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## Thermoregulatory behavior in the small island flying fox, *Pteropus hypomelanus* (Chiroptera: Pteropodidae)

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### Abstract

We investigated the thermal responses and thermoregulatory behavior of five small island flying foxes, *Pteropus hypomelanus* exposed to ambient temperatures ranging from 13.5 to 38.9°C. Bats tended to increase body temperature during the heat of the day. With increasing ambient and body temperatures, bats increased their exposed wing surface and the frequency of wing-fanning behavior. When ambient temperature approached body temperature, bats exposed less wing area and decreased wing-fanning. © 1999 Elsevier Science Ltd. All rights reserved.

**Keywords:** Thermoregulation; Bats; Behaviour; *Pteropus hypomelanus*

### 1. Introduction

Most flying foxes (genus *Pteropus*) and other members of the family Pteropodidae are known mostly from the Paleotropics (Corbet and Hill, 1991); only a few species have penetrated into temperate regions (Pierson and Rainey, 1992). These relatively large, frugivorous bats, are often exposed to high ambient temperature ( $T_a$ ) while roosting in trees during the daytime (Nelson, 1965; Jones, 1972). In captive situations, pteropodids are able to maintain a constant body temperature ( $T_b$ ) over a wide range of values of  $T_a$  (Robinson and Morrison, 1957; Bartholomew et al., 1964).

Given that wing membranes of bats are naked and highly vascularized (Cowles, 1947; Reeder and Cowles, 1951), they should provide a route for losing significant amounts of body heat. This avenue for heat dissipation may be enhanced by an increased blood flow through the wings (Kluger and Heath, 1970), by an

increase in the amount of wing surface exposed, or by both. Wing fanning has been observed in *Pteropus* in response to high  $T_a$  (Nelson, 1965), suggesting that this behavior plays an important role in thermoregulation. Members of the Pteropodidae typically lack sweat glands (Robinson and Morrison, 1957; Quay, 1970), and some species are known to enhance evaporative cooling at high  $T_a$  by salivating and licking their wing membranes (Nelson, 1965).

The objectives of this study were to investigate the thermoregulatory responses of captive *Pteropus hypomelanus* by recording changes in  $T_b$  and skin temperature ( $T_s$ ) in response to differences in  $T_a$ , and to examine the relationships between these temperatures and the occurrence of thermoregulatory behaviors during the roosting period. We hypothesized that the proportion of wing membrane exposed to the environment, its rate of vascular perfusion, and extent of wing fanning should be associated with thermoregulatory adjustments to  $T_a$ . Because wing-fanning can increase forced convection, we predicted that the amount of wing area exposed and the extent of wing-fanning should increase as  $T_a$ s increased. However, the amount of wing area exposed and the occurrence of wing fan-

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ning should decrease after a certain  $T_a$  is reached, because the temperature differential between the body and the environment is sufficiently small as to impede or even reverse heat flow from the body to the environment.

## 2. Material and methods

### 2.1. Study animals

Five captive *Pteropus hypomelanus* (three adult males and two adult females, mean body mass = 540 g, SD =  $\pm$  136 g) were used in these experiments. The bats were originally collected in Kalimantan, Indonesia, and since 1990 have been housed as part of a captive breeding and research program at The Lube Foundation, Inc. (Gainesville, Florida). Animals were housed in a large flight cage (1.5 m high and 8 m diameter). The cage was shaded and exposed to normal daily  $T_a$  fluctuations. Bats were fed daily a diet that consisted of chopped fruit and vegetables (bananas, apples, grapes, carrots, and lettuce) supplemented with monkey chow and multiple vitamins (Vionate, Arc Laboratories).

### 2.2. Temperature measurements

Small (2.5–2.7 g) temperature sensitive radiotransmitters (PD-2 T, Holohil Systems, Ltd.) were used to measure both  $T_b$  and  $T_s$  of bats. Each radiotransmitter was coated with water-resistant epoxy to prevent damage from internal body fluids or from direct transfer of moisture from the skin.

Before radiotransmitters were implanted or attached to the bats, they were calibrated to the nearest 0.1°C using a series of water baths (at 5°C intervals) ranging from 5–40°C. We determined  $T_b$  and  $T_s$  by measuring the time it took for 10 pulses to be emitted by the radiotransmitters, and then converting it to  $T_b$  or  $T_s$  using calibration curves. Because our calibration curves differed slightly from those provided by the manufacturer, we used our own curves in subsequent analysis. No drift was

detected when radiotransmitters were re-calibrated at the end of the study.

Bats were anesthetized with isoflourane, and a sterilized radiotransmitter was inserted intraperitoneally through a small incision made in the body wall. One month after surgery, bats were again anesthetized, a small patch of hair on the dorsal area of the neck was clipped, and a temperature-sensitive radiotransmitter, with a 100-mm whip antenna was attached to the skin with a latex-based surgical adhesive (SkinBond). This radiotransmitter was held in position by attaching it to a small leather collar made from soft (tanned) sheep skin (Spencer et al., 1991).

A digital thermometer was placed near the bats to measure  $T_a$  ( $\pm$ 0.1°C) throughout the study.

### 2.3. Data collection

We recorded  $T_a$ ,  $T_b$ , and  $T_s$  and made behavioral observations every 10 min from 0700 to 1900 h, for 10 consecutive days in May 1993. The temperature sensitive radiotransmitter implanted intraperitoneally in bat 90 ceased to operate immediately before we began our observations, thus we report  $T_b$  from only four bats.

We measured the relative amount of wing surface exposed, and the occurrence of wing fanning and licking behavior for each bat using a standard scan sampling protocol (Altmann, 1974). We marked each bat with a uniquely colored wire and plastic tag attached to the leather neck collar. This device made it possible to readily distinguish each individual during behavioral observations. For each wing, the amount of wing surface exposed (wing opening) was estimated based on an arbitrary scale ranging from 1 to 5. Degrees of wing opening were defined as follows: 1) 100–76%; 2) 75–51%; 3) 50–26%; 4) 25–1%) and 5) 0%. A 0% opening indicated that the wings were completely wrapped around the body.

### 2.4. Data analysis

Data analysis was performed using the AUTOREG procedure from the SAS/ETS statistical

Table 1  
Yule-Walker estimates for the autocorrelation-corrected regression of  $T_b$  against  $T_a$  and time of day in five *Pteropus hypomelanus*

Bat No.	$r^2$	Intercept	$T_a$			Time of day		
			Parameter	$t$	$P$	Parameter	$t$	$P$
33	0.03	32.44	0.1763	1.96	0.0508	1.2836	3.19	0.0015
84	0.26	30.35	0.1876	11.19	0.0001	2.3087	4.77	0.0001
83	0.10	37.45	0.0387	3.39	0.0008	2.1656	6.07	0.0001
92	0.11	28.19	0.2653	6.62	0.0001	2.5914	0.84	0.3996

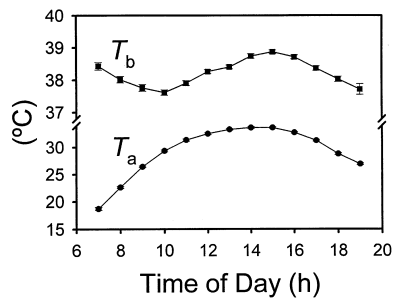


Fig. 1. Mean body temperature ( $T_b$ ,  $\pm$ SE) of four captive *Pteropus hypomelanus* and ambient temperature ( $T_a$ ,  $\pm$ SE) at which they were exposed in relation to time of day.

package (SAS Institute Inc., 1993). This procedure uses the Yule–Walker method to produce parameter estimates corrected for the autocorrelation introduced in the data by sequential sampling of temperatures and behaviors. All regression models included time of day as an independent variable. Percentage data were arcsin transformed before statistical tests were run.

### 3. Results

#### 3.1. Thermal responses to ambient temperature

Individuals of *Pteropus hypomelanus* were exposed to outdoor, naturally occurring  $T_a$  that averaged  $30.0^\circ\text{C}$  ( $\text{SD} = \pm 4.99$ ,  $n = 509$ ), and ranged from  $13.9$  to  $38.9^\circ\text{C}$ .  $T_b$  averaged  $38.3^\circ\text{C}$  ( $\text{SD} = \pm 1.12$ ,  $n = 2017$ ) for all bats tested and ranged from  $35.6$  to  $40.2^\circ\text{C}$ .

As can be seen in Fig. 1,  $T_b$  decreased until 1030 h and then increased following the increase in  $T_a$  throughout the day. For this reason, analyses of the effect of  $T_a$  on  $T_b$  and  $T_s$  were conducted using time of day as an independent factor.

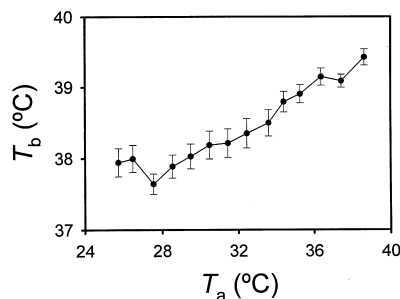


Fig. 2. Mean body temperature ( $T_b$ ,  $\pm$ SE) of four captive *Pteropus hypomelanus* in relation to outdoor ambient temperature ( $T_a$ ), utilizing only data collected after 1030 h.

Averaging all bats,  $T_b$  was significantly influenced by  $T_a$  ( $t = 6.854$ ,  $P < 0.0001$ ) but not by time of day ( $t = -1.311$ ,  $P < 0.1903$ ) (Table 1). As can be seen in Fig. 2,  $T_b$  increased steadily with  $T_a$  above  $28^\circ\text{C}$ .

$T_s$  averaged  $35.9^\circ\text{C}$  ( $\text{SD} = \pm 1.336$ ,  $n = 1901$ ), ranging from  $30.3$  and  $39.8^\circ\text{C}$ . Averaging all bats,  $T_s$  was significantly influenced by  $T_a$  ( $t = 21.80$ ,  $P < 0.0001$ ), and by  $T_b$  ( $t = 15.62$ ,  $P < 0.0001$ ), but not by time of day ( $t = -0.04$ ,  $P < 0.9651$ ).

#### 3.2. Behavioral thermoregulatory responses

A total of 445 scan samples of roosting behavior were obtained for each of five bats. All bats exhibited thermoregulatory behaviors such as wing fanning and body licking. Bats never clustered together and always maintained a distance of at least two body widths from each other (25 cm). During the period of observation, the animals spent most of their time resting ( $\bar{x} = 90.9\%$ ,  $\text{SD} = \pm 13.75\%$ ,  $n = 2262$ ). Activity level was not significantly influenced by  $T_a$ ,  $T_b$ , nor by time of day.

As  $T_a$  increased, bats exposed a larger proportion of their wing surface to the environment. Consequently, bats increased the wing surface exposed as  $T_b - T_a$  got smaller (Fig. 3). Averaging all bats, wing opening was significantly influenced by  $T_a$  ( $t = 7.03$ ,  $P < 0.0001$ ), and by  $T_b$  ( $t = 5.23$ ,  $P < 0.0001$ ), but not by time of day ( $t = 0.13$ ,  $P < 0.8973$ ). This pattern was also observed in most individual bats (Table 2). Following a peak in the amount of wing surface exposed at about  $36^\circ\text{C}$ , further increases in  $T_a$  were followed by a decrease in the amount of wing surface exposed.

Wing fanning was a conspicuous thermoregulatory behavior in *P. hypomelanus*, and its prevalence increased as  $T_b - T_a$  decreased (Fig. 4). On average, bats spent 24% ( $\text{SD} = \pm 24.01\%$ ,  $n = 2262$ ) of their time fanning. This behavior consisted of high frequency (200–300 per min) wing movements of one wing away from and towards the body. During these

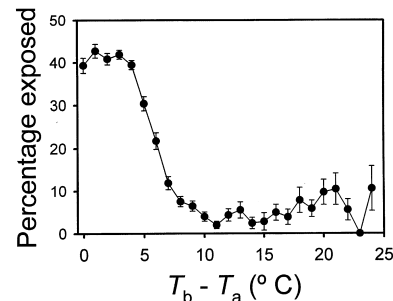


Fig. 3. Mean percentage ( $\pm$ SE) of wing surface exposed to the environment by four captive *Pteropus hypomelanus* in relation to the temperature differential  $T_b - T_a$ .

Table 2  
Significance of the Yule–Walker autocorrelation-corrected regression estimates of different behaviors against  $T_a$ ,  $T_b$ , and  $T_s$  in five individuals of *Pteropus hypomelanus*

Regressor	Bat No.	Wing Opening	Wing Fanning	Body Licking
Time of Day	33	0.2837	0.2672	0.8282
	83	0.1116	0.3009	0.5366
	84	0.4197	0.3619	0.7661
	90	0.5121	0.4681	0.4980
	92	0.6279	0.1986	0.9658
$T_a$	33	0.0001	0.0004	0.6678
	83	0.0001	0.0001	0.9093
	84	0.0004	0.0001	0.5251
	90	0.0033	0.0003	0.8045
	92	0.0002	0.0001	0.2560
$T_b$	33	0.0002	0.0464	0.8043
	83	0.2799	0.2544	0.8782
	84	0.0056	0.0001	0.2103
	92	0.0001	0.0060	0.1668

movements, the wing was partially flexed with the elbow joint forming an angle ranging from 30 to 45°. The occurrence of wing fanning increased with  $T_a$ , reaching a maximum at about 36°C. Averaging all bats, time spent fanning was influenced by  $T_a$  ( $t = 6.93$ ,  $P < 0.0001$ ), and by  $T_b$  ( $t = 5.54$ ,  $P < 0.0001$ ), but not by time of day ( $t = 1.04$ ,  $P < 0.2993$ ). As with wing opening, fanning was not influenced by  $T_b$  in bat 83 (Table 2).

Salivation and body licking appeared to be a last resort in response to overheating. In these situations, individuals most frequently licked their wing membranes, thumb, and wrist. Averaging all bats, the occurrence of this behavior was not significantly influenced by  $T_a$  ( $t = 0.26$ ,  $P < 0.7950$ ),  $T_b$  ( $t = 0.50$ ,  $P < 0.6152$ ), nor by time of day ( $t = 0.54$ ,  $P < 0.5858$ ). The same pattern was observed in individual bats (Table 2). However, bats spent significantly more time licking their bodies at  $T_a$ s above 35°C than

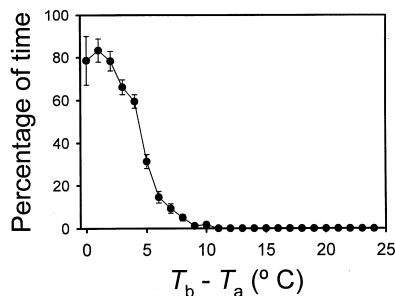


Fig. 4. Mean percentage of time ( $\pm SE$ ) spent wing fanning by four captive *Pteropus hypomelanus* in relation to the temperature differential  $T_b - T_a$ .

below this temperature (14.03 vs. 1.44%, two tailed  $t$ -test = 16.58,  $P < 0.0001$ ).

## 4. Discussion

### 4.1. Possible biases with the use of temperature transmitters

A potential bias in the estimation of  $T_s$  of free ranging pteropodids under field conditions would be the effect of solar radiation on the temperature-sensitive radiotransmitter glued to the skin surface. In our study, we shaded the entire cage in order to minimize the effect of direct solar radiation. Recent advances in the development of small, temperature-sensitive radiotransmitters, have made recording of  $T_s$  possible by attaching them directly to the animal's skin. Although this approach has not been widely used, the use of radiotransmitters offers the only practical approach for transmitting radio signals at distances that incorporate the home ranges of free-ranging bats (Audet and Thomas, 1996; Barclay et al., 1996; Hickey and Fenton, 1996). For large mammals, implantable temperature-sensitive radiotransmitters can be used to monitor  $T_b$ s over relatively large distances. Alternatively, surface-mounted, radiotransmitters offer the potential to assess  $T_b$  of free-ranging bats. Several investigators have used these devices to monitor the thermoregulatory responses of small insectivorous bats to changes in  $T_a$  (Audet and Fenton, 1988; Webb et al., 1993; Grinevitch, 1995; Hickey and Fenton, 1996), and only recently have reports been published on the accuracy or reliability of  $T_b$ s derived from such radiotransmitters (Audet and Thomas, 1996; Barclay et al., 1996).

A considerable body of research has been conducted on thermoregulation in bats, but only a few studies have been performed on the Megachiroptera (reviewed in Lyman, 1970; Kurta and Fujita, 1988; also see Laburn and Mitchell, 1975; Korine and Arad, 1993). Reliable measurements of  $T_b$  under field conditions are crucial for the interpretation of both behavioral and theoretical models of thermoregulation.

### 4.2. Thermal responses to ambient temperature

The observed decrease in  $T_b$  with time of day before 1030 h may have been due to the gradual dissipation of heat produced by activity and feeding during the night. The fact that activity did not change with the time of day makes it unlikely that the increase in  $T_b$  after 1030 h was due to this factor.

Our finding that  $T_b$  was significantly influenced by  $T_a$  is consistent with observations made on other species of pteropodids. In our study,  $T_b$  tended to

increase steadily above 28°C  $T_a$  (Fig. 2). Rectal temperatures of restrained *Pteropus poliocephalus* and *P. scapulatus* increased when bats were exposed to a  $T_a$  of 35, 37.5, and 40°C (Morrison, 1959; Bartholomew et al., 1964). Similar observations have been reported for *P. giganteus* and *Rousettus aegyptiacus* (Kulzer, 1963a,b; Korine and Arad, 1993; McNab and Bonaccorso, 1995). Jones (1972) reported that the  $T_b$  of other pteropodids (*Eidolon helvum*, *Epomops franqueti*, and *Micropteropus pusillus*) also increased when the animals were exposed to extremely high  $T_a$ . An increase in  $T_b$  during the day may help to maintain an adequate temperature differential to facilitate heat loss without having to increase evaporative cooling. On average, bats in our study increased  $T_b$  by about 1.3°C during the heat of the day (average increase in  $T_a = 7^\circ\text{C}$ ).

#### 4.3. Behavioral thermoregulatory responses

That bats in the present study were generally inactive during the daylight hours was expected, although behaviors involving change in roosting location may be more prevalent in natural conditions than in captivity. In the wild, there is often loud vocalization and movement within roost areas, and some individuals may fly from one place to another (Nelson, 1965; Lekagul and McNealey, 1977).

The ability to regulate the amount of wing surface exposed to the environment seems to be an important characteristic of the thermoregulatory strategy of *P. hypomelanus*. In the present study, bats responded to increases in  $T_a$  and  $T_b$  by exposing a larger wing surface to the environment. The hypothesis that exposure of a larger wing area, coupled with increased vascular perfusion, may facilitate thermoregulation at high temperatures was supported by our observation that wing opening increased with increasing  $T_a$  and  $T_b$ . Although we did not measure wing vascular perfusion, our results strongly suggest that wing membranes are an important route for heat dissipation in *P. hypomelanus*.

Our study demonstrates that wing-fanning behavior is an important means of heat dissipation of pteropodids at high  $T_a$ . Wing-fanning behavior has been reported in several species of bats. Leitner and Nelson (1967) postulated that the occurrence of this behavior in some species (*Pteropus* spp.), but not in others (*R. aegyptiacus*, *Macroderma gigas*) may reflect the fact that the latter two species roost in caves, whereas *Pteropus* roost in trees and thus are exposed daily to high  $T_a$ . Wing fanning would be important when  $T_b - T_a$  is small, because it would increase forced convection and evaporative cooling (Laburn and Mitchell, 1975).

Robinson and Morrison (1957) proposed two explanations for their observation that *P. poliocephalus* con-

tinued wing fanning even when  $T_a$  was greater than  $T_b$ . First, they suggested that there was no provision for bats to stop this behavior at the experimentally-imposed high temperatures, given that such temperatures are not normally encountered in the wild. They further postulated that a high  $T_a$  may trigger a mechanism that controls the synchronization of breathing with rates of wing fanning. Our observations suggest that *P. hypomelanus* is able to control wing fanning at high temperatures, and that the prevalence of this behavior decreases when  $T_a - T_b$  approaches zero (Fig. 4).

We found that the frequency of body licking increased ten times above 35°C  $T_a$ . Evaporative cooling is the only effective mechanism to dissipate heat when  $T_a$  exceeds  $T_b$ . Because pteropodids do not have active sweat glands (Robinson and Morrison, 1957; Quay, 1970), they often deposit large amounts of saliva on themselves to avoid overheating. Bartholomew et al. (1964) reported that body licking in *P. poliocephalus* began when  $T_a$  approached 40°C, and our observations are consistent with these findings.

In summary, although *P. hypomelanus* maintains a relatively constant  $T_b$  over a wide range of  $T_a$ s, individuals of this species tend to increase  $T_b$  through the heat of the day. The behavioral thermoregulatory response of these bats involves changes in the amount of wing surface exposed to the environment and forced convection from wing fanning. In addition, when  $T_a$  approaches  $T_b$ , evaporative cooling based on salivation and licking becomes a significant mechanism of heat dissipation.

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