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# Heat Exchange from the Toucan Bill Reveals a Controllable Vascular Thermal Radiator

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The toco toucan (*Ramphastos toco*), the largest member of the toucan family, possesses the largest beak relative to body size of all birds. This exaggerated feature has received various interpretations, from serving as a sexual ornament to being a refined adaptation for feeding. However, it is also a significant surface area for heat exchange. Here we show the remarkable capacity of the toco toucan to regulate heat distribution by modifying blood flow, using the bill as a transient thermal radiator. Our results indicate that the toucan's bill is, relative to its size, one of the largest thermal windows in the animal kingdom, rivaling elephants' ears in its ability to radiate body heat.

In the hall of animal oddities, the toucan's enlarged bill is the avian example of exaggeration, being a source of debate since Buffon labeled it a "grossly monstrous" appendage (1). Even Darwin was intrigued, stating that "toucans may owe the enormous size of their beaks to sexual selection, for the sake of displaying the diversified and vivid stripes of colour with which these organs are ornamented" (2). More recent explanations for the oversized bill include fruit peeling (3), nest predation (4–6), social selection in the context of territorial defense (7), and, finally, serving as a visual warning (6). Although the selective

forces that led to the large bills of present-day toucans remain elusive, the current use, costs, and proximal consequences can be examined. We investigated the role of the toucan bill in thermoregulation. As must any endothermic organism, toucans regulate their body temperature primarily by balancing metabolic heat production with heat exchange with the environment. Therefore, a large and uninsulated appendage, such as the bill, may be an important avenue for heat exchange (8–11).

We focused on the toco toucan (*Ramphastos toco* Muller, 1776), which has the largest bill of all the toucans (12). The bill has a network of superficial blood vessels supporting the horny ramphotheca (13, 14) (Fig. 1). Therefore, the toucan's bill combines all the important features of a candidate thermal radiator: It is enlarged, uninsulated, and well vascularized (8, 9, 11, 15). It is, however, crucial that blood flow be ad-

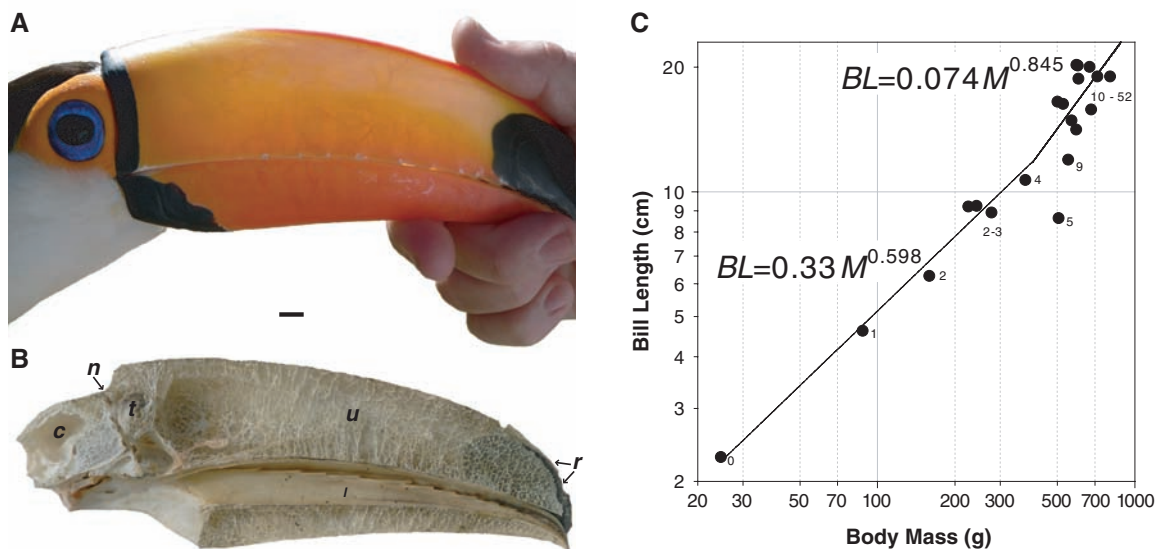
justable in order to control heat exchange from the bill. We examined whether the toucan's bill can operate as a thermal window for heat loss, capable of being "opened" within and above the thermal neutral zone and "closed" to conserve metabolic heat at lower temperatures. We used infrared thermography (15) to examine the effects of changing ambient temperature ( $T_a$ ) on the heat exchange profile of different regions of the bird's body (16).

The bill of the toucan attains its remarkable size through a steep ontogenetic growth (Fig. 1), leading to a bill surface area 25 to 40 times larger than that predicted from scaling relationships (17). Changes in bill length follow a moderate trajectory during the first 4 to 5 weeks of life, scaling with positive allometry, relative to body mass (bill length = 0.33 body mass<sup>0.598</sup>). Thereafter, when the juvenile attains nearly 80% of its adult mass, the bill exhibits more rapid allometric growth, with the scaling exponent ( $b$ ) increasing to 0.845, nearly three times predictions from isometry. This positive allometry in bill growth led us to examine whether juvenile toucans ( $n = 2$ , mass = 503 g, bill length = 10.7 cm) with actively growing bills would have the same ability to modify heat exchange as adults ( $n = 4$ , mass = 676 ± 42 g, bill length = 18.7 ± 0.4 cm; table S1).

As  $T_a$  changed, significant alterations were detected in the superficial temperature of the birds' backs (a feather-covered area with no practical ability to adjust heat exchange,  $F_{21,105} = 5.56$ ,  $P = 1 \times 10^{-14}$ ), the eye/peripalpebral region ( $F_{21,105} = 78.5$ ,  $P = 1.7 \times 10^{-54}$ ), and the proximal ( $F_{23,69} = 2.12$ ,  $P = 0.0087$ ; adults only) and distal ( $F_{23,69} = 12.1$ ,  $P = 4 \times 10^{-16}$ ; adults only) regions of the bill (Fig. 2 and fig. S1). As expected, the temperature of the feather-

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**Fig. 1.** (A) Side view of an adult toco toucan bill with visible blood vessels. (B) A sagittal section of a museum specimen demonstrating the lightweight bone (c, cranium; n, nares; t, turbinates; u, upper bill; l, lower bill; r, ramphotheca). Horizontal scale bar = 1 cm. (C) Bill length in toco toucans scales with positive allometry. Values are derived from digital photographs and measurements of toucans of known mass and age (numbers adjacent to data points indicate age in weeks). Equations describe the scaling relationship for the first 5 weeks [ $b = 0.598 \pm 0.055$ ; 95% confidence interval (CI), correlation coefficient ( $r$ ) = 0.993] separately from that for toucans older than 5 weeks ( $b = 0.845 \pm 0.503$ ; 95% CI,  $r = 0.634$ ). Both exponents were significantly greater than isometry [ $t_{df-7} (t_7) = 9.1$ ,  $P = 2 \times 10^{-5}$ , and  $t_{17} = 1.8$ ,  $P = 0.045$ , respectively].



covered areas was only slightly above ambient temperature and varied significantly only at the lowest temperatures (Fig. 2). Temperature in the eye region was kept nearly constant [30° to 36°C; compare to toucan body temperature of ~38° to 39°C (18)] at all  $T_a$ , indicating continuous blood flow to the naked skin around the eye regardless of  $T_a$ . Proximal and distal bill regions were more variable, but the prevailing trend was for larger gradients to occur between 20° and 25°C in the proximal region (in adults), with the distal region not exhibiting sustained dilation until  $T_a$  was above 25°C (Figs. 2 and 3). Thus, the proximal region of the bill was used mainly to dump heat at lower  $T_a$  (>16° to 25°C), and as temperature rose, the distal region began to receive increased blood flow, becoming warmer, helping the bird cope with the extra heat load. The greatest variance in bill surface temperatures occurs within the toucan's thermal neutral zone (~18° to 30°C) (18), according to the expectations of a thermal window. These results show that vasomotory adjustments to the bill's surface in toucans serve a thermoregulatory function. Furthermore, breathing frequency and expired air temperatures changed suddenly at air temperatures below ~21°C, paralleling the thresholds for bill vasodilation (fig. S2).

Heat loss from the bill is highly variable, and, depending on air speed and  $T_a$ , could account for as little as 25% (minimum) to as much

as 400% (maximum) of resting heat production in adults (Fig. 4), the largest reported for an animal. It is, therefore, remarkable that the toucan bill, which represents ~30 to 50% of body surface area (table S1), is capable of playing such a critical role in heat transfer, whereas other species' thermal windows, such as the duck's bill and the elephant's ear, have been estimated to account for 9 to 91% of resting heat production (19, 20). This capacity for heat loss might become a liability at low temperatures. However, toucans and toucanets are well known for tucking their bills beneath their wings and orienting their tail feathers rostrally during sleep (12) (movie S1); this posture increases insulation of the bill and mitigates heat loss incurred during sleep.

The remarkable heat exchange capacity of the bill may also be instrumental when metabolic heat production is increased, as would occur during flight [when heat production is 10 to 12 times that at rest (21)]. For one bird (fig. S3), bill temperatures ( $T_{\text{bill}}$ ) started at ~30° to 31°C and began to rise within 4 min of flight, until eventually reaching a maximum of 37°C by the 10th minute, after which the bird voluntarily terminated its flight. Thus, the heat loss from the bill could prove essential for maintaining adequate thermal balance when heat production increases.

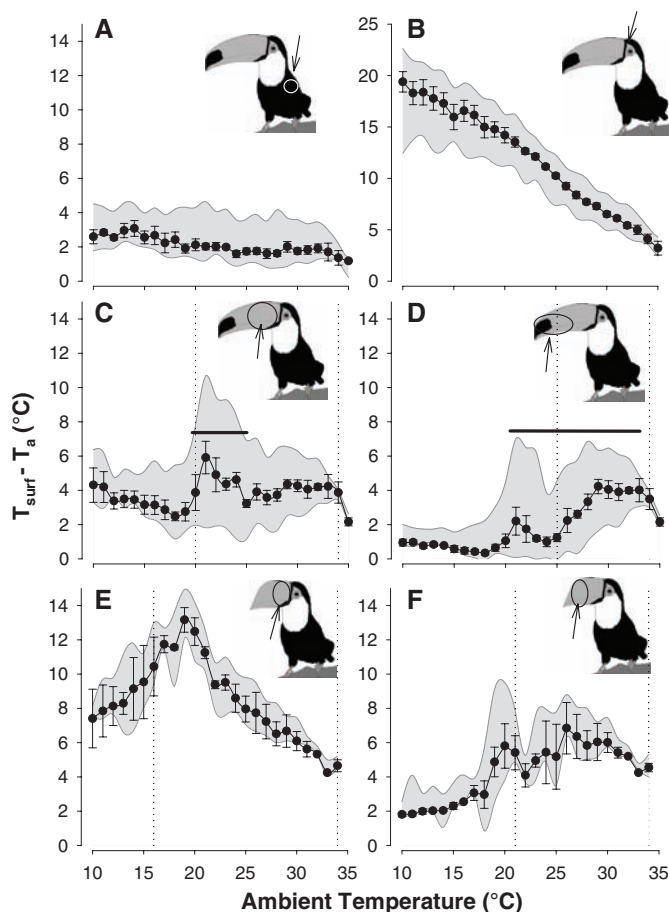
As a proportion of total heat loss, the bill routinely accounted for 30 to 60% of heat loss

in adults and juveniles. However, adults could adjust heat loss from the bill to account for as little as 5% ( $T_{\text{bill}} - T_a \sim 0$ ), and, for short periods, up to 100% of total body heat loss (Fig. 4). In contrast, juvenile toucans were unable to adjust circulation to the bill to any great extent (Fig. 4), even at very low  $T_a$  (<15°C), when such a response would confer considerable heat conservation. Therefore, even 2-month-old toucans exhibit high obligatory heat loss from the bill, which cannot be down-regulated in the cold. As young, toucans remain blind and naked for the first 3 weeks, begin plumage growth at 4 weeks, and fledge only after 6 weeks of age (5, 22), at which point the bill is less than half the adult size. During this period, the young are not brooded by the adults during the day (5) and shiver at temperatures as high as 26° to 27°C (5). Thus, even in subtropical climates, young toucans would incur thermoregulatory costs, made more challenging by their poor ability to control bill heat exchange. The need for substrate delivery to the rapidly growing bill must demand high and steady blood flow, conflicting with the vasoconstriction required for heat conservation. Furthermore, the complexities of the vasculature and controlling mechanisms needed to adjust the blood flow to the bill may not be completely developed until adulthood.

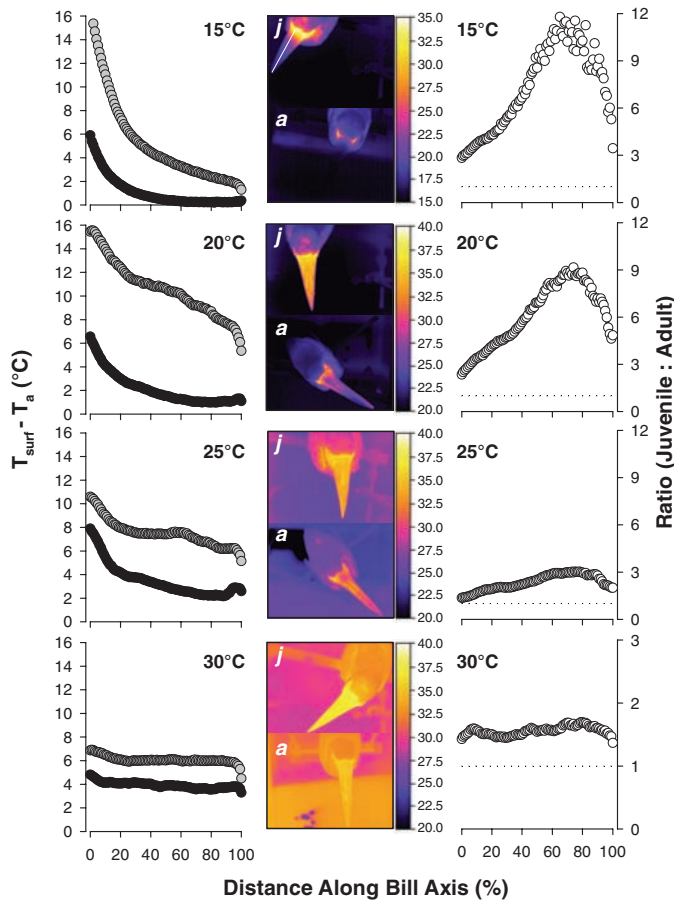
Temporal changes in the adult bill's surface temperatures are rapid and reversible, occurring within minutes (fig. S1), which was most evident when we observed the birds while they were sleeping. As the birds begin to sleep, a transient bill vasodilation occurs (movie S1). Because birds, like most endotherms, reduce body temperature during their nocturnal sleep, our results show that toucans have the ability to use their bill to rapidly dump body heat as the thermal set-point declines (23). Furthermore, we found that sleeping birds show transient changes in bill surface temperature without evidence of awakening, indicative of sleep-state transitions associated with changes in thermoregulatory state (24) (movie S2).

Ultimately, the changes in heat loss from the bill derive from the underlying vasculature. Little is known about the vascular anatomy of the toucan bill; however, a fine network of vessels ramifies within the dermis between the horny and bony parts of the bill (Fig. 1) (14, 19). Because surface temperatures in the distal and proximal regions often follow distinct and unique patterns, separate vessels must supply the distal and proximal regions; indeed, arteriovenous anastomoses (AVAs) are found in abundance in the tip of the duck's bill (14, 15). Nevertheless, because of the steepness of the temperature gradient profile along the bill and the fact that distal regions approach  $T_a$  in the cold (Fig. 3), counter-current mechanisms of heat conservation might be at play at low temperatures. At high  $T_a$ , however, the distal region of the bill can exhibit surface temperatures equal to or in excess of the proximal region (fig. S1F), indicating that counter-

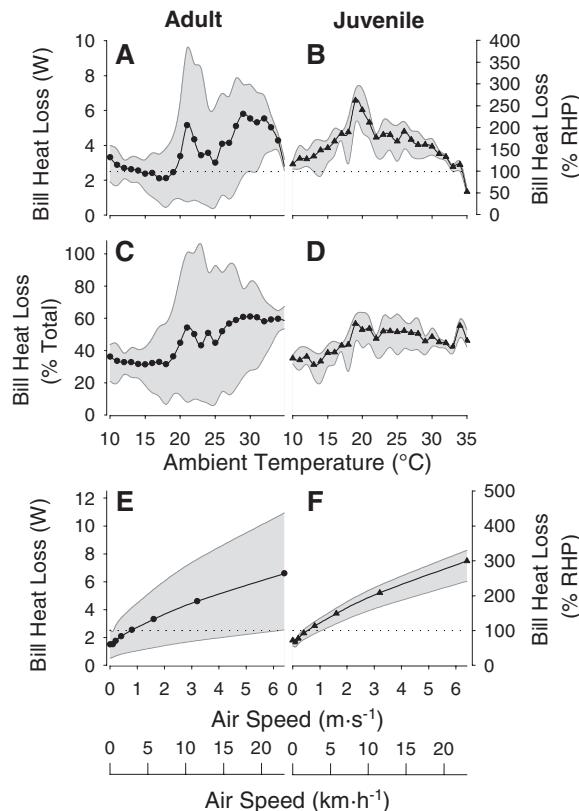
**Fig. 2.** Bill surface temperatures ( $T_{\text{surf}}$ ) (mean  $\pm$  SE) obtained from toucans exposed to a range of  $T_a$  (10° to 35°C), expressed as differential values ( $T_{\text{surf}} - T_a$ ). (A)  $T_{\text{surf}}$  of the external back feathers ( $n = 6$  toucans). (B)  $T_{\text{surf}}$  of the eye ( $n = 6$ ). (C) and (D) The differential values for the proximal and distal bill regions of adult toucans ( $n = 4$ ). (E) and (F) Bill surface temperature differentials from juveniles ( $n = 2$ , no statistics reported). Solid horizontal lines in (C) and (D) denote the range of statistically significant differences from values assessed at  $T_a = 32^\circ\text{C}$ .



**Fig. 3.** Temperature profiles of surface temperature differentials of the toucan bill at four different  $T_a$  (15°, 20°, 25°, and 35°C). The lefthand plots depict the average  $T_{\text{surf}} - T_a$  differences for adults ( $n = 4$ , black circles) and juveniles ( $n = 2$ , gray circles), expressed against the relative distance along the bill (white line in top middle panel; 0 = proximal end; 100 = distal tip). The middle column depicts thermographic images from adult (a) and juvenile (j) toucans at the respective  $T_a$ . The ratio of the juvenile:adult values for the  $T_{\text{surf}} - T_a$  differences is shown in the righthand panels. The horizontal dotted line indicates the line of equality, where the ratio = 1.



**Fig. 4.** Estimated rates of heat loss from toucan bills (average values are depicted as symbols and minimum and maximum values as gray shading). (A and B) Estimated bill heat loss for adults (circles) and juvenile (triangles) toucans at an air speed of  $5 \text{ m s}^{-1}$ . The horizontal dotted line indicates resting heat production (RHP) (18). (C and D) Bill heat loss expressed as a percentage of total heat body loss from all sources. (E and F) The summarized influence of air speed at  $T_a = 21^\circ\text{C}$  on heat loss from the bill in adult and juvenile toucans.



current arrangements can be bypassed through AVAs when needed.

Our results demonstrate that the constraints of heat exchange and the bill's potential use as a thermoregulatory organ should be considered in understanding the distribution, ecology, and behavior of toucans. Furthermore, given the rapid radiation of bill structures and diversity of beak morphologies of birds (3, 25), thermal constraints from bill heat loss may prove to be a common feature among many avian fauna.

**References and Notes**

1. G. L. L. Buffon, *Histoire Naturelle, Générale et Particulière avec la Description du Cabinet du Roi* (L'Imprimerie Royale, Paris, 1780).
2. C. Darwin, *The Descent of Man: And Selection in Relation to Sex* (J. Murray, London, 1871).
3. J. S. Jones, *Nature* **315**, 182 (1985).
4. H. Sick, *Ornitologia Brasileira* (Editor Nova Fronteira, Rio de Janeiro, Brazil, 1997).
5. J. Van Tynne, *The Life History of the Toucan Ramphastos brevicarinatus* (Museum of Zoology, Univ. of Michigan, Ann Arbor, MI, 1929).
6. P. Buhler, in *Tropical Biodiversity and Systematics*, H. Ulrich, Ed. (Zoologisches Forschung Institut und Museum, Bonn, Germany, 1997), pp. 305–310.
7. M. J. West-Eberhard, *Q. Rev. Biol.* **58**, 155 (1983).
8. P. K. Phillips, A. F. Sanborn, *J. Therm. Biol.* **19**, 423 (1994).
9. G. J. Tattersall, W. K. Milsom, *J. Exp. Biol.* **206**, 33 (2003).
10. W. C. Lancaster, S. C. Thomson, J. R. Speakman, *J. Therm. Biol.* **22**, 109 (1997).
11. J. J. Klir, J. E. Heath, N. Bennani, *Comp. Biochem. Physiol. A* **96**, 141 (1990).
12. H. Alvarenga, *Toucans of the Americas* (M. Pontual Edições e Arte, Rio de Janeiro, Brazil, 2004).
13. T. S. Traill, *Trans. Linn. Soc. London* **11**, 288 (1815).
14. U. Midtgard, *Zoomorphology* **104**, 323 (1984).
15. G. R. Scott, V. Cadena, G. J. Tattersall, W. K. Milsom, *J. Exp. Biol.* **211**, 1326 (2008).
16. See supporting material on Science Online.
17. G. E. Walsberg, J. R. King, *J. Exp. Biol.* **76**, 185 (1978).
18. B. K. McNab, *Auk* **118**, 916 (2001).
19. A. A. Hagan, J. E. Heath, *J. Therm. Biol.* **5**, 95 (1980).
20. P. K. Phillips, J. E. Heath, *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **101**, 693 (1992).
21. V. A. Tucker, *J. Exp. Biol.* **48**, 67 (1968).
22. A. F. Skutch, *Condor* **60**, 201 (1958).
23. H. C. Heller, *Can. J. Zool.* **66**, 61 (1988).
24. P. Alfoldi, G. Rubicsek, G. Cserni, F. Obal, *Pflügers Arch.* **417**, 336 (1990).
25. A. Abzhanov *et al.*, *Nature* **442**, 563 (2006).
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**Supporting Online Material**

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