

Are Tropical Small Mammals Physiologically Vulnerable to Arrhenius Effects and Climate Change?*

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Accepted 7/28/2013; Electronically Published 10/1/2013

Online enhancement: appendix figure.

ABSTRACT

There is some urgency in the necessity to incorporate physiological data into mechanistic, trait-based, demographic climate change models. Physiological responses at the individual level provide the mechanistic link between environmental changes and individual performances and hence population dynamics. Here we consider the causal relationship between ambient temperature (T_a) and metabolic rate (MR), namely, the Arrhenius effect, which is directly affected by global warming through increases in average global air temperatures and the increase in the frequency and intensity of extreme climate events. We measured and collated data for several small, free-ranging tropical arboreal mammals and evaluated their vulnerability to Arrhenius effects and putative heat stress associated with climate change. Skin temperatures (T_{skin}) were obtained from free-ranging tarsiers (*Tarsius syrichta*) on Bohol Island, Philippines. Core body temperature (T_b) was obtained from the greater hedgehog tenrec (*Setifer setosus*) and the gray brown mouse lemur (*Microcebus ravelobensis*) from Ankaramantsika, Madagascar. T_{skin} for another mouse lemur, *Microcebus griseorufus*, was obtained from the literature. All four species showed evidence of hyperthermia during the daytime rest phase

in the form of either T_{skin} or T_b that was higher than the normothermic T_b during the nighttime active phase. Potentially, tropical arboreal mammals with the lowest MRs and T_b , such as tarsiers, are the most vulnerable to sustained heat stress because their T_b is already close to T_a . Climate change may involve increases in MRs due to Arrhenius effects, especially during the rest phase or during torpor and hibernation. The most likely outcome of increased Arrhenius effects with climate change will be an increase in energy expenditure at the expense of other critical functions such as reproduction or growth and will thus affect fitness. However, we propose that these hypothetical Arrhenius costs can be, and in some species probably are, offset by the use of hyperthermic daily torpor, that is, hypometabolism at high T_a .

Introduction

Over the past decade, climate envelope models have been the most widely used approaches to forecast climate change impacts on species distributions, abundance, and extinctions. However, these approaches seldom account for the key mechanisms by which the species' demographic performances change, leading to biased estimations of the risks for biodiversity (sensu Dawson et al. 2011). To predict the sensitivity of species to environmental change, mechanisms underlying the causative relationship between environmental variability and population changes need to be identified (Fuller et al. 2010; Lavergne et al. 2010; Huey et al. 2012; Seebacher and Franklin 2012; Somero 2012) and incorporated into trait-based demographic models (Williams et al. 2008; McMahon et al. 2011; Huey et al. 2012). Physiological responses at the individual level provide the mechanistic link between environmental change and individual performances but remain generally overlooked (Angilletta et al. 2002; Ricklefs and Wikelski 2002).

The causal relationship between ambient temperature (T_a) and metabolic rate (MR) is affected directly by global warming through the increases in global average air temperatures and the increase in the frequency and intensity of heat waves (Dillon et al. 2010; IPCC 2011). The effect can be described by the Arrhenius equation:

$$\ln\left(\frac{\text{MR}_1}{\text{MR}_2}\right) = -\frac{E_a}{R}\left(\frac{1}{T_1} - \frac{1}{T_2}\right) \quad (1)$$

(Withers 1992), where MR_1 and MR_2 are metabolic rates at body temperature (T_b) of T_1 and T_2 , respectively; E_a is the

* This paper was submitted in response to a call for papers for a Focused Issue on "Conservation Physiology."

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apparent enthalpy of activation; and R is the gas constant ($8.314 \text{ J K}^{-1} \text{ mol}^{-1}$). The formula for the temperature coefficient, Q_{10} , the change in rate with a 10°C change in temperature, is widely used as a simple measure of the Arrhenius effect on rate processes:

$$Q_{10} = \left(\frac{R_2}{R_1} \right)^{10/(T_2 - T_1)},$$

where R_1 and R_2 are rate processes at T_1 and T_2 , respectively.

To develop causal, mechanistic explanations of population changes, specific physiological responses and physiological tolerance limits to T_a need to be understood (Angilletta et al. 2002; Chown et al. 2010; Hofmann and Todgham 2010). To date, most research on the metabolic impacts of climate change has focused on ectotherms. The relationship between T_a and T_b in ectotherms is evident as they depend on exogenous heating and are therefore highly vulnerable to Arrhenius effects (Huey et al. 2009, 2012; Dillon et al. 2010). On the other hand, endotherms are believed to be less dependent on T_a , and therefore, most climate studies have focused on resource or water availability (Durant et al. 2007; Adams 2010; Angilletta et al. 2010).

Arrhenius effects can theoretically affect endotherms when T_a approaches or exceeds T_b and also during hibernation and daily torpor when T_b follows an ectotherm-like state when T_a is higher than the torpor setpoint T_b (Humphries et al. 2002, 2004; Dausmann et al. 2005, 2009; Lovegrove and Génin 2008; Kobbe et al. 2011). Endothermic thermoregulation is characterized by a thermoneutral zone where maintenance or basal metabolic rate (BMR) is all that is necessary to maintain a relatively stable T_b independent of T_a and hence Arrhenius effects. At T_a higher than the upper critical limit of thermoneutrality (T_{uc}), T_b will continue to increase with increasing T_a until the animal dies of hyperthermia if it cannot minimize the rate of heat storage through evaporative cooling. In mammals, death through hyperthermia occurs at $T_b \sim 41^\circ\text{--}42^\circ\text{C}$ (Lepock 2003), although there is interspecific variation (reviewed in Boyles et al. 2011). Thus, at T_a higher than T_{uc} , the endotherm is exposed to the same exponential Arrhenius heating effects that thermoconforming ectotherms experience at all T_a . For example, using equation (1) and assuming a common mammalian E_a of 74 kJ mol^{-1} (Low et al. 1973), the MR of a hypothetical endotherm with $T_b = 37^\circ\text{C}$ at T_{uc} would increase by 10%, 22%, and 45% with T_b increases of 1° , 2° , and 4°C , respectively. Thus, while climate change will have an indirect effect on energy acquisition of endotherms through changing resource or water availability (Durant et al. 2007), it will theoretically also have direct effects on energy expenditure.

Endotherms generally avoid hyperthermia because the $T_b - T_a$ gradient is sufficiently large to allow heat dissipation from the body to the ambient. However, mammals with low T_b , namely, basoendotherms ($T_b \leq 35^\circ\text{C}$; sensu Lovegrove 2012), are theoretically more likely to suffer hyperthermia with elevated T_a than mesoendotherms and supraendotherms ($T_b > 35^\circ\text{C}$; sensu Lovegrove 2012). For basoendotherms, the $T_b -$

T_a gradient is small relative to nonbasoendotherms (Lovegrove 2012). For example, the $T_b - T_a$ gradient of a basoendotherm with $T_b = 33^\circ\text{C}$ would be about $2^\circ\text{--}3^\circ\text{C}$ at $T_a = 30^\circ\text{C}$. Low T_b places basoendotherms at higher risks of T_b exceeding the normothermic setpoint T_b at lower T_a compared with nonbasoendotherms.

In terms of the untested endotherm thermal performance models, basoendotherms would probably be considered thermoregulatory “generalists” with lower and higher critical thermal minima and maxima, respectively (Angilletta et al. 2002; Boyles et al. 2011). However, the endotherm performance curve concepts were borrowed from ectotherm models, and it is not known whether basoendotherms/generalists can indeed tolerate higher critical thermal maxima on a sustained basis (Boyles et al. 2011). In tropical and semitropical mammals, BMR and T_b are closely associated with unpredictable climate and resource availability rather than high thermal extremes (Lovegrove 2003; Withers et al. 2006). Little information is available about whether the thermal tolerance range during hyperthermia in basoendotherms ($T_b > 35.0^\circ\text{C}$) would have the same adverse effect, for example, as in supraendotherms ($T_b > 39.7^\circ\text{C}$).

To date, the Northern Hemisphere latitudes have been the focus of most studies on climate change. Little attention has been paid to the potential vulnerability of tropical endotherms to the direct and indirect effects of global warming. Fewer than 1% of the long-term climate change data sets come from the tropics (Rosenzweig et al. 2008). Warming has been slower in the tropics, and predictions show smaller increases than at higher latitudes (IPCC 2007; Dillon et al. 2010). However, there has been an increase in the intensity and frequency of extreme climate events related to climate change (Easterling et al. 2000; IPCC 2011; Coumou and Rahmstorf 2012; Rummukainen 2012; Wang et al. 2012). Tropical and semitropical species are potentially the most vulnerable to hyperthermia and related Arrhenius effects because (a) warming will occur in an environment that is already warm (Dillon et al. 2010), (b) relative humidity is high during the wet season (low capacity for evaporative cooling), (c) most are confined on islands or inhabit fragmented habitats from where they have limited or no dispersal opportunities (Şekercioğlu et al. 2012), and (d) they have significantly lower T_b and BMR (most are basoendotherms) than their nontropical counterparts (Lovegrove 2000, 2003, 2012; Şekercioğlu et al. 2012). However, the reaction norms of tropical organisms dwelling in the most unpredictable environments, such as those under strong El Niño Southern Oscillation influences, are likely to be adaptive over very large climatic gradients, much larger than for organisms from stable, temperate systems (Canale and Henry 2010). The high flexibility of physiological traits would extend thermal tolerance limits. However, present reaction norms may not be adaptive under the new climatic conditions (Visser 2008).

Insularity, that is, an island existence, is an important consideration because climate envelope models predict spatial range shifts to cooler climes, either to higher altitudes or higher latitudes (Davis et al. 1998; Humphries et al. 2002, 2004; Huey et al. 2009; Rowe et al. 2010). However, these options are not

available to island-dwelling species; they have nowhere to go. Similar range shift constraints will apply in isolated continental forests, for example, forests fragmented by anthropogenic activities (Pearson and Dawson 2005). Moreover, many islands or fragmented forests do not offer altitudinal gradients for spatial relocation (Laurance et al. 2011), and even for those that do, dispersal routes are often disrupted by habitat loss and fragmentation (Pearson and Dawson 2005).

Here we test the hypothesis that insular arboreal endotherms display daytime rest phase elevations of T_b that exceed the normothermic, active phase, nighttime T_b . We obtained T_{skin} and core T_b data from a number of nocturnal species that inhabit tropical and subtropical regions: the Philippine tarsier *Tarsius syrichta*; the greater hedgehog tenrec *Setifer setosus*; and two species of mouse lemur, the golden-brown mouse lemur *Microcebus ravelobensis* and the reddish-gray mouse lemur *Microcebus griseorufus*. We also used these data to formulate working hypotheses on putative vulnerability to Arrhenius effects and heat stress and a concept of hyperthermic torpor (heat-induced hypometabolism). From these working hypotheses we pose several pertinent questions—the answers to which should aid in the development of mechanistic, trait-based models that focus on tropical endotherms. Our data emphasize the urgency for laboratory investigations to establish the thermal performance thresholds of small mammals in response to high T_a and relative humidity. We support the call that these physiological data on free-ranging, insular, arboreal mammals are essential for the further development of mechanistic models in climate change adaptation programs (Angilletta et al. 2002; Boyles et al. 2011; Huey et al. 2012).

Material and Methods

Tarsius syrichta

Data from the Philippine tarsier were collected at the Tarsius Project at Bilar (see table 1 for details). Tarsiers are small (80–160 g) nocturnal prosimians and are debatably the basal primates (Rosa et al. 1996; Matsui et al. 2009). Relative humidity recordings at the research site (table 1) showed modal values between 95% and 100% (two loggers) and between 90% and 95% (one logger; e.g., fig. A1, available online). Relative humidity was highest during the coolest times of the night when T_a decreased to 20°–22°C. During the heat of the day, when T_a reached a maximum of ~31°C, the relative humidity attained a minimum of ~70% (fig. A1).

The T_{skin} of four tarsiers, three females and one male (mean body mass = 122.5 ± 18.0 g; male mass = 148 g; female mass = 106–120 g), was measured using custom-constructed programmable data loggers based on digitally readable temperature sensors (MCP 9800, Microchip Technology, Chandler, AZ; resolution: 0.0625°C, individually calibrated; storage capacity: 104,832 values). Loggers were embedded into epoxy, together with commercially available tracking transmitters (MIP 1A, Reimesch, Bergisch-Gladbach, Germany) programmed to emit 10-ms pulses in the 150-MHz range with a power of 1 mW at 20-s intervals for 15 h per day. The electronic

logging/tracking units (size: 19 mm × 11 mm × 9 mm, including a button cell battery) were attached to a size-adjustable plastic collar that also included a 7.5-cm wire aerial. The entire collar and electronic parts were enclosed by heat shrink tubing and fastened around the neck of animals, with the temperature logger component in direct contact with the skin. The weight of the entire device was 5.5 g. Previous studies have shown that collar-mounted transmitters had no adverse effects on tarsiers (Gursky 1998).

Recent studies have employed small collar-mounted UHF transmitters that incorporate devices for measuring T_{skin} as a proxy for T_b (e.g., Kobbe et al. 2011). For some very small mammals, such as bats, or rare, endangered mammals, such as tarsiers in this study, these T_{skin} proxies are the only data that we are ever likely to obtain. It is therefore important to identify the potential limitations of T_{skin} proxies.

In bats fitted with temperature-sensitive collars located between the scapula, Willis and Brigham (2003) showed that T_{skin} was influenced by heat production from interscapular brown adipose tissue located immediately underneath the transmitter. During deep torpor and arousal, T_{skin} exceeded T_b by as much as 9.5°C. During normothermy, however, the $T_b - T_{\text{skin}}$ gradient in bats was about 3°C, which is a fairly typical core T_{skin} gradient in normothermic small mammals (Lovegrove et al. 1991). In animals fitted with collar-mounted transmitters where the T_{skin} of the throat region was measured, much smaller differences between T_{skin} and T_b were measured. For example, in dwarf lemurs (*Cheirogaleus medius*) in Madagascar, the $T_b - T_{\text{skin}}$ gradient was small (about -0.1°C; i.e., T_{skin} slightly higher than T_b) during the daytime rest phase, and T_{skin} explained 98% of the variance in T_b . During the nighttime active phase, T_{skin} was slightly lower than T_b by about 0.37°C and explained 79% of the variance in T_b (Dausmann 2005). Thus, in the latter study, T_{skin} was a good predictor of T_b during the daytime rest phase. We argue that, when correctly fitted, collar-mounted temperature loggers provide reliable measures of temporal changes in T_b . However, reliance on quantitative active phase T_{skin} measures should acknowledge and recognize unusual T_{skin} variability. For example, during normothermy, decreases in T_{skin} by as much as ~15°C between the daytime rest phase and the nocturnal active phase clearly indicate very poor approximation of T_b , probably as a consequence of loose collars (Blanco and Rahalinarivo 2010; Dausmann 2012).

Microcebus ravelobensis and *Setifer setosus*

These species were studied at two research sites, Jardin Botanique A (JBA) and Jardin Botanique B (JBB), adjacent to the Ampijoroa Forestry Station in Ankarafantsika National Park, Madagascar (table 1). *Microcebus ravelobensis* (Cheirogaleidae) is a small nocturnal heterothermic primate (63.2 ± 7.5 g; this study) inhabiting the area between the Betsiboka River and the Mahajamba River (Olivieri et al. 2007). Ten individuals (five males, five females) were captured in April and May 2011 with Elliott live traps (30 cm × 8 cm × 7 cm) baited with banana. The animals were kept for a maximum of 3 d in an outdoor

Table 1: Key information on study species and environmental conditions at the field sites

	Sleeping sites	Location	Time of year	Type of habitat	Mean annual rainfall (mm)	T_a	T_a measurements
<i>Tarsius syrichta</i> T_{skin} ($n = 4$)	Dense foliage ¹	Bohol Island, (9°44'N, 124°06'E), Philippines	Aug–Dec 2010	Secondary rainforest with deep gullies and gorges	1,307 ¹	Annual mean minimum T_a 21°C, maximum T_a 33°C ²	Thermometer/hygrometer data loggers at 1.5 m aboveground in research area ^a
<i>Microcebus ravelobensis</i> (male) T_b ($n = 1$)	Tree holes, branches, lianas, and leaves; ³ 1.3–7 m ⁴	JBB, Ankarafantsika National Park (16°19'S, 46°48'E), Madagascar	May 25–Sep 11, 2011; dry, nonreproductive season	Dry deciduous forest ⁵	1,538 ⁶	Dry season, mean minimum T_a 18°C, maximum T_a 33°C ⁶	iButtons at 1 m aboveground in shaded area of research area (JBB) ^b
<i>Setifer setosus</i> (female) T_b ($n = 1$)	Tree holes 0 to >2 m, underground burrows (7.4% of recordings) ⁷	JBA, Ankarafantsika National Park (16°19'S, 46°48'E), Madagascar	May 26–Nov 10, 2011; dry, nonreproductive season	Dry deciduous forest ⁵	1,538 ⁶	Dry season, mean minimum T_a 18°C, maximum T_a 33°C ⁶	iButton placed in tree cavity previously used as nest site in JBA ^b
<i>Setifer setosus</i> (male) T_b ($n = 3$)	Tree holes 0 to >2 m, underground burrows (7.4% of recordings) ⁷	JBA, Ankarafantsika National Park (16°19'S, 46°48'E), Madagascar	Dec 2010–Feb 2011 ($n = 1$); Nov 2011–Jan 2012 ($n = 2$); rainy, reproductive season	Dry deciduous forest ⁵	1,538 ⁶	Rainy season, mean minimum T_a 22°C, maximum T_a 34.1°C ⁶	iButton placed in tree cavity previously used as nest site in JBA ^b

Note. Superscript letters denote equipment used. a = model S3120 (Comet Systems); b = DS1922L Thermocron iButtons (Dallas Semiconductor). T_a = ambient temperature; T_b = body temperature; T_{skin} = skin temperature. JBA = Jardin Botanique A; JBB = Jardin Botanique B.

Sources. 1 = Neri-Arbodela et al. (2002); 2 = Norwegian Meteorological Institute (<http://met.no/>); 3 = Radespiel et al. (2003); 4 = Thoren et al. (2010); 5 = Alonso et al. (2002); 6 = Durrell Wildlife Conservation Trust, Ampijoroa 1997–2010; 7 = Levesque et al. (2012).

enclosure (100 cm × 80 cm × 140 cm) provided with two wooden nest boxes and water and banana ad lib. They were released during the early evening at the site of capture 1–2 d later to allow for postoperative observations. A high predation rate in this species (C. Canale, personal observation) meant that only six of the 10 were recaptured in September. Of the six iButtons recovered, five malfunctioned, and the data were lost.

The data collected on *S. setosus*, a nocturnal tenrec (supraorder: Afrotheria), are part of a larger study on the thermoregulation and ecology of this species (D. Levesque and B. G. Lovegrove, unpublished data). Only a small portion of these data are included in this study. A detailed description of the study site, population, and general methods are provided by Levesque et al. (2012). The study was conducted over two rainy seasons, from September 2010 to February 2012 (table 1). All animals were caught by hand by walking the established trails in the area at night. They were housed in plastic containers lined with paper towel and provided with live insects and sardines. The tenrecs were kept for a maximum of 5 d before surgery to allow for the measurement of metabolic data for a concurrent study. Telemeters were recovered either after successful recapture following a dry season (one individual) or after the animal's death (eaten by a snake or due to road accident; Levesque et al. 2013). Data presented here were obtained from one adult female (whose mass ranged from 140 g post-hibernation to 256 g prehibernation) between May 26, 2011, and the date of explantation on November 10, 2011. The small amount of data collected from this individual when active (11 d) were supplemented with data obtained from three adult males (169 ± 11 g).

Surgical Procedures

DS1922L Thermocron iButtons (Dallas Semiconductor, Dallas, TX) were miniaturized (Lovegrove 2009), encapsulated in surgical wax (Paramat Extra-Merck, Darmstadt, Germany; weight = 1.86 ± 0.13 g, 2.9% of the animal's body mass), and surgically implanted into the peritoneal cavity of *M. ravelobensis*. Data were recorded every 40 min with a resolution of $\pm 0.0625^\circ\text{C}$. For the larger *S. setosus*, two miniaturized DS1922L Thermocron iButtons were fitted alongside a modified two-stage transmitter (Merlin Systems, Boise, ID) to allow subsequent location and recapture. The entire waxed transmitter/iButton package weighed around 13.0 g (mean: 13.0 g; range: 11.7–13.5 g; 5%–8% of the animal's body mass). The iButtons were programmed to record once every 32 min at a resolution of $\pm 0.5^\circ\text{C}$. Both species were also injected subcutaneously with a transponder (Small Animal Marking System, Trovan, Melton, East Yorkshire, UK) to allow for identification at recapture.

The data loggers were implanted via ventral midline laparotomies under sterile conditions in an enclosed laboratory site at the research camp. Oxygen and vaporized anesthetic (isoflurane) were delivered to the animals through a mask at a rate of 700 mL min^{-1} . Anesthesia was induced at 1%–2% isoflurane

and maintained at 0.5%. An intramuscular injection of antibiotics (1 mL 10 g^{-1} of Duplocillin or 10^{-3} mL 10 g^{-1} of Duphamox) was administered to prevent postoperative infection. Following surgery, an anti-inflammatory pomade (Sulmidol) was applied, and mouse lemurs were given an analgesic ($0.04 \text{ mL } 100 \text{ g}^{-1}$; Metacam). All procedures involving the use of animals were approved by the Madagascar National Parks (permits 218/09/MEF/SG/DGF/DCB.SAP/SLRSE, 158/10/MEF/SG/DGF/DCB.SAP/SCBSE, 017/11/MEF/SG/DGF/DCB.SAP/SCB) and comply with all national Malagasy laws.

Environmental Data

Sunrise and sunset times were obtained for each day from the US Naval Observatory website (<http://www.usno.navy.mil/USNO/>).

Microcebus griseorufus

To expand our description of T_{skin} data and daytime hyperthermia, we digitized various sections of the data from figure 2 in Kobbe et al. (2011) using Techdig V2 (R. B. Jones, Mundelein, IL). These data were measured during the dry season in Madagascar and were interpreted in the context of this study.

Data and Statistical Analyses

In all species we evaluated the number of times in which T_b or T_{skin} was higher during the animal's rest phase than it was during the previous and preceding active phases. Torpor expression was also quantified in all species. A threshold T_b of 33°C was used for *M. ravelobensis* in keeping with previous studies on mouse lemurs (Ortmann et al. 1997; Genin and Perret 2003). *Setifer* were considered torpid when T_b tracked T_a (thermoconforming; see Canale et al. 2012). Unless otherwise stated, all data are presented as mean \pm SD. The daytime and nighttime maximum and minimum T_{skin} and T_a were obtained from data for the four tarsiers. We performed a general least squares repeated-measures analysis of variance examining the influence of factor (day and night maxima and minima) and between subject effects. To test the hypothesis that T_a has an influence on daytime T_{skin} , we performed an ordinary least squares regression on maximum daytime T_{skin} as a function of maximum daytime T_a . All statistics were performed using SPSS, ver. 18, and compared to an α value of 0.05.

Results

Torpor Patterns

Three of the four studied species, namely, *Setifer setosus*, *Microcebus ravelobensis*, and *Microcebus griseorufus*, entered torpor, either prolonged (hibernation) or <24 h, during the rest phase (daily heterothermy) during the dry season in western Madagascar.

Hibernation in the female *S. setosus* commenced around April 25, 2010 (D. Levesque, personal observation), but a data

logger malfunction caused a loss of data from the first part of the hibernation period. However, T_b data obtained from the second data logger demonstrated that the female was in torpor between May 26 and October 22. During hibernation T_b closely tracked T_a measured in a nearby tree hole ($P < 0.001$, $r^2 = 0.61$; fig. 1A). During the period of activity following emergence from hibernation, the mean nighttime (active phase) T_b for this individual was $33.1^\circ \pm 0.2^\circ\text{C}$, whereas the maximum T_b recorded during hibernation was 36.0°C (fig. 1A, 1). On two occasions, as indicated by a reduction in the T_b amplitude, the animal moved to a more insulated nest site (fig. 1A, 2). After the hibernation period, the female appeared to remain active each night until the date of recapture.

This study demonstrated for the first time that *M. ravelobensis* employs daily torpor, as has been previously found in other congeneric species (*Microcebus murinus*, *M. griseorufus*, *Microcebus myoxinus*). Over 109 d of recordings, the individual entered daily torpor on 43% of days (see, e.g., fig. 1B, 3). The average T_b was $35.5^\circ \pm 2.1^\circ\text{C}$ during the daytime rest phase and $37.6^\circ \pm 1.4^\circ\text{C}$ during the nighttime active period.

Kobbe et al. (2011) demonstrated that *M. griseorufus* show highly flexible thermoregulatory patterns, ranging from short torpor bouts to hibernation bouts lasting more than 2 wk. We digitized data from a 30-d trace of T_{skin} of an individual *M. griseorufus* (fig. 2b in Kobbe et al. 2011) during the winter dry season. The animal entered torpor daily during the latter half of the nighttime active phase. The mean maximum daytime T_{skin} was 33.7°C (range: $31.3^\circ\text{--}36.1^\circ\text{C}$). The mean minimum T_{skin} during the night when the animals were torpid, most commonly measured after midnight, was 15.5°C (range: $11.1^\circ\text{--}22.5^\circ\text{C}$). The mean T_{skin} at midnight, which is a period during the active phase immediately prior to torpor entry, was 26.3°C (range: $23.1^\circ\text{--}31.3^\circ\text{C}$). Thus, the highest maximum active phase T_{skin} measured (31.3°C) was equal to the lowest maximum daytime T_{skin} measured. *Microcebus griseorufus* clearly experience notable heat storage during their daytime rest phase (fig. 1C).

Over a total of 141 d of observation, no pronounced daily torpor and/or hibernation was recorded in tarsiers. However, a slight relaxation of normothermy was observed on several nights (fig. 2A, 4). We presume that at the time of the year when the measurements were made on tarsiers, energy stresses were minimal. Whether tarsiers are heterothermic could be confirmed at other times of the year, for example, during the short dry season in the Philippines (January and February).

Daytime Rest Phase Hyperthermia

All four species we describe here experienced higher T_b or T_{skin} during the daytime rest phase than during their active nighttime period (fig. 2, 1). All four tarsiers showed the same pattern of T_{skin} in response to T_a (fig. 2A, 1). T_{skin} was elevated when daytime T_a was high (fig. 2A) but not when T_a was lower on periodic cooler days (fig. 2A, 2). Elevated tarsier daytime T_{skin} was indeed induced by elevated T_a because for the pooled tarsier data, there was a significant positive correlation between the daily maximum T_a and the daily maximum T_{skin} ($n = 141$ d,

$r^2 = 0.374$, $P \ll 0.001$; fig. 3A). The slopes for the four individuals ranged from 0.32 to 0.79 (mean \pm SD: 0.55 ± 0.18). There was no significant correlation between the minimum night T_{skin} as a function of minimum night T_a ($P \gg 0.05$, $r^2 = 0.02$; fig. 3A), confirming that the collar-mounted telemeters were not influenced by T_a at night (fig. 2A, 3). There were significant differences between T_{skin} measures (SPSS, ver. 18., general linear model, repeated-measures ANOVA, $F_{3,137} = 31.17$, $P \ll 0.001$). A Bonferroni post hoc test showed significant differences between maximum day T_{skin} ($33.27^\circ \pm 0.96^\circ\text{C}$) and maximum night T_{skin} ($31.95^\circ \pm 0.67^\circ\text{C}$).

In *S. setosus*, daytime rest phase T_b was higher than the previous night's active T_b on 6.1% of all days (range: 3.1%–7.7%). This high T_b occurred mostly before the onset of the rainy season from November to December. Whereas on some days the effects of T_a on T_b were highly evident (fig. 2B, 1), on others the animal maintained a lower T_b , likely due to behavioral recourse to a more insulated nest site (fig. 2B, 2). Each absolute maximum T_b (35.5° , 34.1° , 36.0° , and 34.4°C) was recorded during the daytime rest phase (1200–1500 hours; fig. 2B, 1) and often after a torpor bout (fig. 2B, 4).

Microcebus ravelobensis had higher T_b during the rest phase than during the active phase on 6 d (5.5%; fig. 2C, 1). Similar to what was observed in *S. setosus*, hyperthermic temperatures often occurred after a shallow torpor bout that was terminated by rising T_a (fig. 2C, 4).

Microcebus griseorufus showed the highest T_{skin} values during the day and lower, more constant T_{skin} during the night, except early on in the third day when the animal entered torpor (fig. 2D, 4). As with *S. setosus*, when *M. griseorufus* hibernated (fig. 1C), the T_{skin} data were identical to those that a typical thermoconforming ectotherm would display, although T_{skin} was phase delayed because of refugium insulation (see Dausmann et al. 2005).

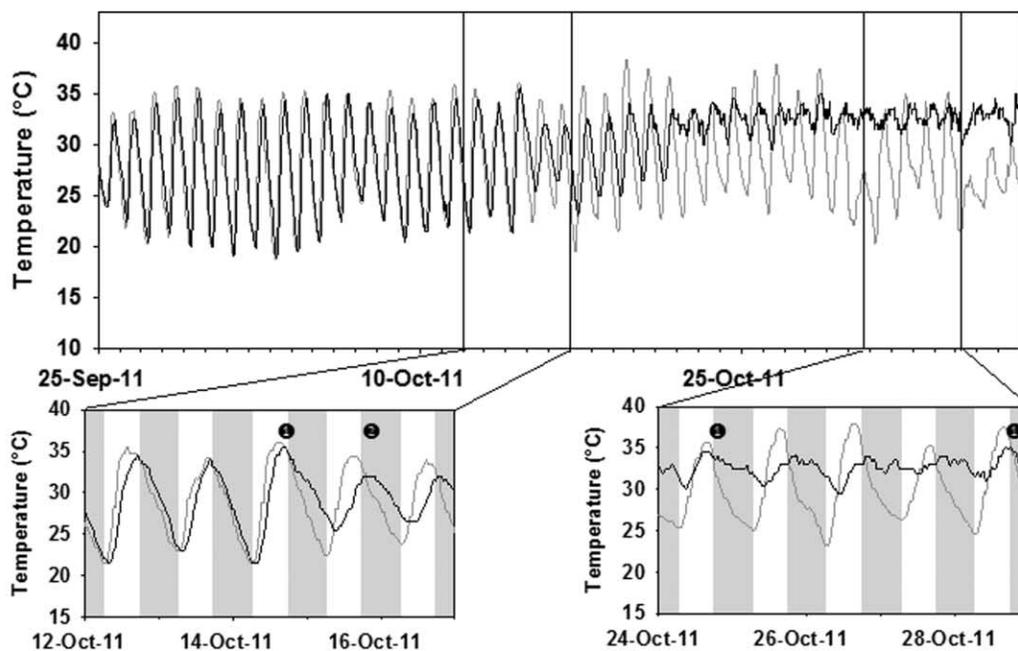
Unlike the tarsiers, the data from *S. setosus* and *M. ravelobensis* showed no relationship between maximum T_b and maximum T_a during the nighttime active phase (*S. setosus*: $P = 0.990$; *M. ravelobensis*: $P = 0.195$) and little to no relationship during the daytime rest phase (*S. setosus*: $P = 0.003$, $r^2 = 0.075$; *M. ravelobensis*: $P = 0.211$).

Discussion

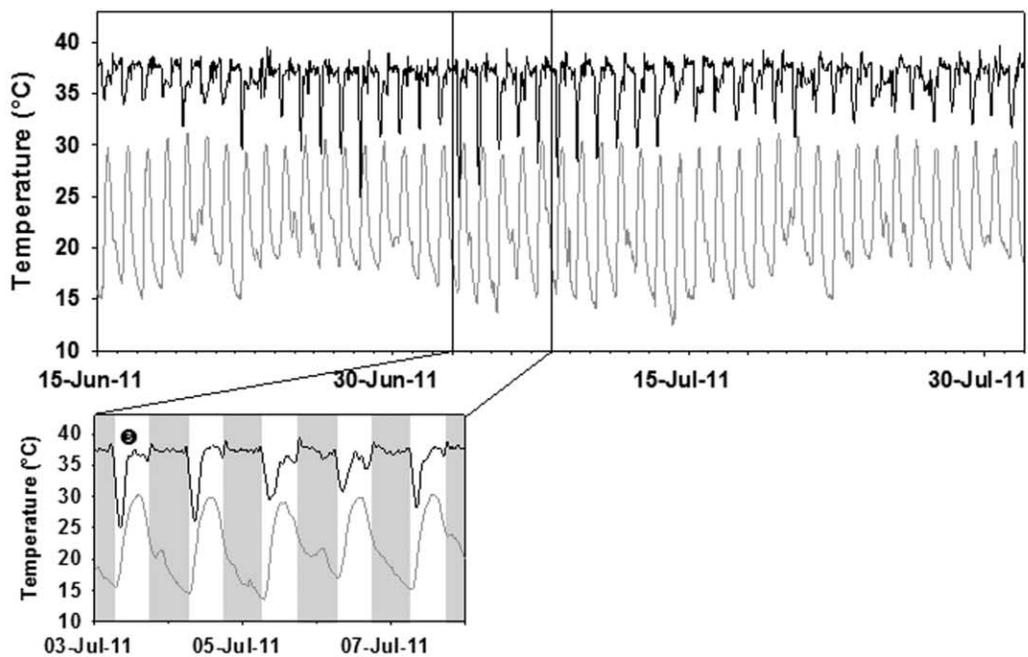
Vulnerability to Arrhenius Effects

In all four small tropical arboreal mammals that we studied, we found evidence of hyperthermia during the daytime rest phase. We use the term “hyperthermia” here to refer to any T_b higher than the normothermic active phase T_b . Hyperthermia is most pronounced in the basoendothermic species, such as the tarsiers, where the maximum daytime rest phase T_{skin} is $\sim 2^\circ\text{--}3^\circ\text{C}$ higher than the maximum active phase T_{skin} (fig. 2A). Thus, our preliminary data on T_{skin} and T_b of free-ranging, tropical arboreal small mammals, albeit admittedly limited in sample sizes, suggest that Arrhenius effects associated with climate change can theoretically impose energetic costs that can affect fitness.

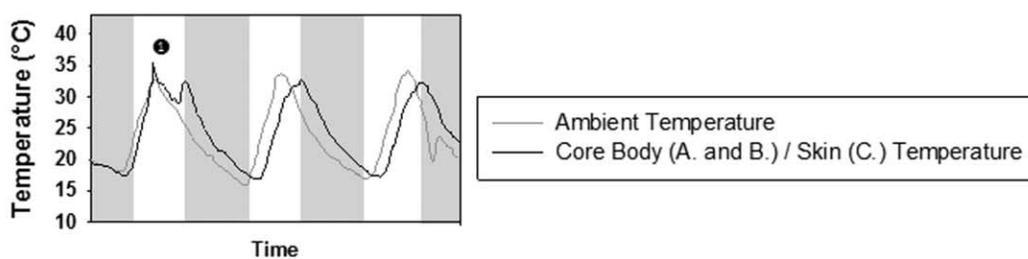
A. *Setifer setosus*



B. *Microcebus ravelobensis*



C. *Microcebus griseorufus*



For the first time, to our knowledge, these data highlight that free-ranging nocturnal mammals show higher maximum rest phase T_b than maximum active phase T_b . Mammals typically display circadian amplitudes in T_b in which the active phase T_b is always higher than that of the rest phase T_b (Aschoff et al. 1982; Refinetti 2010). Indeed, in all mammals used in the latter two data sets, the active phase T_b was higher than the rest phase T_b , irrespective of whether the mammal was diurnal or nocturnal. In the laboratory, T_a did not influence the circadian T_b rhythm of mammals and birds, except at lower T_a (10° – 15° C), where some species displayed an elevated amplitude in the daily rhythm (Refinetti 2010).

The unusual elevated daytime T_b has not been observed in free-ranging mammals before because very few data have been measured in free-ranging arboreal small mammals at high T_a . Arboreality is important in this context because some small arboreal mammals do not exploit the cooler, thermally buffered underground realms during the day, as do many small nocturnal mammals. These latter species can enter torpid states throughout the daytime because there is a sufficiently large $T_b - T_a$ gradient to facilitate core T_b cooling. They can thus also avoid potential daytime increases in T_a induced by climate change (although see Humphries et al. 2002). The behavioral recourse to thermally buffered refugia is, however, effectively exploited by some arboreal tropical species, such as dwarf lemurs (*Cheirogaleus* spp.; Dausmann et al. 2009; Blanco and Rahalinarivo 2010) and *Setifer setosus* (Levesque et al. 2012). Indeed, dwarf lemurs and *S. setosus* occasionally hibernate in underground refugia (Blanco et al. 2013; D. Levesque, personal observation). For other species, such as tarsiers, these extreme behavioral responses are not known. Specialized arboreality presumably limits the full range of behavioral response options that are possible.

Arrhenius effects are potentially most energetically threatening when arboreal mammals are torpid (see also bats in Humphries et al. 2002). Cheirogalid primates and tenrecs employ either daily torpor or hibernation during the dry season to profoundly reduce energetic demands when resources are scarce (Racey and Stephenson 1996; Dausmann et al. 2005, 2009; Lovegrove and Génin 2008; Kobbe and Dausmann 2009; Kobbe et al. 2011). These species display an ectotherm-like pattern of T_b during torpor when T_a exceeds the torpor T_b setpoint; T_b essentially tracks that of the T_a quite precisely day after day. For example, T_b fluctuates between a minimum of $\sim 16.5^{\circ}$ C at night to a maximum of $\sim 36.0^{\circ}$ C during the daytime in hibernating *S. setosus*. MR also fluctuates in a similar daily pattern (Dausmann et al. 2009), presumably reflecting Arrhenius effects (but see discussion below of putative hyperthermic torpor). Thus, it is theoretically likely that any increase in the maximum and minimum daily temperature with climate

change will influence T_b and hence related Arrhenius effects on MR.

With the exception of the tarsiers, which did not appear to employ daily torpor regularly during the period of measurement (August–December 2010), *S. setosus* (during the active/rainy season) and both species of mouse lemur in this study entered daily torpor during the latter stages of the active phase or during the first part of the daytime rest phase (e.g., fig. 2B–2D, 4). Indeed, this is the only time that nocturnal arboreal heterotherms can employ torpor because the gradient between normothermic T_b and T_a is sufficiently large to promote core temperature cooling. For example, the lowest T_b attained by torpid *S. setosus* when not hibernating occurred on nights when activity ended an hour or two before sunrise. In this respect there must be a trade-off between time spent in torpor conserving energy and time spent foraging and acquiring energy. Under laboratory conditions, starved mouse lemurs were hyperactive in the first hour of the night, and activity time was reduced to 4 h, resulting in longer torpor bouts compared to animals fed ad lib. to maintain their body mass (Canale et al. 2011). In free-ranging *M. griseorufus*, fatter individuals displayed longer torpor bouts than lean individuals (Kobbe et al. 2011).

We have yet to quantify Arrhenius effects in free-ranging tropical mammals. However, under the most extreme climate change predictions, that is, a 4° C increase in average global T_a by the end of the century (IPCC 2011), the Arrhenius equation predicts increases in MR as high as 45% during the hottest times of the day. This prediction assumes, of course, that there is no concomitant endogenous reduction in MR, which may not necessarily be true. Thus, our preliminary data on T_{skin} and T_b of free-ranging tropical arboreal small mammals suggest that Arrhenius effects associated with climate change can theoretically impose energetic costs during torpor that can result in less energy being allocated to growth and/or reproduction, which will seriously affect fitness.

Hyperthermic Torpor?

Whether small mammals can offset Arrhenius effects through endogenous reductions in metabolism, that is, heat-induced hypometabolism, is not known. Indeed, when small arboreal mammals display hyperthermia during the daytime rest phase, we need to question whether they may be in a state of “hyperthermic torpor.” As counterintuitive as this term may sound, we present a working hypothesis here that argues that endotherms could theoretically minimize the energetic consequences of daytime hyperthermia through hyperthermic daily torpor (HDT). Such metabolic downregulation could minimize the

Figure 1. Patterns of ambient and body temperature of free-ranging *Setifer setosus* (A) and *Microcebus ravelobensis* (B) and skin temperature of *Microcebus griseorufus* (C) during the austral winter (dry season). A, 1 = periods where torpid T_b was greater than the average active phase T_b ; 2 = when *S. setosus* moved to a different hibernaculum (indicated by the reduction in T_b amplitude). B, 3 = a torpor bout in *M. ravelobensis* (sensu Ortmann et al. 1997).

$T_b - T_a$ gradient and hence the absolute hyperthermic T_b and partially negate Arrhenius effects.

One problem in testing for putative hypometabolism, as usually reflected in patterns of T_b or T_{skin} in free-ranging animals, is that torpor patterns are masked or smothered by passive exogenous heating and heat storage at high T_a . Another problem is that there are no data, to our knowledge, of free-ranging MRs measured simultaneously with core T_b in heterothermic basoendotherms. There are, however, metabolic and T_{skin} data measured in the dwarf lemur *Cheirogaleus medius* during hibernation in the austral winter (dry season) in Madagascar (Dausmann et al. 2009). *Cheirogaleus medius* is a lower mesoendotherm (rest phase normothermic $T_b \sim 36.0^\circ\text{C}$; Dausmann et al. 2005).

Theoretically, if T_b influences MR as predicted by the Arrhenius effect, Q_{10} should be 2–3. However, if metabolism is downregulated as T_a approaches T_b , as proposed by the HDT hypothesis, then we should predict $Q_{10} < 2$ in torpid animals during the daytime rest phase when T_b is elevated due to endogenous passive heating.

In Dausmann et al.'s (2009) study T_{skin} of *C. medius* during the daytime during hibernation seldom exceeded 30°C , so these can probably not be considered true hyperthermic T_b . Nevertheless, Q_{10} values calculated using T_{skin} of hibernating *C. medius* showed mean $Q_{10} = 2.11 \pm 0.97$ ($n = 11$; Dausmann et al. 2009). The graphs of six of these 11 individuals showed Q_{10} values of 1.29, 1.35, 1.70, 1.86, 1.91, and 3.96 (Dausmann et al. 2009). These data show a large variance (one large outlier), but five of the six animals did display $Q_{10} < 2$ where T_{skin} was elevated during the daytime rest phase. Although these Q_{10} values should be evaluated with some caution because they were (a) calculated from skin rather than core temperatures and (b) were not calculated from true hyperthermic T_b , small tropical heterotherms may display Q_{10} values lower than those predicted by the Arrhenius effect. The test of this hypothesis is highly worthy of further investigation, most feasibly in the laboratory.

Another test for the presence of HDT would be to examine the patterns of T_b at the end of the daytime rest phase when T_b cools rapidly with cooling T_a . If animals maintain our proposed rest phase torpor into the entire period of the following active phase, then T_b will closely track T_a , as is seen in hibernating *C. medius* (Dausmann et al. 2009) and *M. griseorufus* (Kobbe et al. 2011). However, if they terminate torpor and become active, the setpoint T_b will be adjusted to the normothermic active phase level and T_b will be controlled, as seen, for example, in the tarsiers (fig. 2A) and *M. ravelobensis* (fig. 2C). The precise timing of when the animals become active at the onset of the active phase can offer a test for HDT, especially in nonbasoendotherms. If, following the rest phase, animals remain in torpor and arouse only after T_b has decreased to below the normothermic active phase setpoint, then, at the initiation of activity, T_b will rapidly “catch up” to the normothermic active phase T_b . Should this occur, it will be reflected as a dip in the T_b pattern at the onset of the active phase. The dip essentially is indicative of the termination of daytime rest phase hyperthermic torpor.

Our data for core T_b of *M. ravelobensis* do indeed illustrate these post-rest phase dips in T_b (fig. 2C, 5). The magnitude of the dips will be dependent on the timing of the onset of activity and the absolute value of the active phase T_b . Dips should be most pronounced when there is a late activity onset and/or an active phase $T_b > 36^\circ\text{C}$. In the latter case, pronounced dips can be seen in free-ranging long-eared bats (*Nyctophilus geoffroyi*) in Australia (Geiser and Stawski 2011; Stawski and Geiser 2012). In these tree-roosting bats, arousal coincided exactly with the onset of the night. Following the late afternoon reduction in T_a , T_{skin} showed a concomitant decline but then increased rapidly from $\sim 31^\circ\text{C}$ to the active phase T_{skin} ($\sim 39^\circ\text{C}$) immediately prior to flight. Note that tarsiers and *Setifer* did not display the dip, although T_b in *Setifer* often decreased at the initiation of activity (fig. 2A, 2B), because, as predicted, their active phase T_b is so low ($\sim 33^\circ\text{C}$).

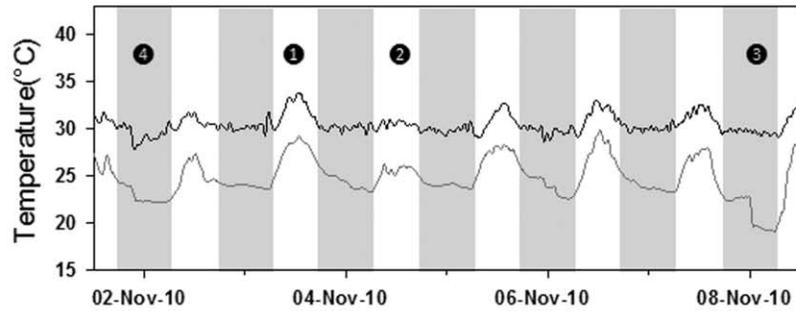
Vulnerability to Hyperthermia: The Humidity Problem

Tropical mammals faced with global warming also face the adversity of high relative humidity (RH) associated with increased precipitation intensity (Meehl et al. 2000; Yeh et al. 2009). At low relative humidity, mammals can easily avoid hyperthermia because evaporative cooling is an extremely effective means of dissipating heat to the ambient when T_a approaches or exceeds T_b . However, in tropical and subtropical forests, where relative humidity is consistently high (see fig. A1), heat dissipation is challenging. First, the driving force for evaporative cooling is limited because the water vapor saturation deficit between the ambient and the animal is small. Second, high relative humidity increases wet bulb temperatures (T_w) and reduces the $T_b - T_w$ gradient and hence the capacity to dissipate heat by convection and radiation (Huber 2008; Sherwood and Huber 2010). A $T_b - T_w$ gradient of $\sim 2^\circ\text{C}$ is generally considered to be about the minimum necessary to offload metabolic heat to the environment through nonevaporative processes (Sherwood and Huber 2010). So, even when shaded and resting, mammals will begin to store heat if T_w approaches T_b .

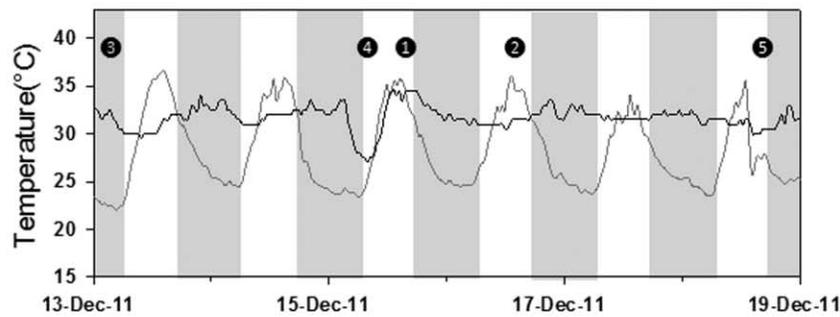
To illustrate the potential influence of relative humidity on T_w , we present a graphic extension of Sherwood and Huber's (2010) predictions. The model shows the full range of T_w that mammals are likely to experience at different T_a and RH% (fig. 4). The model is not intended to be quantitative but serves merely to emphasize and develop predictions which incorporate RH% as a confounding variable in climate change models. As an example, in humans a sustained $T_w > 35^\circ\text{C}$ would be lethal (Sherwood and Huber 2010), which would occur when RH% reaches 80%–100% at T_a between 35° and 38°C (fig. 4). At present, maximum global T_w seldom exceeds 31°C , so, apart from short-term heat waves, humans are not currently vulnerable to sustained heat stresses (Sherwood and Huber 2010).

However, depending on their critical thermal maxima, the situation for small tropical endotherms may be much more critical. Tarsiers, for example, may be vulnerable to sustained heat stress with climate change. These prosimians are excellent

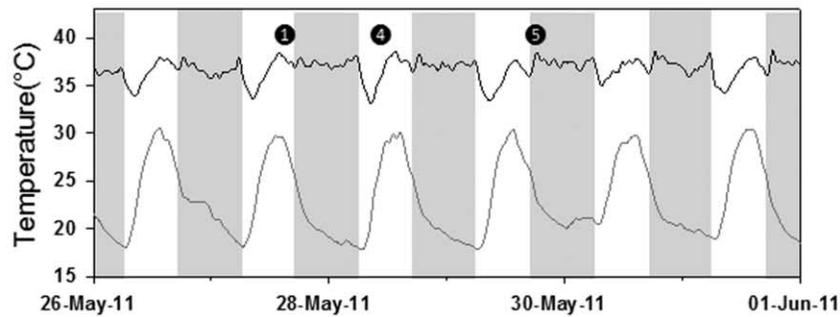
A. *Tarsius syrichta*



B. *Setifer setosus*



C. *Microcebus ravelobensis*



D. *Microcebus griseorufus*

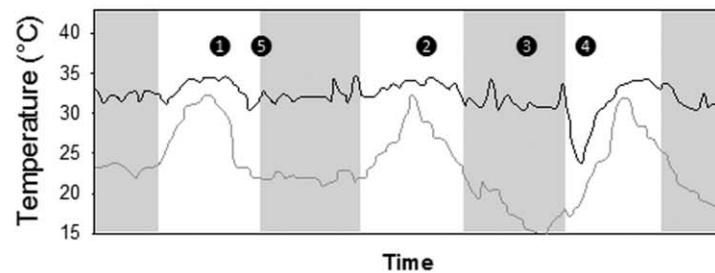


Figure 2. Patterns of ambient temperature (T_a) and body temperature (T_b) or skin temperature (T_{skin}) of free-ranging *Tarsius syrichta* (A; T_{skin}), *Setifer setosus* (B; T_b), *Microcebus ravelobensis* (C; T_b), and *Microcebus griseorufus* (D; T_{skin}). 1 = periods of putative hyperthermic daily torpor; 2 = days when T_b did not follow T_a because of nest insulation (e.g., *S. setosus*) or a cooler than average day (e.g., *T. syrichta*); 3 = periods where the basoendotherms (*Tarsius* and *Setifer*) were capable of maintaining high active T_b , indicated by days where the animal maintained a high T_b during the active phase despite cold T_a ; 4 = periods of torpor were observed in all species and are terminated by rising T_a , which may, as we argue in the text, lead to putative hyperthermic torpor (1) and the dip in T_b (C; 5) followed by an increase to normothermia at the onset of the active phase.

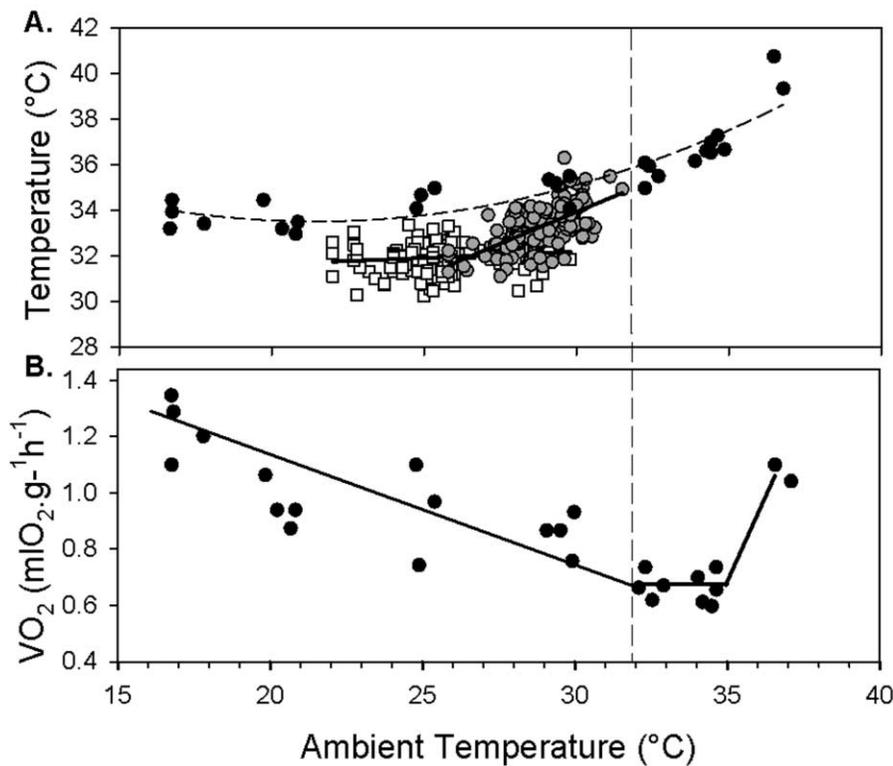


Figure 3. Body temperatures and metabolic rate (filled circles) of *Tarsius syrichta* measured in the laboratory in resting animals (data digitized from McNab and Wright 1987). A, Maximum nighttime active phase T_b (squares) and maximum daytime rest phase T_b (shaded circles) of free-ranging tarsiers. There is a significant ordinary least squares regression of the daily maximum T_{skin} as a function of daily maximum T_a ($n = 141$ d; slope = 0.55; $r^2 = 0.374$, $P \ll 0.001$). B, Lines representing the thermal profile were fitted by eye for easier graphic representation. The dashed line indicates the lower critical limit of thermoneutrality.

models to investigate potential daytime hyperthermia with climate change in arboreal small mammals. They are strictly nocturnal and in the laboratory displayed the lowest body temperature ($T_b = 33.8^\circ\text{C}$) and basal metabolic rate (BMR = 65% of expected) of all primates (McNab and Wright 1987).

In our study, the daytime T_{skin} of tarsiers was heavily influenced by daytime T_a (figs. 2A, 3). The telemeter temperatures were not influenced by direct solar radiation because tarsiers retire to densely shaded retreats during the day (Dagosto 2001; Řeháková-Petrů et al. 2012). During the daytime, T_{skin} tracked T_a with a consistent differential of $\sim 3^\circ\text{C}$. When our free-ranging data are compared with rest phase T_b and resting MRs measured by McNab and Wright (1987) in the laboratory (fig. 3), one observation is noteworthy. The highest daytime T_a measured in the forests in Bohol (31.5°C) in our study was approximately equal to the lower critical limit of thermoneutrality and about 4°C lower than T_{uc} (McNab and Wright 1987; fig. 3). Thus, these laboratory data suggest that increases in T_a by as much as 4°C will theoretically have no influence on the MR of resting tarsiers, despite their elevated T_b .

However, if we take humidity into account and assume a conservative 1°C differential between the animal's normothermic T_b and T_w required to maintain normothermy, then sustained heat stress for tarsiers would commence at $T_w \approx 32.9^\circ\text{C}$

under a 4°C climate change increase model ($T_a \approx 34^\circ\text{C}$) at RH% = 80% (fig. 4; see also fig. A1 for station RH% and T_a). This exercise illustrates that laboratory data measured in dry air, i.e., RH% < 10%, cannot realistically predict the likely effects of climate change hyperthermia in free-ranging tropical endotherms, especially in basoendotherms. Similar arguments have been made for ectotherms (Niehaus et al. 2012).

The real vulnerability of tropical small mammals to relative humidity occurs during the rainy season, when relative humidity remains consistently high and the capacity for evaporative cooling is very low. However, it is very difficult at this stage to model this potential influence because there is a surprising dearth of information on the influence of RH% on mammalian T_b and MRs. Baudinette (1972, p. 57) argued that in Californian ground squirrels (*Spermophilus beechyi*), "the dimension of the thermoneutral zone is independent of ambient humidity." Similarly, studies on rodents and brush-tailed possums have shown little to no effect of humidity on MRs or T_b below the upper limit of thermoneutrality (Edwards and Haines 1978; Cooper and Withers 2008). We find it hard to imagine that an endotherm's T_b at or above T_{uc} will not be influenced by T_w . Ironically, taking physiology to the field is producing questions that can now seemingly be answered only by returning to the laboratory, and the role of RH% in mam-

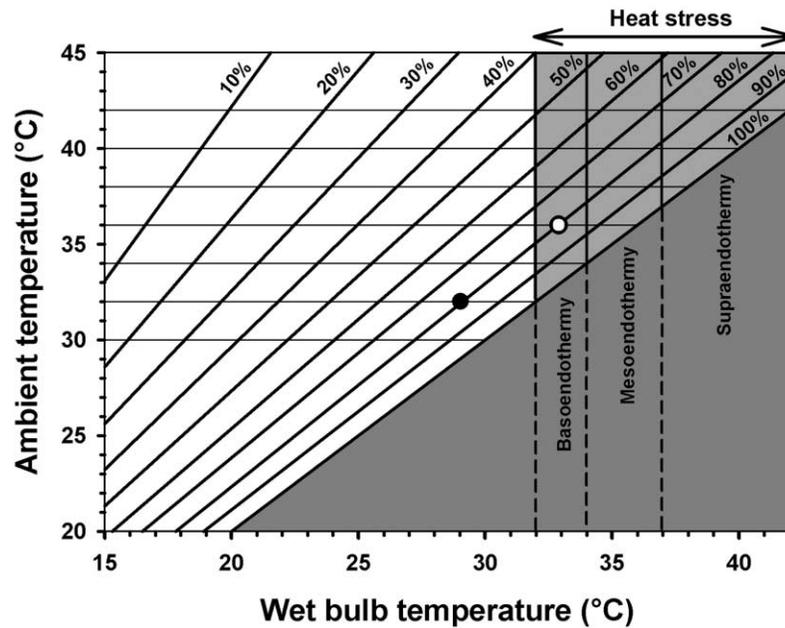


Figure 4. Graphic illustration of the range of wet bulb temperatures (T_w) that mammals endure in macro- and microclimates. Heat stress is predicted to occur when the $T_b - T_w$ differential decreases below about 1°C (see also Sherwood and Huber 2010). Station ambient temperature (T_a) is plotted noncausally as a function of T_w for a range of relative humidity (RH) calculated from Martinez (1994). The lower limit of basoendotherm heat stress ($T_w = 32^\circ\text{C}$) assumes a body temperature (T_b) of 33°C and a gradient between T_b and T_w of 1°C . In a similar fashion, the lower limits for mesoendotherms ($35^\circ\text{C} \leq T_b \leq 37.9^\circ\text{C}$) and supraendotherms ($T_b > 37.9^\circ\text{C}$; sensu Lovegrove 2012) are also indicated. The horizontal lines provide a quick method of evaluating T_w from a station T_a and RH%. An example is provided for the tarsier (filled circle) based on field data from the study site on Bohol Island, Philippines (barometric pressure = 760 mm Hg; maximum $T_a = 32^\circ\text{C}$; RH% = 80%; note that fig. A1, available online, shows an example of the relationship between T_a and RH% at the site). The open circle shows the same estimate but under the most severe climate change prediction (T_a increase of 4°C).

malian hyperthermia is certainly one of them. Figure 4 may be a useful preliminary aid in this regard because it can be used to predict heat stress vulnerability in different macro- and microclimates under different climate change predictions.

Water Availability

Another major consideration related to relative humidity that has yet to be explored in physiologically founded climate change models is the availability of water required to balance losses through evaporative cooling. Rates of evaporative water losses will increase dramatically with hyperthermia because the rate of respiratory water loss increases in direct proportion to increases in the rate of gas exchange (Cooper and Withers 2008; Woods and Smith 2010). Krockenberger et al. (2012) have argued that the distributional range of the green ringtail possum (*Pseudochirops archeri*) in Australia's Wet Tropics is constrained by the availability of free water and dietary water, in addition to high T_a , in the forest canopy during the dry season. These authors propose the novel hypothesis that one of the adaptive advantages of tropical heterothermy may be the reduction of the amount of water required to maintain water balance at normothermy.

Climatic Extremes

Heat wave die-offs following extreme climate events, such as 4–5-d heat waves (Easterling et al. 2000; Meehl and Tebaldi 2004), occur frequently in semitropical arid regions (McKechnie and Wolf 2010), but they also occur in the tropics. For example, several mass die-offs of tree-roosting flying foxes (*Pteropus alecto*) have occurred in tropical Australia, for example, in Townsville ($19^\circ 13'S$), when the maximum daily dry bulb temperature reached 44.3°C (Welbergen et al. 2008). In these examples, bats had limited recourse to behavioral responses. One mass die-off of *P. alecto* that occurred on January 12, 2002, in New South Wales, Australia, was closely observed and documented (Welbergen et al. 2008). A total of 1,453 bats (5%–6% of the colony) died, with deaths commencing about 1 h prior to T_a attaining a maximum of 42.9°C (Welbergen et al. 2008). Unfortunately, in all documented mass die-offs reported, it is not known, to our knowledge, whether dehydration or pathological cellular heat damage was the direct cause of death.

This example of tropical bat die-offs highlights the major difference in vulnerability faced by relatively immobile island-bound mammals and highly mobile mammals, such as bats, which have the capacity to migrate to cooler climes at higher

latitudes or altitudes. Over the past 8–9 decades, *P. alecto* has expanded its distribution southward and now overlaps with *Pteropus poliocephalus* (Welbergen et al. 2008). Thus, although *P. alecto* periodically experience 100% mortality, during which entire colonies die out, the population as a whole is distributed over a sufficiently wide geographic distributional range to avoid extinction. The same cannot be said for mammals such as *M. ravelobensis*, which is limited to a single small, isolated forest fragment in Madagascar. A single heat wave, like those that have occurred in Townsville, Australia, could potentially lead to the extinction of this primate within a single day.

Conclusions

In this study we have measured and reevaluated published data illustrating examples of free-ranging T_b and T_{skin} in tropical small mammals. Our data showing that all species displayed the highest T_{skin} or T_b during the daytime rest phase are completely contrary to what would be predicted by chronobiology. Indeed, taking physiology to the field, specifically to the tropics, might compel us to rethink certain concepts on thermal adaptation. In terms of both slow long-term global warming and short-term heat waves, our data suggest that insular, tropical basoendotherms, especially those that cannot retire to buffered underground refugia or caves and that also have little or no opportunity for altitudinal or latitudinal migration, are vulnerable to heat stress with global warming. Species that are particularly vulnerable are those with limited recourse to thermoregulatory behavioral responses and those that currently have very limited distributions on islands.

Our data also question whether small tropical arboreal mammals will indeed experience Arrhenius energetic costs and consequent effects on fitness. Although Arrhenius effects theoretically cannot be avoided during the daytime rest phase in both normothermic and torpid tropical mammals in thermally unbuffered retreats, we propose that hyperthermic torpor (hyperthermia-induced hypometabolism) at high T_a can offset Arrhenius effects. This being the case, we then need to question whether a torpid, small tropical endotherm is any different physiologically in terms of its thermal response to high T_a to a similar-sized tropical ectotherm. If not, then the “grim” predictions that have been made for tropical ectotherms (Huey and Berrigan 2001; Deutsch et al. 2008; Huey et al. 2009, 2012) should be equally applicable to small tropical baso- and mesoendotherms. Despite the comparatively slow warming of the tropics relative to high latitudes between 1980 and 2010, tropical ectotherms and endotherms will display the largest metabolic increases simply because “tropical warming took place in an environment that was initially warm” (Dillon et al. 2010, p. 704).

Our mechanistic understanding of the metabolic responses to hyperthermia under different water vapor pressure environments in small tropical mammals is very poor. There is also a critical lack of information on the importance of water availability and relative humidity associated with the ability of small arboreal tropical mammals to cope with global warming. Very

few relative humidity data have been collected simultaneously with free-ranging physiological data. The lack of these data limits the capacity of climate change models to estimate the gradient between the ambient T_w and T_b in macro- and microclimates. These data are particularly important for small tropical basoendotherms because their thermal biology interfaces very closely with that of the ambient.

Acknowledgments

The research was financed by incentive grants from the University of KwaZulu-Natal and incentive grants and an ad hoc travel grant from the National Research Foundation to B.G.L., a Claude Leon Foundation Postdoctoral Fellowship to C.C., and a postgraduate scholarship from the National Science and Engineering Research Council (Canada) to D.L. Data-logging devices used in tarsiers were developed within a project supported by the city of Vienna, the province of Lower Austria, and an Austrian Science Fund grant (FWF project P20534-B17) to T.R. We thank Idea Wild for a grant to purchase several GPS devices. We thank the Tarsius Project for financial support, especially the Decin Zoo and various funding agencies and sponsors (Hedvábná Stezka, Koktejl, Humi, Storm, Comet Systems, and others). We thank our local partners in the field, Simply Butterflies Conservation Centre, MICET (Madagascar), Bohol Island State University, and the Departement de Biologie Animale of the University of Antananarivo for cooperation and support. Special thanks to Lubomír Peške, Václav Řehák, Cristy Burlace, Felix Sobiono, Monika Papoušková, Olivia Lovasoa Malala Andriambola, and volunteers who helped us in the field. We thank Julius Baslot and his assistants for help with catching of tarsiers. We thank the DENR Philippines for providing the permits necessary for our research.

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