

# Thermoregulation during Flight: Body Temperature and Sensible Heat Transfer in Free-Ranging Brazilian Free-Tailed Bats (*Tadarida brasiliensis*)

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## ABSTRACT

Bat wings are important for thermoregulation, but their role in heat balance during flight is largely unknown. More than 80% of the energy consumed during flight generates heat as a by-product, and thus it is expected that bat wings should dissipate large amounts of heat to prevent hyperthermia. We measured rectal ( $T_r$ ) and surface ( $T_s$ ) temperatures of Brazilian free-tailed bats (*Tadarida brasiliensis*) as they emerged from and returned to their daytime roosts and calculated sensible heat transfer for different body regions (head, body, wings, and tail membrane). Bats'  $T_r$  decreased from 36.8°C during emergence flights to 34.4°C during returns, and  $T_s$  scaled positively with ambient temperature ( $T_a$ ). Total radiative heat loss from bats was significantly greater for a radiative sink to the night sky than for a sink with temperature equal to  $T_a$ . We found that free-ranging Brazilian free-tailed bats, on average, do not dissipate heat from their wings by convection but instead dissipate radiative heat ( $L$ ) to the cloudless night sky during flight ( $L_{\text{sky}} = 0.85 \pm 0.12$  W). However, within the range of  $T_a$  measured in this study, *T. brasiliensis* experienced net heat loss between evening emergence and return flights. Regional hypothermia reduces heat loss from wings that are exposed to potentially high convective fluxes. Additional research is needed to establish the role of wings in evaporative cooling during flight in bats.

## Introduction

Powered flight enables bats to rapidly move long distances while foraging, dispersing, and migrating, but this activity also poses unique challenges with respect to energy expenditure, thermoregulation, and water balance. Physical and physiological models predict that less than 20%, and as little as 4%, of the metabolic power that is used by bats and birds during flapping flight is converted to mechanical power, while the remaining energy expenditure generates by-product heat (Carpenter 1986; Speakman and Thomas 2003). It has long been expected that bats dissipate body heat from their naked and highly vascular wing membranes (Cowles 1947; Reeder and Cowles 1951; Kluger and Heath 1970). However, small-bodied bats have a large body surface area-to-volume ratio even when wings are excluded, resulting in potentially high rates of heat loss during flight. The balance between thermogenesis and heat loss may be especially important for bats that fly for prolonged periods or in warm air. Euthermic body temperature during flight is important for promoting efficient muscle activity, enzymatic functions, and other physiological processes (Reeder and Cowles 1951; Nelson et al. 1977). Recent technological developments in thermal infrared (TIR) imaging make it possible to quantify surface temperature ( $T_s$ ) and heat transfer in free-ranging bats.

The Brazilian free-tailed bat (*Tadarida brasiliensis*) is common in subtropical regions of the Americas. In North America, this species forms large colonies in caves, bridges, and buildings (Kunz and Reynolds 2003; McCracken 2003; Keeley and Keeley 2004; Betke et al. 2008; Hristov et al. 2010), where maternity roost temperatures may reach 40°C in summer (Herreid 1963; Kunz and Robson 1995; Allen et al. 2010). Brazilian free-tailed bats emerge nightly to commute and feed on insects at altitudes near 800–1,100 m, potentially reaching 3,000 m (Williams et al. 1973; McCracken et al. 2008) and flying as far as 56 km from the roost to foraging grounds (Best and Geluso 2003; T. H. Kunz and M. Wikelski, unpublished data). Reproductive females often participate in two or more foraging bouts each night, returning to the roost to suckle offspring between bouts (McCracken and Gustin 1991; Kunz et al. 1995). Although some individuals may use separate night roosts (T. H. Kunz and M. Wikelski, unpublished data), it is expected that, on average, Brazilian free-tailed bats are on the wing for up to 8 h per night (Kunz et al. 1995). Dietary analysis suggests that this species may rely largely on metabolic water, given that free water for drinking can be limited throughout much of its geographic range in southern United States and northern Mexico

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(Kunz et al. 1995). Elevated nighttime humidity also reduces the potential for evaporative cooling. Thus, sensible (nonevaporative) heat loss through radiative and convective cooling should assume an important role in maintaining appropriate body temperature and water balance during flight. As Brazilian free-tailed bats disperse and forage outside the boundary layer near the ground, they are exposed to greater convective and radiative fluxes to the cool night sky above or the warmer ground below.

Theoretically, bat wings should be suitable for regulating heat exchange because they can be flushed with warm blood from the body (Cowles 1947). The Brazilian free-tailed bat has a relatively high thermoneutral zone, ranging from 33° to 38°C (Herreid and Schmidt-Nielsen 1966), which is above typical nighttime ambient temperature ( $T_a$ ) in the southwestern United States. However, Soriano et al. (2002) reported a lower thermoneutral zone (26°–33°C) in *T. brasiliensis* from higher-elevation forests. Thus, heated blood traveling through naked wing membranes should cool rapidly when bats are flying, causing wing temperatures to be significantly influenced by air temperature (Bartholomew et al. 1964; Lancaster et al. 1997). This cooling can be accelerated by high convective forces during flight. Although bats may upregulate blood flow through the flight membranes and flap their wings to dissipate heat when roosting under heat stress (Reeder and Cowles 1951; Ochoa-Acuña and Kunz 1998), blood can be shunted away from the wings to sustain muscle activity during flight (Reeder and Cowles 1951; Stones and Wiebers 1965). While research on the roosting ecology of bats is critical to our understanding of bat biology (Kunz 1982; Kunz and Lumsden 2003), such studies have limited ecological relevance to the role of wings in dissipating heat during flight.

We measured rectal temperature ( $T_r$ ), as an estimate of body temperature ( $T_b$ ), and  $T_s$  of free-ranging Brazilian free-tailed bats to estimate sensible heat transfer ( $G_s$ ) and determine the relative capacity for radiative and convective dissipation of heat from different regions of the body. We used TIR imaging to measure  $T_s$  before and after sustained foraging flights (i.e., during evening emergence from the roost and returns near midnight and sunrise, respectively). TIR imaging provides detailed measurement of  $T_s$  without interfering with natural activity or physiology and has led to important discoveries in the field of thermal biology (Phillips and Heath 1995; Mauck et al. 2003; Scott et al. 2008; Tattersall et al. 2009; Reichard et al. 2010). However, this technology has been employed more often in captive situations than in the wild (Lancaster et al. 1997) and often on stationary or constrained subjects (McCafferty 2007). To our knowledge, this and a companion study (Reichard et al. 2010) are the first studies to use TIR technology to quantify heat transfer from flying bats in their natural environment.

Using standard equations for convective and radiative heat transfer, we estimated  $G_s$  for the body, head, wings, and tail membrane over a range of  $T_a$  and compared  $G_s$  to expected flight-related thermogenesis predicted from allometric models (Speakman and Thomas 2003). We tested the hypothesis that heat loss to the environment balances estimated thermogenesis

during flight, making it possible for bats to avoid hyperthermia while foraging, commuting, or migrating. If heat loss exceeds heat production during sustained flight, then  $T_b$  would be expected to decrease. Newton's Law of Cooling is that heat exchange is driven by temperature gradients. Thus, as  $T_b$  decreases, the resulting smaller gradient between  $T_b$  and  $T_a$  will lessen  $G_s$  and approach a balance between thermogenesis and sensible heat loss. However, if equilibrium  $T_b$  is too low, then animals will incur an additional energetic cost to maintain adequately elevated  $T_b$ . This cost has implications for trade-offs in energy and time budgets during foraging and migration. Alternatively, if  $G_s$  is less than heat production,  $T_b$  may be expected to increase unless there is adequate dissipation of heat through evaporative cooling. We predicted that  $T_s$  for all body regions would vary with  $T_a$  but that  $T_s - T_a$  would increase if bats increased peripheral blood flow to dissipate heat. We conducted this study to establish relationships between  $T_r$ ,  $G_s$ , and  $T_a$  under natural conditions typically experienced by the Brazilian free-tailed bat.

## Material and Methods

### Study Species and Site

The Brazilian free-tailed bat (*Tadarida brasiliensis*) is a relatively small, insectivorous bat (body mass = ca. 12 g for a non-pregnant adult female) that has a transcontinental range extending from Argentina to southern Oregon in the United States (Wilkins 1989). Frio Cave, located near Concan, Uvalde County, Texas, houses a large maternity colony of up to 1,000,000 *T. brasiliensis* in midsummer (Betke et al. 2008). In summer, this colony consists almost exclusively of adult females that emerge predominantly from two main openings to the cave (Reichard et al. 2009). During evening emergences, the large numbers and predictable flight trajectories of Brazilian free-tailed bats at Frio Cave greatly facilitate TIR imaging and capture without interference with normal activities of the majority of emerging individuals.

### Weather

Relative humidity (RH) and  $T_a$  were recorded at 10-min intervals in a shaded location outside the mouth of the cave (iButton Hygrochron DS1923, Maxim Integrated Products, Sunnyvale, CA), adjacent to where TIR images were recorded. During TIR imaging,  $T_a$  ranged between ~21° and ~37.5°C under natural conditions (Table 1). The location for TIR imaging was naturally sheltered from prevailing winds, but recordings were suspended during rain or severe weather to minimize effects of these variables on convective flux parameters and to avoid damage to equipment.

### Internal (Rectal) Temperature

We captured bats with a 0.5-m-diameter hoop net along two flight trajectories in front of the cave as they emerged near dusk or returned from foraging ( $N = 60$ ). Bats'  $T_r$  was recorded with

Table 1: Environmental conditions during thermal infrared imaging and flight speeds of Brazilian free-tailed bats recorded during emergence and return flights from Frio Cave

	Emergence	Return
Ambient temperature ( $^{\circ}\text{C}$ )	29.6 $\pm$ 4.4 (21.0–34.3)	25.2 $\pm$ 2.0 (22.8–30.0)
Relative humidity (%)	34.8 $\pm$ 9.7 (22.5–50.0)	69.5 $\pm$ 16.9 (42.1–87.5)
Flight speed ( $\text{m s}^{-1}$ )	5.95 $\pm$ 1.13 (4.23–8.76)	7.12 $\pm$ 1.87 (4.05–10.69)

Note. Values are reported as means  $\pm$  SD, with range in parentheses.

a lubricated 2-mm-diameter quick-reading cloacal thermometer (Avinet, Dryden, NY) inserted 1 cm into the rectum immediately upon capture. The  $T_r$  was recorded after the thermometer had stabilized, usually within 15 s, but never more than 30 s, of capture. Thick cotton gloves were worn to minimize heat transfer between the handler and the bat. Once  $T_r$  was recorded, sex, age, and reproductive condition were recorded for each captured bat before it was released. Bats in these large colonies emerge in a more or less linear fashion from the cave. Once evening emergence is underway, it is rare that bats return to the cave against the large volume of dispersing individuals. Moreover, large colony sizes make it highly unlikely that a released bat would subsequently fly through the field of view of the TIR camera. The  $T_r$  was recorded during the same periods as TIR imaging (below), but with the specific objective of measuring  $T_s$  without interfering with the bats' typical behavior, we did not measure  $T_r$  and  $T_s$  on the same individuals. All protocols followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007) and Boston University's Institutional Animal Care and Use Committee.

### Surface Temperatures

We used calibrated Merlin Mid TIR cameras (hereafter, the Merlin; Indigo Systems, Santa Barbara, CA) to collect TIR images near cave openings. The Merlin uses ThermaCAM Rdac data acquisition software (FLIR Systems, Portland, OR) to record digital files ( $320 \times 256$  pixels) for up to 5 h continuously at 60 frames per second (fps). The Merlin was configured with a  $22^{\circ}$  (25-mm) or a  $5.5^{\circ}$  (100-mm) lens with focal plane established before the onset of bat activity: 2–3 m with the  $22^{\circ}$  lens and 7–9 m with the  $5.5^{\circ}$  lens. Thus, all bats analyzed in this study were  $<9$  m from the camera lens. The Merlin was calibrated by the manufacturer for distances and temperatures appropriate for this study:  $0.018^{\circ}\text{C}$  resolution and  $\pm 2^{\circ}\text{C}$  accuracy from  $0^{\circ}$  to  $350^{\circ}\text{C}$ . The close focal plane meant that absorption of radiation by atmospheric moisture did not significantly affect  $T_s$  measurements. Evening emergence activity was recorded during flights from the cave between dusk and 2200 hours. Returning flights were recorded during two periods: 2300 to 0100 hours and again from 0500 hours to sunrise (typically about 0700 hours). The large number of bats emerging or returning during imaging periods meant that occasionally bats passed through the focal plane with a suitable orientation to the camera with wings extended and the ventral

surface facing the camera (Fig. 1). Although Brazilian free-tailed bats may emerge before sunset, depending on weather and foraging conditions (Reichard et al. 2009), we recorded TIR images between dusk and dawn to minimize incident solar radiation affecting  $T_s$  measurements.

The TIR images were viewed and analyzed with ThermaCAM Rview (FLIR Systems). For each bat in proper orientation and focus, the “lasso” tool was used to designate four regions of interest: head, body, tail membrane, and wings (consisting of both left and right wings). We excluded the edges between the bat images and background from the regions of interest because these regions may not depict accurate  $T_s$  due to the curvature of the subject relative to the camera lens (McCafferty et al. 1998) and averaged values for pixels that included both subject and background. Emissivity was set at  $\epsilon = 0.98$  for skin and pelage (Monteith and Unsworth 1990). We recorded mean  $T_s$  for 209 bats (156 emerging and 53 returning).

### Surface Areas and Characteristic Dimensions

Fifty bats were captured and digitally photographed on a flat surface with one wing extended (Fig. 2). For scale, a penny (diameter = 1.89 cm) was included on the same plane as the bat wing in each photograph. Average surface areas (SAs) for the wings and tail membrane were estimated by counting the number of pixels in these regions and converting to square meters with ImageJ processing and analysis software (ver. 1.42q, National Institutes of Health). The SA measurement from a single wing was multiplied by 4 to estimate the total area ( $\text{SA}_{\text{wing}}$ ) for the ventral and dorsal surfaces of two wings. Likewise,  $\text{SA}_{\text{tail}}$  was twice the area of the tail membrane measured in the photograph.  $\text{SA}_{\text{head}}$  was estimated as the lateral area of a cone with height from the tip of the nose to the shoulder girdle and base diameter equal to the cranial width (Fig. 2).  $\text{SA}_{\text{body}}$  was estimated as the lateral area of a truncated cone with base diameters equal to the lateral girth at the shoulders and waist (Fig. 2). Mean SA for each region was assumed to be the same for photographed and TIR-imaged bats (Table 2). These estimates were used to calculate total convective and radiative heat transfer.

Convective heat transfer depends on the shape and size of the body as well as the direction and velocity of airflow across the surface (Gates 1980). The characteristic dimension ( $x$ ) for each region was estimated as the length along the direction of airflow:  $x_{\text{wing}}$  was the distance from the base of the thumb to the trailing edge of the wing at the fifth digit;  $x_{\text{tail}}$  was the

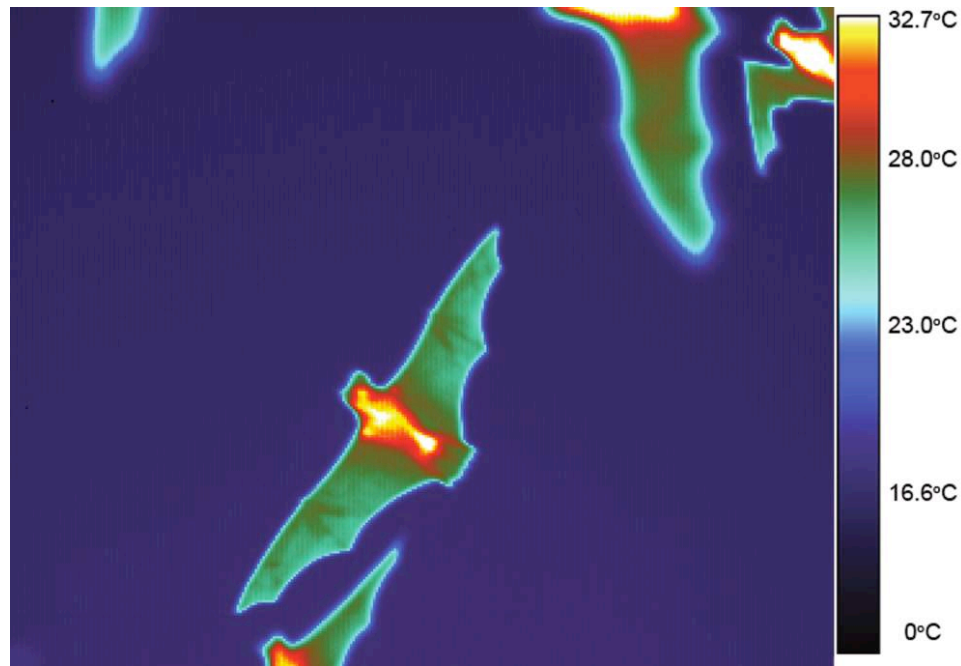


Figure 1. Thermal infrared (TIR) image representing surface temperatures of a Brazilian free-tailed bat emerging from Frio Cave against the night sky, recorded with a Merlin Mid TIR camera running FLIR software at 60 fps ( $320 \times 256$ -pixel array). See “Analytic Methods” for additional details.

distance from the base of the tail to the distal edge of the tail membrane. The exposed surfaces of the head and body were also treated as plates because airflow was parallel to the medial axis of the body (Ward et al. 1999). Thus,  $x_{\text{head}}$  and  $x_{\text{body}}$  surfaces were the length from the tip of the nose to the shoulder girdle and from shoulder girdle to base of the tail, respectively (Fig. 2).

#### Flight Speed

We estimated flight speeds for two flight trajectories (emerging [ $n = 30$ ] and returning [ $n = 30$ ] bats) between 2 and 10 m in front of the cave opening. We oriented the Merlin perpendicular to the bats’ flight paths with a  $22^\circ$  lens and collected data at 60 fps for 25 min for each trajectory. Two padded poles were placed within the field of view of the flying bats to provide scale for distance measurements. The distance between reference poles was 6.7 m during emergence and, because the trajectories of descending bats were more erratic, 2.5 m during return flights.

Individual bats passing along the same plane as the reference poles were manually tracked through consecutive frames with ThermaCAM RView, creating a nonlinear path on the digital image. The time span for each trajectory was determined from time stamps associated with the thermal images. The resulting images were exported to ImageJ, where scale was determined from known lengths and distances between reference poles in the fields of view and used to convert length in pixels to distance (m). Velocity was estimated as  $V = \text{path distance}/\text{time}$  ( $\text{m s}^{-1}$ ).

This method assumes two-dimensional trajectories, with bats flying parallel to the camera’s focal plane for the duration of the tracked path. However, because bats inevitably move in three dimensions, our estimates of flight speed likely underestimate the actual emergence and return speeds.

#### Sensible Heat Transfer in Flight

Sensible heat transfer ( $G_s$ ;  $\text{W m}^{-2}$ ) from the surfaces of bats during flight consists of only radiative and convective vectors because conductive heat transfer between the outer surface of an animal and the free atmosphere is negligible (Monteith and Unsworth 1990). Thus, our model for sensible heat loss in flying Brazilian free-tailed bats was similar to one adapted for musk-oxen (Monteith and Unsworth 1990; Munn et al. 2009):

$$G_s = C + L, \quad (1)$$

where  $C$  is convective heat transfer ( $\text{W m}^{-2}$ ) and  $L$  is long-wave radiative heat transfer ( $\text{W m}^{-2}$ ; Monteith and Unsworth 1990). Values of  $C$ ,  $L$ , and  $G_s$  were estimated for each of four body regions: head, body, tail membrane, and wings.

Convective heat transfer occurs predominantly by forced convection as bats propel themselves through the air. Although turbulence can affect convective heat transfer, we assumed laminar flow over all surfaces of this small-bodied animal (Ward et al. 2004). We calculated convective heat transfer for static wing positions and thus did not account for increased con-

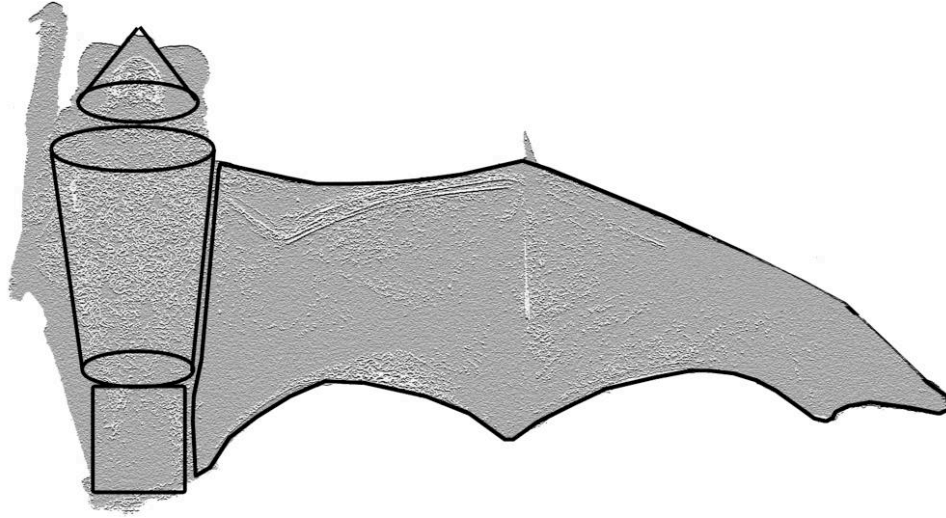


Figure 2. Digital photograph of a Brazilian free-tailed bat with left wing extended. Surface area of the wing was determined by converting the number of pixels in the outlined area to square meters. Other dimensions were measured linearly via pixel conversion, and then surface areas were calculated according to the approximate shape of the region: the head as a cone, the body as a truncated cone, and the tail membrane as a rectangular plate.

vective transfer due to flapping motion of the wings. We estimated  $C$  according to Holman (1986),

$$C = h \times (T_s - T_a), \quad (2)$$

where  $h$  is the convective heat transfer coefficient ( $\text{W m}^{-2} \text{ } ^\circ\text{C}^{-1}$ ). For the head and wings,

$$h = \text{Nu} \times \frac{k}{x}, \quad (3)$$

where  $k$  is the thermal conductivity of air ( $0.02624 \text{ W m}^{-1} \text{ K}^{-1}$  at 300 K; Holman 1986) and  $x$  is the length of the body region in the direction of air flow (m). Nu is the mean Nusselt number,

$$\text{Nu} = 0.664 \times \text{Re}^{0.5} \times \text{Pr}^{0.333}, \quad (4)$$

where Pr is the dimensionless Prandtl number (0.708 for air at 300 K; Holman 1986; Ward et al. 1999). Re is the Reynolds number and is proportional to the wind speed and characteristic dimension of the surface:

$$\text{Re} = V \times \frac{x}{\nu}, \quad (5)$$

where  $V$  is the air velocity ( $\text{m s}^{-1}$ ), estimated as equal to the flight speed (above), and  $\nu$  is the kinematic viscosity of air ( $15.69 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  at 300 K; Holman 1986; Ward et al. 1999).

The mean value of  $h$  decreases with an increasing thermal boundary layer from the leading to the trailing edge of a plate (Gates 1980). For example, the thermal boundary layer of the body will be greater because of the effect of the head on airflow toward the body. Thus, we modified  $h$  for the body and the tail membrane according to method 2 of Ward et al. (1999):  $h'_{\text{body} + \text{head}}$  and  $h'_{\text{tail} + \text{body} + \text{head}}$  were calculated as above (eq. [3])

with  $x$  equal to the combined lengths of the region and the upwind regions ( $x_{\text{body} + \text{head}}$  and  $x_{\text{tail} + \text{body} + \text{head}}$ ). Then,  $h'_{\text{body}}$  and  $h'_{\text{tail}}$  were calculated to account for the lengths of the upwind body regions (Ward et al. 1999):

$$h'_{\text{body}} = (h_{\text{body} + \text{head}} \times x_{\text{body} + \text{head}}) - (h_{\text{head}} \times x_{\text{head}}), \quad (6a)$$

$$h'_{\text{tail}} = (h_{\text{body} + \text{head} + \text{tail}} \times x_{\text{body} + \text{head} + \text{tail}}) - (h_{\text{body} + \text{head}} \times x_{\text{body} + \text{head}}). \quad (6b)$$

Subsequently,  $h'_{\text{body}}$  and  $h'_{\text{tail}}$  were substituted for  $h$  in equation (2) for these regions.

Long-wave radiative heat transfer was estimated from

$$L = \sigma \times \varepsilon_{\text{bat}} \times \varepsilon_{\text{sky}} \times (T_s^4 - T_{\text{sink}}^4), \quad (7)$$

where  $\sigma$  is the Stefan-Boltzmann constant ( $5 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$ ),  $\varepsilon_{\text{bat}}$  is the emissivity of the bat (0.98; Monteith and Unsworth 1990), and  $\varepsilon_{\text{sky}}$  is the emissivity of the sky (Swinbank 1963),

$$\varepsilon_{\text{sky}} = 0.398 \times 10^{-5} \times (T_a + 273.15)^{2.148}. \quad (8)$$

Radiative flux occurs between a flying bat and radiative sinks of the ground or sky at radiative temperature  $T_{\text{sink}}$ . Thus, we calculated  $L$  for two different  $T_{\text{sink}}$ :  $L_{\text{air}}$ , where  $T_{\text{sink}} = T_a$  recorded near ground level, and  $L_{\text{sky}}$ , where  $T_{\text{sink}}$  was estimated from  $T_a$  according to Gates (1980):

$$T_{\text{sky}} = T_a - 20.4 + T_a \times 0.22. \quad (9)$$

Table 2: Surface areas (SA) and coefficients of convection ( $h_c$ ) for different body regions for emerging and returning Brazilian free-tailed bats

Body Region	SA $\pm$ SD (m <sup>2</sup> )	% Total SA	Convection Coefficient $h_c$ (W m <sup>-2</sup> °C <sup>-1</sup> )	
			Emerging	Returning
Head	.0005 $\pm$ .0001	2.5	59.93	65.56
Body	.003 $\pm$ .0003	14.8	38.16	41.75
Tail membrane	.0008 $\pm$ .0002	3.9	33.20	36.31
Wings	.016 $\pm$ .002	78.8	44.27	48.33

### Analytic Methods

Statistical analyses were performed in JMP 5.0.1 (SAS Institute, Cary, NC) and R 2.9.0 (<http://www.r-project.org>). Unless otherwise indicated, values are reported as mean  $\pm$  SD. Data were tested for normality with Shapiro-Wilk tests,  $\alpha = 0.05$ . Non-normal data were tested with one-way Wilcoxon rank sum and Kendall's tau-b ( $\tau$ -b) rank sum tests for nonparametric comparison and correlation, respectively. To test the effect of environmental conditions and activity on  $T_r$ , we used a multi-variable model with  $T_r$  as the dependent variable and  $T_a$ , RH, and flight trajectory (emerging or returning) as independent variables.

### Results

#### Internal (Rectal) Temperature

Mean  $T_r$  declined from  $36.8 \pm 0.96$ C during emergence flights to  $34.4 \pm 1.20$ C during return flights (Wilcoxon test:  $W = 7,814$ ,  $P < 0.001$ ,  $N = 193$ ; Fig. 3). However,  $T_r - T_a$  was significantly lower during emergence than during return flights: mean  $T_r - T_a = 5.4 \pm 2.01$  and  $9.0 \pm 2.27$ C, respectively (Wilcoxon test:  $W = 922$ ,  $P < 0.001$ ,  $N = 193$ ; Fig. 3). Mean  $T_r$  was correlated with  $T_a$ , RH, and flight trajectory, with trajectory explaining most of the variation in  $T_r$  (Table 3).

#### Surface Temperatures

For each of the four body regions,  $T_s$  was positively correlated with  $T_a$  for all bats ( $N = 209$ ) and for returning bats (Kendall's  $\tau$ -b test:  $P < 0.001$ ,  $n = 53$ ). The  $T_s$  of the tail membrane on emerging bats was not significantly correlated with  $T_a$  (Kendall's  $\tau$ -b test:  $P = 0.60$ ,  $n = 156$ ), while those of the head, body, and wings were positively correlated with  $T_a$  ( $P < 0.001$ ). Similarly,  $T_s - T_a$  was negatively correlated with  $T_a$  for all regions for all bats ( $N = 209$ ) and for emerging bats alone ( $n = 156$ , Kendall's  $\tau$ -b test:  $P < 0.001$ ; Fig. 4). For returning bats alone ( $n = 53$ ),  $T_s - T_a$  was negatively correlated with  $T_a$  for head and body regions (Kendall's  $\tau$ -b test:  $P < 0.05$ ), but  $T_s - T_a$  was positively correlated with  $T_a$  for the wings and tail membrane (Kendall's  $\tau$ -b test:  $P < 0.01$ ).

#### Flight Speed and Sensible Heat Transfer

Sixty flight trajectories of bats were tracked for 1.9–9.6 m. Mean flight speeds for emerging ( $n = 30$ ) and returning ( $n = 30$ )

bats were  $5.95 \pm 1.13$  and  $7.12 \pm 1.87$  m s<sup>-1</sup>, respectively (Table 1). The  $V_{\text{return}}$  was  $1.2$  m s<sup>-1</sup> faster than the  $V_{\text{emerge}}$  (one-way ANOVA:  $t = -2.19$ ,  $P = 0.03$ ,  $df = 1, 2$ ). Area-specific radiative or convective heat transfer (W m<sup>-2</sup>) for the head, body, or tail membrane did not differ between emerging and returning bats (Wilcoxon test:  $P > 0.05$ ). However, wings of returning bats had significantly different  $L_{\text{air}}$  (Wilcoxon test:  $P = 0.01$ ),  $L_{\text{sky}}$  (Wilcoxon test:  $P = 0.01$ ), and  $C$  (Wilcoxon test:  $P = 0.003$ ), compared to those of emerging bats (Table 4). Area-specific rates of heat transfer differed among body regions for both emerging and returning bats (Wilcoxon test:  $P < 0.001$ ,  $df = 3$ );  $L_{\text{air}}$  and  $C$  each indicated heat loss from the body and head but sensible heat gain to the wings and tail membrane for both emerging and returning bats (Table 4). Radiative heat loss to the night sky ( $L_{\text{sky}}$ ) was recorded from all body regions (Table 4). For both emerging and returning bats, significant differences were evident when  $L_{\text{air}}$ ,  $L_{\text{sky}}$ , and  $C$  were compared (Wilcoxon test:  $P < 0.001$ ,  $df = 2$ ; Table 4).

Overall,  $L_{\text{air}} \times \text{SA}$  differed among body regions during both evening emergence and return (Wilcoxon test:  $P < 0.001$ ,  $df = 3$ ); it was significantly more negative for wings than for the head, body, and tail membrane (Tukey-Kramer HSD:  $\alpha = 0.05$ ; Fig. 5A). Convective transfer  $C \times \text{SA}$  was positive from the head and body but negative from the tail membrane and wings, with significant differences among body regions during both emergence and return flights (Wilcoxon test:  $P < 0.001$ ,  $df = 3$ ; Fig. 5B). Radiative heat  $L_{\text{sky}} \times \text{SA}$  also differed among body regions for both emerging and returning bats (Wilcoxon test:  $P < 0.001$ ,  $df = 3$ ; Fig. 5C). The wings exhibited significantly greater  $L_{\text{sky}} \times \text{SA}$  than other body regions (Tukey-Kramer HSD:  $\alpha = 0.05$ ; Fig. 5C).

Total sensible heat transfer to air ( $L_{\text{air}} + C$ )  $\times \text{SA}$  became significantly more negative for returning bats than for emerging bats ( $-1.032 \pm 0.088$  vs.  $-0.912 \pm 0.148$  W [mean  $\pm$  SEM]; Wilcoxon test:  $P = 0.016$ ,  $df = 1$ ; Fig. 6). Total sensible heat loss to the night sky ( $L_{\text{sky}} + C$ )  $\times \text{SA}$  was significantly greater for emerging bats than for returning bats ( $0.304 \pm 0.145$  vs.  $0.172 \pm 0.089$  W; Wilcoxon test:  $P = 0.015$ ,  $df = 1$ ; Fig. 6). For both flight trajectories, ( $L_{\text{sky}} + C$ )  $\times \text{SA}$  was greater than ( $L_{\text{air}} + C$ )  $\times \text{SA}$  (Wilcoxon test:  $P < 0.001$ ,  $df = 1$ ; Fig. 6).

### Discussion

Brazilian free-tailed bats (*Tadarida brasiliensis*) experience a net heat loss between emergence from their daytime roost at dusk

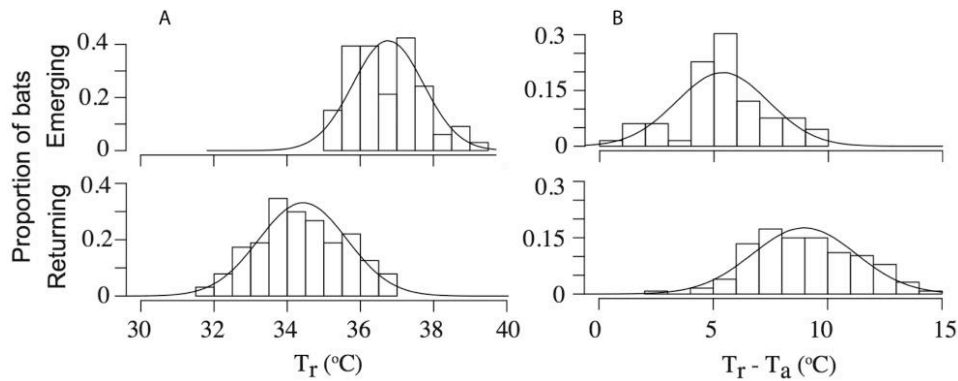


Figure 3. A, Variation in rectal body temperature ( $T_r$ ; °C) of emerging (top) and returning (bottom) Brazilian free-tailed bats. B, Difference between  $T_r$  and ambient temperature ( $T_a$ ; °C) of emerging (top) and returning (bottom) Brazilian free-tailed bats.

and return after foraging, as indicated by a drop in  $T_r$  over that period. The measured decline in  $T_r$  correlates with declining  $T_a$  over that time interval, although returning bats maintain a greater difference between  $T_r$  and  $T_a$  than do emerging bats, suggesting a greater contribution of metabolic heat to sustain elevated  $T_b$ . Slightly reduced  $T_b$  during flight effectively reduces sensible heat loss by diminishing the temperature gradient between the bat and the environment, a condition that is consistent with heat retention strategies (Henshaw 1970; Bakken 1976; Speakman and Racey 1989; Webb et al. 1993). Reduced  $T_b$  may also reduce evaporative water loss (O'Farrell and Bradley 1977) and oxygen demand for animals flying in hypoxic environments (Scott et al. 2008). This type of low-oxygen environment would be expected at high altitudes or while flying at high speeds, two conditions regularly encountered by *T. brasiliensis* (Williams et al. 1973; McCracken et al. 2008). Although  $T_r - T_a$  increased in our study, there was no significant difference in sensible heat loss from the body and head between emerging and returning bats. Radiative heat loss to the night sky is largely balanced by convective heat gain to relatively cool wings. However, the wings and tail membrane became cooler relative to  $T_a$  between emergence from and return to the cave, suggesting that bats may transition rapidly from cooler environments before passing the camera's field of view. We expect that the thin membranes would equilibrate rapidly with temperature fluxes and thus cool wings are more likely the result of evaporative and radiative fluxes.

The effect of  $T_a$  on  $T_b$  varies, depending on the range of  $T_a$ , species, and behavior (O'Farrell and Bradley 1977; Thomas et al. 1991). Lancaster et al. (1997) recorded no significant change in  $T_b$  related to elapsed flight time, and others have suggested that  $T_b$  increases during flight for bats (Thomas and Suthers 1972), although both of these studies were conducted within smaller ranges of  $T_a$  or in laboratory settings that may not account for the ecological variables that bats encountered in our study. It is expected that bats lose substantial heat from the large surfaces of their wings during flight (Thomas and Suthers 1972; Thomas et al. 1991); however, convective dissi-

pation of heat from Brazilian free-tailed bats may be limited largely to the head and body, not the flight membranes. The relatively high  $T_s$  of these regions is consistent with the location of heat-generating flight muscles in the pectoral and scapular regions of bats (Vaughan 1966) and vital organs that require maintenance of euthermic body temperature. In addition to the much smaller SAs of these regions, evaporative cooling from the mouth and nasal cavities or combined heat fluxes from the hairless pinnae can maintain locally low  $T_{s-head}$ . Thus, as a whole, the body accounts for an order-of-magnitude greater sensible heat loss than the head. Because the wings and tail membrane are consistently cool relative to  $T_a$ , on average these surfaces dissipate sensible heat through radiative flux to the night sky and not by convection.

Thermoregulatory strategies of homeothermic endotherms are frequently discussed in terms of maintaining appropriately low  $T_b$  during strenuous activities such as flight. Speakman et al. (1994) proposed that hyperthermia may limit daytime flight for bats but concluded that this would be true only for larger species. Thus, heat dissipation during active periods may be more important for animals that inhabit terrestrial boundary layers buffered from strong convective forces than for nocturnal flying animals. Nocturnal flight, however, exposes animals to even greater  $G_s$  because of high radiative flux to the night sky (Léger and Larochelle 2006), and flight exposes animals to con-

Table 3: Multiple linear regression estimates

Parameter	Estimate	SE	<i>P</i>	Cumulative $R^2$
$T_a$	.26	.05	<.001	.035
RH	.02	.01	.003	.021
Trajectory	1.63	.27	<.001	.494
Intercept	26.26	1.84		
Model			<.001	.549

Note. Rectal temperature of the Brazilian free-tailed bat is the dependent variable, and the independent variables are ambient temperature ( $T_a$ ), relative humidity (RH), and flight trajectory (emerging = 1, returning = 0).  $N = 193$ ,  $F_{3,189} = 76.75$ .

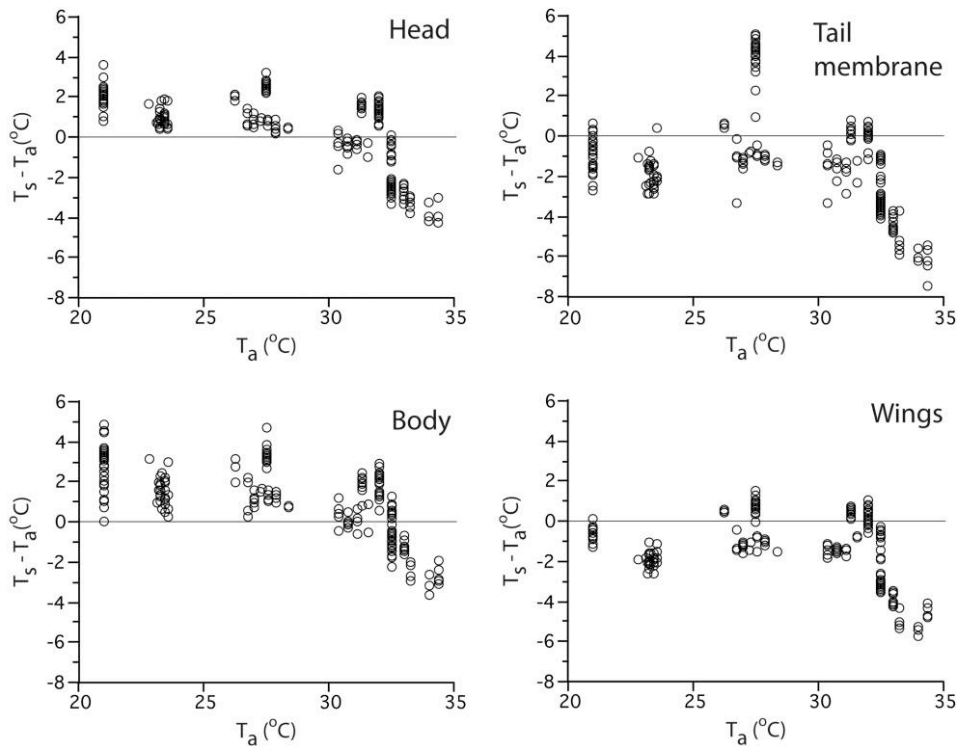


Figure 4. Surface temperature of Brazilian free-tailed bats relative to ambient temperature,  $T_s - T_a$  ( $^{\circ}\text{C}$ ), plotted against  $T_a$  for the head ( $N = 209$ ), body ( $N = 209$ ), wings ( $N = 207$ ), and tail membrane ( $N = 209$ ). For all body regions of bats,  $T_s - T_a$  was significantly correlated with  $T_a$  (Kendall's  $\tau$ -b:  $P < 0.01$ ).

tinuous strong convective forces. Activity-related thermogenesis may compensate for thermoregulatory costs of running or hopping birds subjected to convective heat transfer (Webster and Weathers 1990; Zerba and Walsberg 1992; Zerba et al. 1999). Although flight is energetically more costly per unit time than terrestrial forms of locomotion (Thomas and Suthers 1972), the cost of flight for small bats may be even greater because of an additional energetic cost associated with maintaining elevated body temperature. This situation would suggest only partial compensation of by-product heat for thermoregulation during flight in Brazilian free-tailed bats. If demand for thermoregulatory heat production increases because of a greater SA-to-volume ratio, smaller bats would be expected to expend relatively more energy than larger bats during flight. In fact, this pattern is evident from studies of field metabolic rates for a variety of bat species for which flight costs have been measured (reviewed in Speakman and Thomas 2003). In suggesting that Brazilian free-tailed bats experience net heat loss during flight, our results are consistent with the hypothesis that hyperthermia may not be a driving force behind nocturnal behavior in small-bodied bats (Reeder and Cowles 1951; Carpenter 1986; Thomas et al. 1991; Speakman et al. 1994).

Allometric relationships predict that metabolic cost of flight for a 12-g bat is ca. 1.7 W (Speakman and Thomas 2003). Thus, assuming that flight muscle efficiency is between 4% and 20%, a Brazilian free-tailed bat would generate 1.3–1.6 W of heat

during flight (Speakman and Thomas 2003). Because  $G_s$  in this study is less than the estimated thermogenesis, latent heat exchange may be responsible for dissipating the remainder. Evaporative cooling in the lungs may be a high source of heat loss, but respiratory rate is expected to be coupled to wing-flapping rates, limiting its flexibility for thermoregulatory purposes (Suthers et al. 1972). Moreover, bats are expected to dissipate only about 10%–15% of heat through respiratory cooling (Thomas and Suthers 1972; Carpenter 1986), leaving more than 1.2 W of heat to dissipate to avoid hyperthermia, which is ca. four times the estimated sensible heat loss to the night sky. Our estimate of convective heat transfer during flight in Brazilian free-tailed bats is based on a conservative estimate of flight speeds. More accurate estimates of flight speed using three-dimensional reconstruction (Wu et al. 2009) would be expected to increase estimates of convective transfer from the body and head. Because the wings and tail membrane, on average, are cooler than air during powered flight, we do not expect that turbulent flow, flapping, or wind speed would significantly increase heat loss from these surfaces. On average, the wings of Brazilian free-tailed bats lose  $0.85 \pm 0.12$  W via radiative flux to the night sky. Thus, there is marked radiative heat loss during nocturnal flights (Léger and Larochelle 2006). Cool wings also provide a temperature gradient for conductive and convective heat transfer through blood circulation between the warm body and the cool wings. In addition to radiative loss to the sky,



Table 4: Mean ( $\pm$  SEM) heat transfer ( $\text{W m}^{-2}$ ) by radiative flux to  $T_a$  ( $L_{\text{air}}$ ), by radiative flux to  $T_{\text{sky}}$  ( $L_{\text{sky}}$ ), and by convective flux ( $C$ ) for each of four body regions of emerging and returning Brazilian free-tailed bats

	$L_{\text{air}}$	$L_{\text{sky}}$	$C$
Emerging ( $n = 156$ ):			
Head	$.29 \pm .82^{\text{Aa}}$	$60.01 \pm .78^{\text{Ab}}$	$8.61 \pm 10.53^{\text{Aa}}$
Body	$4.03 \pm .74^{\text{Ba}}$	$63.75 \pm .71^{\text{Bb}}$	$35.91 \pm 6.18^{\text{Ac}}$
Tail membrane	$-5.57 \pm 1.04^{\text{Ca}}$	$54.15 \pm 1.02^{\text{Cb}}$	$-.031 \pm .006^{\text{Bc}}$
Wings	$-6.09 \pm .71^{\text{Ca}}$	$53.63 \pm .69^{\text{Cb}}$	$-57.03 \pm 6.55^{\text{Bc}}$
Returning ( $n = 53$ ):			
Head	$3.88 \pm .27^{\text{Ec}}$	$62.93 \pm .27^{\text{Ef}}$	$59.22 \pm 4.20^{\text{Ef}}$
Body	$6.27 \pm .41^{\text{Fc}}$	$65.32 \pm .40^{\text{Ff}}$	$60.71 \pm 3.99^{\text{Ff}}$
Tail membrane	$-6.12 \pm .51^{\text{Ge}}$	$52.92 \pm .54^{\text{Gf}}$	$-.042 \pm .004^{\text{Fg}}$
Wings	$-6.19 \pm .38^{\text{Ge}}$	$52.85 \pm .42^{\text{Gf}}$	$-71.20 \pm 4.53^{\text{Gg}}$

Note. Flux rates differed among body regions; values labeled with different capital letters within columns are significantly different (Tukey-Kramer HSD:  $\alpha = 0.05$ ). Flux rates also differed among flux types within body regions; values labeled with different lowercase letters within rows are significantly different (Tukey-Kramer HSD:  $\alpha = 0.05$ ).

thermal windows on the flanks of the body and pelvic region may experience locally high rates of heat loss (Reichard et al. 2010).

We measured instantaneous  $G_s$  as bats emerged from and returned to the cave, but we were unable to measure  $T_s$  during all moments of their foraging bouts. Although a rough estimate of heat loss throughout the foraging bout could be extrapolated by assuming that fluxes measured at ground level remain constant while the bat is away from the cave, such estimates are likely to be misleading. Brazilian free-tailed bats commute and forage at high altitudes (McCracken et al. 2008), and  $T_a$  at 1,000 m can be  $>6^\circ\text{C}$  less than that at ground level, depending on humidity (Moore 1956). Heat transfer rates would vary greatly, depending on  $T_a$  and flight speeds at different altitudes. It is also possible that Brazilian free-tailed bats glide or soar on wind currents at high altitude, thus reducing metabolic heat production. However, Ruck (1946) noted that smaller bats were less likely to glide than larger bats, even in warm weather (see Thomson et al. 2002). It is possible that relatively cool wing temperatures measured at ground level reflect rapid transition between different  $T_a$  regimes such that bats are not at thermal equilibrium with the surrounding air. Still, the very thin wing membranes and the high rate of convective heat transfer should mean  $T_{s\text{-wing}}$  would equilibrate rapidly with  $T_a$ . Also, we measured relatively low  $T_{s\text{-wing}}$  on returning and emerging bats, the latter having just emerged from subterranean airspace where, between dusk and dawn,  $T_a$  inside the outer chambers of the cave is similar to outside  $T_a$ .

Surface temperatures of wings, on average, were below  $T_a$ . Such regional hypothermia has been demonstrated to help maintain elevated  $T_b$  by reducing heat loss from appendages exposed to cold (Gordon 1968; Schmidt-Nielsen 1997; Butler 2004). Although sweat glands are absent from bat wings (Crowley and Hall 1994), transcutaneous water loss may be significant for animals in arid habitats (Muñoz-García et al. 2008). We expect that wings were cool because of evaporative cooling as

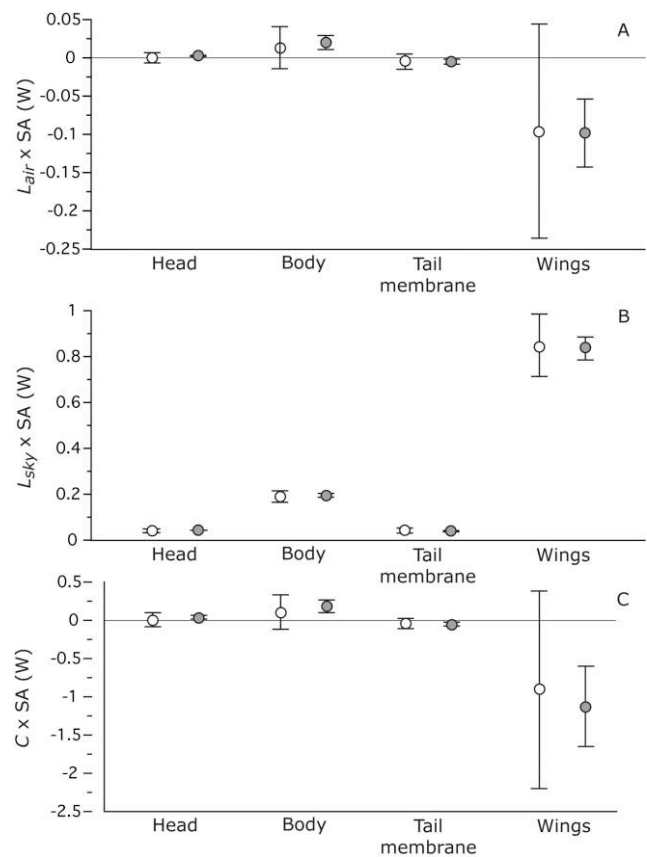


Figure 5. Mean heat transfer ( $\text{W}$ ) by radiative fluxes  $L_{\text{air}} \times \text{SA}$  (A) and  $L_{\text{sky}} \times \text{SA}$  (B) and convective flux  $C \times \text{SA}$  (C) in Brazilian free-tailed bats. Circles represent means, and error bars represent 1 SD. Within body regions, rates did not differ between emerging and returning bats (Wilcoxon test:  $P > 0.1$ ), except for borderline significance for the wings (Wilcoxon test:  $P < 0.1$ ).

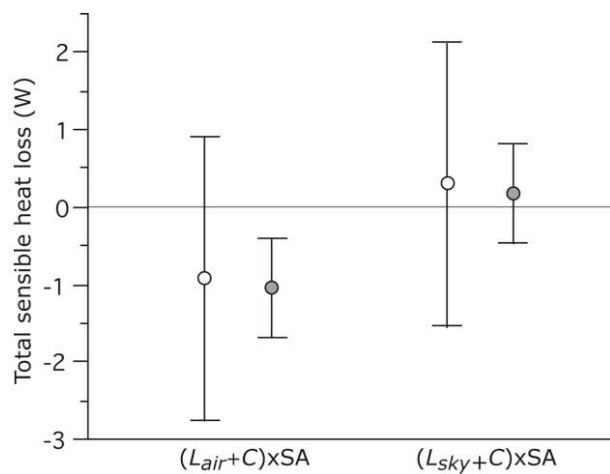


Figure 6. Total sensible heat loss (W):  $(L_{air} + C) \times SA$  and  $(L_{sky} + C) \times SA$  for emerging (white circles;  $n = 156$ ) and returning (gray circles;  $n = 53$ ) Brazilian free-tailed bats. Circles represent means, and bars represent 1 SD.

well as radiative heat loss. The  $L_{sky} + C$  recorded from wings of Brazilian free-tailed bats in flight was ca.  $-7.22 \text{ W m}^{-2}$ . Thus, using the latent heat of vaporization ( $2,430 \text{ J g}^{-1} \text{ H}_2\text{O}$  at  $30^\circ\text{C}$ ), we estimated that water loss from wing surfaces of  $0.003 \text{ g H}_2\text{O m}^{-2} \text{ s}^{-1}$  would be needed to maintain cool wings. Preliminary analysis of water loss from wing surfaces using a leaf respirometry chamber (LI6400 LI-COR Biosciences, Lincoln, NE) revealed mean water loss from Brazilian free-tailed bat wings to be  $0.004 \text{ g H}_2\text{O m}^{-2} \text{ s}^{-1}$  (J. D. Reichard, unpublished data). Unfortunately, this rate was below the respirometer's sensitivity, and thus measurements must be repeated to confirm their accuracy. Moreover, this rate of water loss was recorded for bats captured during emergence and return flights and may not be representative of water loss throughout the feeding period. The air at high altitudes is likely to be significantly cooler than and to differ in humidity from ground-level air. Moreover, even at ground level, RH often increases as the night progresses. Thus, the potential for evaporative cooling can be expected to vary with altitude and time. Notwithstanding these caveats, low rates of water loss estimated for heat balance and from the respirometer data suggest that this species may be adapted for low evaporative water loss in arid regions in the southwestern United States (Kunz et al. 1995). This preliminary analysis of water flux also does not identify the source of water being measured. It is entirely possible that wings become moist from the surrounding air by condensation and thus that water already on the surface of the wings when we attached the leaf respirometry chamber would not be distinguished from transcutaneous water loss. RH is high inside Frio Cave, and water vapor may also condense on wings as bats circle inside the cave before emerging. Thus, passing from this higher-humidity environment could lead to evaporation of moisture from the wings as the bats leave the cave. Additional studies are needed

to identify the extent and source of evaporative cooling from the wings during flight in *T. brasiliensis*.

Many cave roosts of Brazilian free-tailed bats exceed  $35^\circ\text{C}$  during midsummer. Bats are often seen flying within the roost throughout the day, presumably to seek temporary refuge from the warm temperatures in roosting clusters (Herreid 1963). TIR imaging of roosting Brazilian free-tailed bats revealed that clusters are more diffuse at midnight and in the early morning, after bats return from foraging (A. J. Frank, unpublished data). At rest, bats lose heat through the same mechanisms as during flight, with additional conductive heat loss to the cave walls (Herreid 1963). However, after the bats enter the warm and humid cave, it is likely that evaporative, convective, and radiative heat loss decrease, and it may take some time for bats to cool down after prolonged flights. Roosting in diffuse clusters has greater potential for convective cooling and lower thermal mass than occupying dense clusters, thus expediting postflight cooling (Canals et al. 1997) and reducing heat gain from other bats in the roost (Licht and Leitner 1967). After sunrise, the density of roosting bat clusters increases, presumably to reduce heat loss after residual flight-related heat has been dissipated (A. J. Frank, unpublished data).

We could not determine the sex, age, or reproductive conditions of bats from TIR images. Thus, we did not test for temperature differences among these cohorts. Although one could expect greater flight-related heat production from a pregnant bat, there is no strong evidence that predictions of flight cost from body mass are reliable within species (Speakman and Thomas 2003). Pregnant bats are expected to select warm roost temperatures to optimize growth of fetuses (Racey and Swift 1981), and temperature preferences of Brazilian free-tailed bats have been studied only in the roost, not in flight (Herreid 1963). Although warm roosts should promote faster growth and development of pups (Allen et al. 2010), lactating bats may benefit from temporary reprieve from high temperatures while foraging. Król and Speakman (2003) demonstrated that elevated  $T_b$  can hinder milk production in mice, leading to the hypothesis that reduced  $T_b$  during flight may increase milk production. A similar study of sensible heat loss examining individuals of known sex, age, and reproductive condition may reveal significant differences in thermoregulation strategies and demands among cohorts with different energetic demands.

Most previous studies of the thermoregulatory roles of bat wings were conducted on immobilized or roosting bats (Cowles 1947; Reeder and Cowles 1951; Kluger and Heath 1970). Our observations do not rule out the hypothesis that bats may flush wings with blood as means of dissipating heat to avoid hyperthermia. However, we suggest that high  $T_b$ , which might elicit this response during flight, is unlikely under natural conditions observed in our study. Even when roosting inside a warm cave, flying Brazilian free-tailed bats have lower  $T_b$  than individuals roosting directly above them (Herreid 1963). However, the large variation in estimated rates of heat transfer suggests that wings retain the potential for dissipating or conserving body heat. Moreover,  $T_b$  maintained above  $T_a$  means that bats can dissipate heat through sensible fluxes and reduce requirements of evap-

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orative cooling. Radiative heat loss differs significantly between loss to the night sky and loss to ambient radiative sinks. Although our estimates of  $L_{\text{sky}}$  are consistent with estimates of by-product heat production, it may not be realistic to assume that all surfaces of the bat radiate to the night sky. Because the ventral surfaces of flying bats are more often facing the ground, radiative exchange would be determined by the difference between the temperatures of the bat and the Earth's surface. Convective heat exchange within the body of the bat (i.e., between the warm body and the cool wings), through blood circulation, deserves attention to better identify patterns of heat transfer from the thermogenic flight muscles. Vasoconstriction and vasodilation utilized by captive bats under heat stress may be employed during flight to regulate convective transfer between the body and wings. Blood may also be directed to or shunted from hot spots on the body to create locally high rates of heat loss (Klir and Heath 1992; Mauck et al. 2003). The unique network of blood vessels, or so-called radiator, in the proximal wing membrane and hairless flanks of Brazilian free-tailed bats and other members of the family Molossidae offers a possible mechanism for adaptable heat dissipation (Reichard et al. 2010), the significance of which may be masked by averaging  $T_s$  for larger body regions in this study. Thus, rapid dissipation of heat through this radiator may help to limit blood flow to the distal wing membranes and potentially optimize the inertial power requirements of flapping flight (Swartz 1998).

Because  $T_r$  decreases from the time Brazilian free-tailed bats leave the cave to when they return, there is a net loss of heat from the body. Thus, depressed  $T_b$  during flight may be an adaptation for a species that is morphologically specialized for high speed and endurance (Vaughan 1966). Alternatively, heat conservation may be more important than heat dissipation in the  $T_a$  range naturally encountered by this species. Brazilian free-tailed bats often leave the cave before sunset, when  $T_a$  and incident radiation can limit radiative and convective heat loss (Speakman et al. 1994). How heat is balanced under these conditions remains an open question. The role of bat wings for sensible heat loss during flight may have been overestimated from studies of immobilized wings and artificial heat sources. Although extended flight membranes result in a nearly fivefold increase in the SA of the bat, it is apparent that the wings reflect air temperature more than they do body temperature and thus are not well suited for dissipation of heat by convection. Wings that are cooler than air may experience potentially high rates of radiative heat loss to the sky, but this may be counterbalanced by convective warming. Thus, the patterns and control of heat exchange between the warm body and the cool wings during flight deserve further attention. This study offers the first analysis of surface temperatures and heat transfer of free-ranging bats flying in their natural environment.

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