 2019) and the tropical lowland distribution of many hornbill species (Kemp and Woodcock 1995), the influence of humidity on the regulation of heat loss from hornbills' beaks warrants further investigation.

Our data suggest the beak as well as the facial and gular skin of SGH play important thermoregulatory roles. This species is relatively intolerant of hot weather, commencing heat dissipation behaviours at T_a as low as 26 °C and typically resting in shaded microsites at $T_a > 26$ °C (Kemp and Kemp 1980). Retaating to shaded microsites greatly affects their movements, especially in the hot, summer months when group were recorded to travel farthest when ambient temperatures were cool (10–15 °C), but then distances covered decreased markedly at temperatures above 25 °C (Zoghby et al. 2015). In light of these observed behavioural thermoregulatory adjustments at $T_a > \sim 25$ °C (Zoghby et al. 2015, Kemp and Kemp 1980), our findings that enhanced heat loss from the beak commences at $T_a = 20\text{-}22$ °C is not surprising, nor is the observation that facial and gular skin show evidence of being fully vasodilated by ~ 22 °C and ~ 30 °C, respectively.

Our estimated maximum rate of Q_r from the beak, facial skin and gular skin combined, 6.2 W, is equivalent to 76 % of the allometrically-expected basal metabolic rate of a 3.77-kg non-passerine (Londoño et al. 2015). Although at best an approximation of maximum rates of heat loss, these estimates nonetheless confirm that the beak and unfeathered skin of SGH provide a powerful mechanism to dissipate heat. Maximum rates of heat loss from the beak in Southern Yellow-billed Hornbills averaged $\sim 8\%$ of total heat loss (van de Ven et al. 2016), compared to typical values of 30-60 % in Toco Toucans (Tattersall et al. 2009); our estimates for SGH are not directly comparable as we expressed maximum Q_t as a fraction of predicted BMR. Our observations concerning the secretion of fluid onto the beak surfaces also reveal that SGH can increase beak heat loss even further using an evaporative pathway. The fluid secretions from the nostrils we observed at high T_a have been previously reported, also

at $T_a = \sim 35^\circ\text{C}$ (Kemp and Kemp 1980). These authors dissected a SGH specimen and found no salt glands, leading them to speculate that the fluid probably represents dilute nasal mucous.

Our study has several limitations. First, individuals were exposed to differing levels of direct solar radiation before images were captured, although we attempted to account for this potential confounding influence by including only images captured after an individual spent a minimum period of 3 min within a shaded area. Second, the lack of detailed measurements of the thermal environments experienced by individual birds precludes accurate calculations of heat exchange across the various body surfaces we investigated here, as previous authors have reported (Tattersall et al. 2009, Tattersall et al. 2018, van de Ven et al. 2016, Eastick et al. 2019).

In conclusion, the regulation of heat exchange across the beak surface of SGH we report here adds to the evidence for the avian beak being an important thermoregulatory organ and reiterates that large-beaked species can dissipate heat rapidly via this avenue. The presence of fine control of beak heat loss in representatives both the hornbills (Bucerotidae; (van de Ven et al. 2016) and ground-hornbills (Bucorvidae; present study) suggests that this capacity is widespread among these distinctive, large-billed Old World taxa. Moreover, the diversity of hornbills across Africa and Asia make them an ideal taxon for testing hypotheses concerning the ecological correlates of heat loss via the beak and unfeathered skin and the evolution of these avian thermoregulatory mechanisms.

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Figure legends

Figure 1. Gradients between the surface temperatures of the beak (top panel), facial skin (middle panel) and gular skin (bottom panel) of Southern Ground-hornbills (*Bucorvus leadbeateri*) and air temperature (T_a) revealed several inflection points indicating that heat transfer across these surfaces is under physiological control. Solid lines represent relationships modelled using linear mixed models as described in the text. Photograph courtesy of Warwick Tarboton.

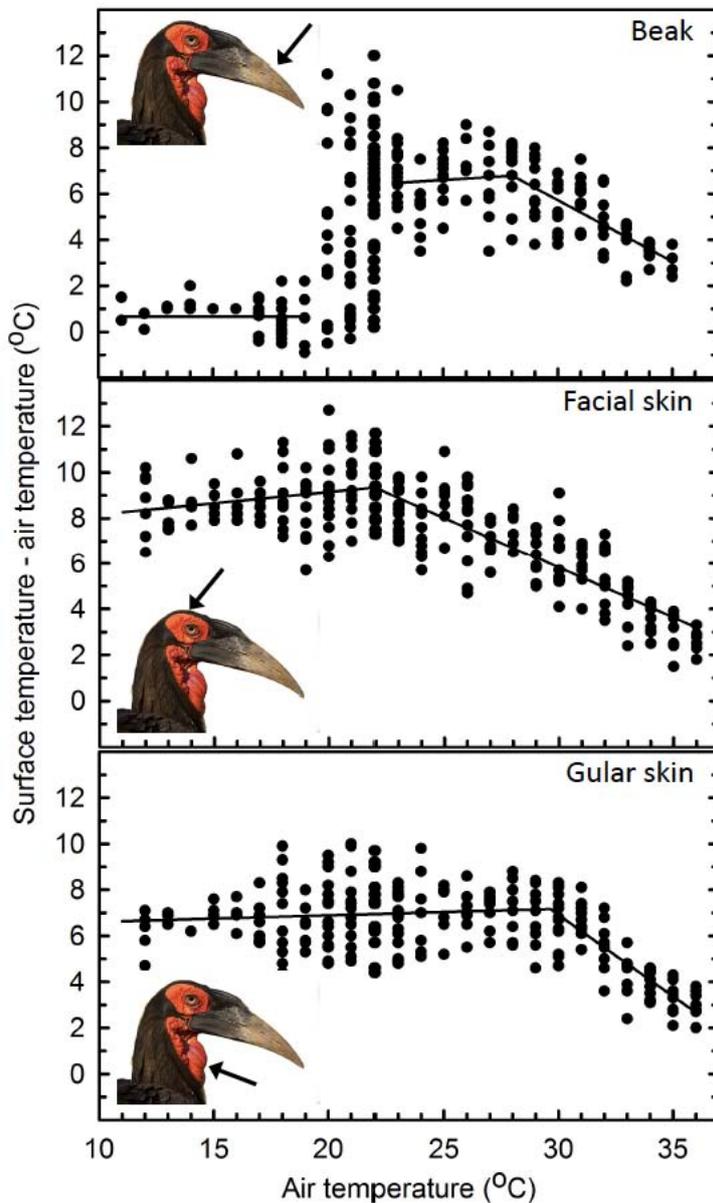


Figure 2. Beak surface temperature (T_{beak}) as a function of air temperature (T_{a}) in Southern Ground-hornbills (*Bucorvus leadbeateri*) held in large outdoor enclosures. The dashed line shows $T_{\text{beak}} = T_{\text{a}}$. Thermal images on the right are of birds at T_{a} values of 15 °C, 25 °C and 30 °C. The average T_{beak} is indicated in each panel.

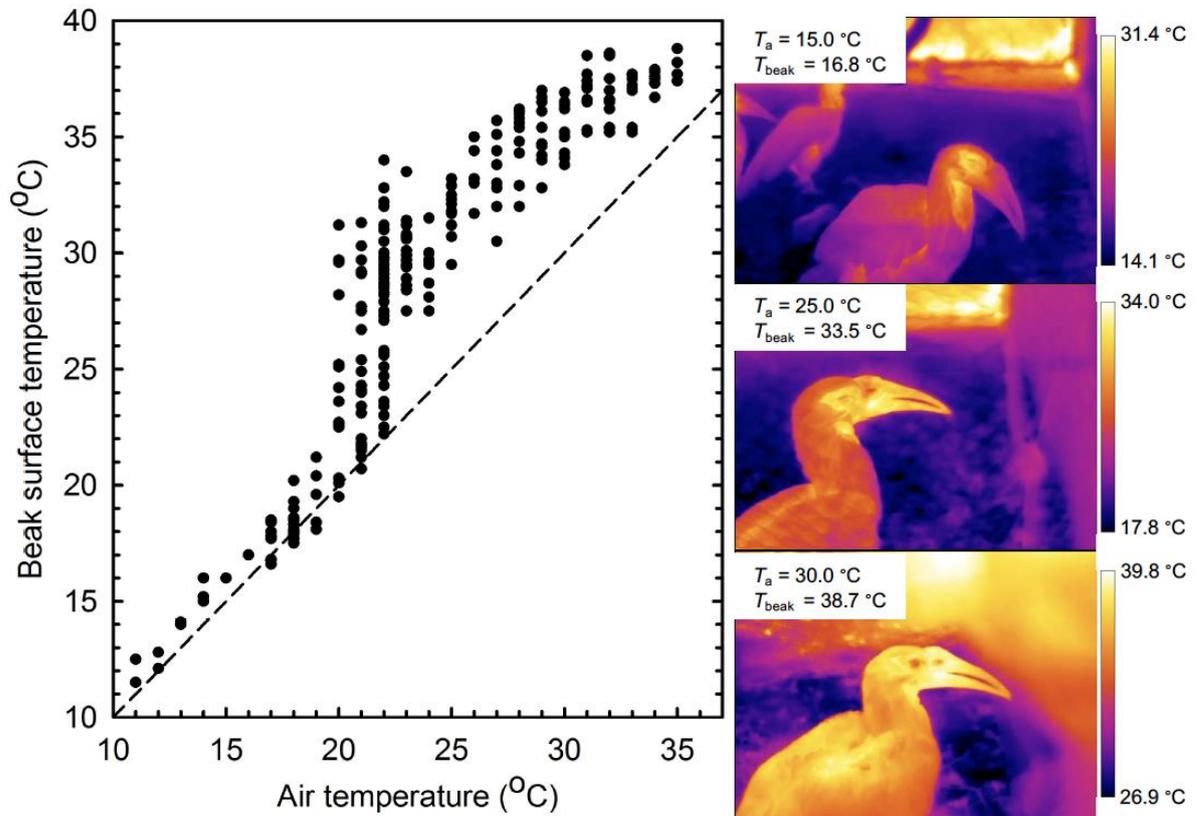


Figure 3. At air temperatures of ~ 35 °C, Southern Ground-hornbills (*Bucorvus leadbeateri*) held in large outdoor enclosures secreted fluid onto the outer surface of the beak, leading to localised areas of reduced beak surface temperature on account of evaporative cooling, indicated on the thermal images using dashed white ovals. This is the same phenomenon referred to “nasal watering” by Kemp and Kemp (1980).

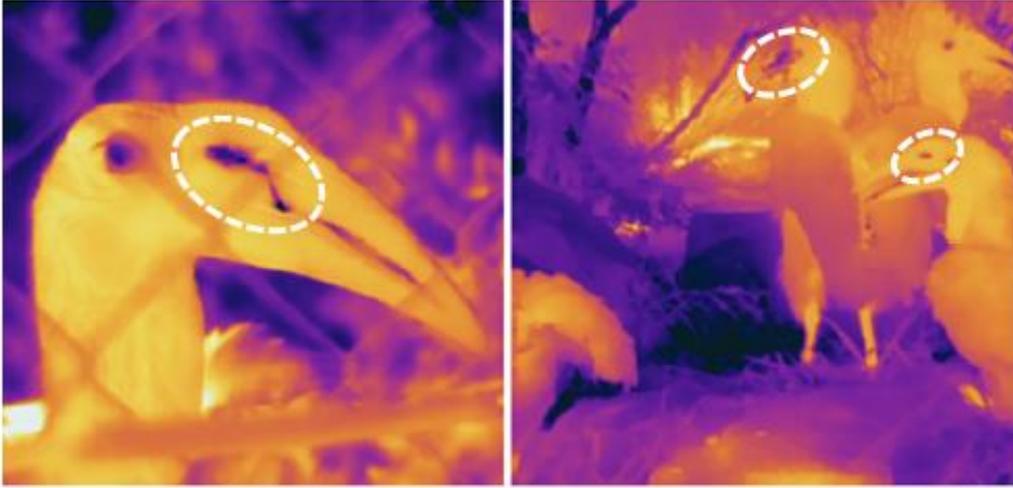


Table Legend:

Table 1: Summary of model selection outcomes for gradients between the surface temperatures of the beak (T_{beak}), facial skin (T_{facial}) and gular skin (T_{gular}) of Southern Ground-hornbills (*Bucorvus leadbeateri*) and air temperature (T_a). Individual was included as a random effect in all candidate models. Degrees of freedom (DF), Akaike Information Criterion corrected for small sample sizes (AICc), ΔAICc and model weight are provided for each candidate model. Ranges of T_a are based on inflection points identified as described in the text.

| Model | DF | AICc | ΔAICc | Weight |
|--|----|-------|---------------------|--------|
| Beak | | | | |
| $T_a < 20^\circ\text{C}$ | | | | |
| Null | 3 | 79.3 | | 0.908 |
| Humidity | 4 | 84.8 | 5.49 | 0.058 |
| T_a | 4 | 86.2 | 6.90 | 0.029 |
| T_a + Humidity | 5 | 90.6 | 11.31 | 0.003 |
| T_a + RH + T_a *Humidity | 6 | 91.9 | 12.61 | 0.002 |
| $23^\circ\text{C} < T_a < 28.01^\circ\text{C}$ | | | | |
| Null | 3 | 232.8 | | 0.903 |
| T_a | 4 | 237.7 | 4.85 | 0.080 |
| Humidity | 4 | 241.3 | 8.42 | 0.013 |
| T_a + RH + T_a *Humidity | 6 | 244.3 | 11.47 | 0.003 |
| T_a + Humidity | 5 | 246.1 | 13.29 | 0.001 |
| $T_a < 28.01^\circ\text{C}$ | | | | |
| T_a | 4 | 181.2 | | 0.987 |
| T_a + Humidity | 5 | 189.9 | 8.75 | 0.012 |
| T_a + RH + T_a *Humidity | 6 | 197.6 | 16.43 | <0.001 |
| Null | 3 | 212.3 | 31.17 | <0.001 |
| Humidity | 4 | 217.7 | 36.54 | <0.001 |
| Facial skin | | | | |
| $T_a < 21.96^\circ\text{C}$ | | | | |
| Null | 3 | 296.0 | | 0.669 |
| T_a | 4 | 297.6 | 1.50 | 0.316 |

| | | | | |
|---------------------------------------|---|-------|--------|--------|
| Humidity | 4 | 304.6 | 8.54 | 0.009 |
| T_a + Humidity | 5 | 305.5 | 9.44 | 0.006 |
| T_a + RH + T_a *Humidity | 6 | 314.0 | 17.95 | <0.001 |
| $T_a > 21.96$ °C | | | | |
| T_a | 4 | 496.3 | | 0.991 |
| T_a + Humidity | 5 | 505.8 | 9.50 | 0.009 |
| T_a + RH + T_a *Humidity | 6 | 518.4 | 22.05 | <0.001 |
| Humidity | 4 | 671.5 | 175.18 | <0.001 |
| Null | 3 | 676.7 | 180.41 | <0.001 |
| Gular skin | | | | |
| $T_a < 29.64$ °C | | | | |
| Null | 3 | 517.0 | | 0.958 |
| T_a | 4 | 523.6 | 6.63 | 0.035 |
| Humidity | 4 | 526.8 | 9.81 | 0.007 |
| T_a + Humidity | 5 | 532.9 | 15.95 | <0.001 |
| T_a + RH + T_a *Humidity | 6 | 546.0 | 28.98 | <0.001 |
| $T_a > 29.64$ °C | | | | |
| T_a | 4 | 179.5 | | 0.989 |
| T_a + Humidity | 5 | 188.6 | 9.10 | 0.010 |
| T_a + RH + T_a *Humidity | 6 | 198.9 | 19.47 | <0.001 |
| Null | 3 | 255.3 | 75.87 | <0.001 |
| Humidity | 4 | 258.8 | 79.29 | <0.001 |