Using thermoregulatory profiles to assess climate change vulnerability in an arboreal tropical bat: heterothermy may be a pre-adaptive advantage

Shaun Welman[1],*, Andrew A. Tuen[2], Barry G. Lovegrove[1]

[1]School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa
[2]Institute of Biodiversity and Environmental Conservation, Universiti Malaysia, Sarawak, Malaysia

ABSTRACT: Many tropical endotherms are already confronted by ambient temperatures (T_a) close to their body temperature (T_b) and risk severe hyperthermia due to global warming. Tropical fruit bats play a vital role in the ecosystem and their absence could have dire consequences for ecosystem health. Many fruit bats have exposed roosting habits that increase their vulnerability to heat stress. We investigated the thermoregulatory capacity of wild caught lesser dog-faced fruit bats *Cynopterus brachyotis* from the Island of Borneo; a heterothermic 32 g foliage-roosting generalist bat. We determined the effect of T_a (21–36°C) on metabolism, T_b and evaporative cooling. We also measured the T_a and relative humidity (RH) at capture sites. The bats displayed a seemingly narrow thermoneutral zone of 30 ± 1°C, a basal metabolic rate of 5.60 ± 0.26 W kg^{-1} (1.01 ± 0.05 ml O$_2$ g^{-1} h^{-1}) and a normothermic T_b of 32.5 ± 0.3°C; all much lower than expected. Evaporative cooling was only effective at $T_a \leq 31$°C, above which heat storage became apparent. Bats typically entered torpor at $T_a < 25$°C and thermoconformed (i.e. allowed their T_b to fluctuate with T_a) at $T_a > 32$°C. The microclimate at capture sites remained cool ($T_a = 24$–25°C) and humid (RH > 90%). Our study supports the argument that tropical endotherms are susceptible to hyperthermia due to their low T_b. Further, we discuss the potential advantage of heterothermy in coping with short-term heatwaves. However, the future of these bats, and likely other low T_b species, depends primarily on their thermally buffered habitats, and decisive conservation action is required to protect thermal refugia.

KEY WORDS: Hyperthermia · Body temperature · Torpor · Global warming · Tropics · Fruit bats

1. INTRODUCTION

The tropics are thought to host the highest diversity of species on the planet (Rohde 1992, den Tex & Leonard 2013, Jablonski et al. 2013, Jansson et al. 2013) yet we have a limited physiological understanding of tropical species (Lovegrove 2000, Dillon et al. 2010). There is now a sense of urgency to fill the gap in our knowledge, as recent studies argue that (1) the rate of climate niche evolution required to keep up with the predicted rate of climate change is 4 orders of magnitude greater than any rate observed in the past (Quintero & Wiens 2013), (2) the rate of

global warming predicted by the IPCC may have been underestimated (Stroeve et al. 2007, van Oldenborgh et al. 2009, Natchimuthu et al. 2016), and (3) tropical species are most vulnerable to global warming (Huey et al. 2012, Lovegrove et al. 2014). Heat tolerance poses a rigid physiological limit to what animals may endure, and is a useful tool with which to gauge species adaptability to global warming (Sherwood & Huber 2010). Many tropical and semi-tropical mammals have comparatively low and thermolabile body temperatures ($T_b < 36$°C; Racey & Stephenson 1996, Lovegrove & Génin 2008, Stawski & Geiser 2012, Lovegrove et al. 2014). Consequently,

they must endure relatively small temperature differentials between their T_b and ambient temperature (T_a). The smaller thermal gradient (i.e. low $\Delta T = T_b - T_a$) compromises their ability to passively dissipate excess body heat or maintain T_b within species-specific ranges, because heat dissipation via conduction and radiation diminishes as ΔT approaches zero (Schmidt-Nielsen 1997, Sherwood & Huber 2010). By contrast, their reliance upon evaporative cooling, a physiologically active form of heat dissipation, increases as T_a increases (Tattersall et al. 2012).

Once $T_a \geq T_b$, evaporative cooling becomes the only means of dissipating heat from the body (McKechnie & Wolf 2004, Cory Toussaint & McKechnie 2012, Withers et al. 2012). Although evaporative water loss (EWL) scales with T_a, the effectiveness of evaporative cooling is ultimately dependent on the water vapour pressure deficit between the animal and its surroundings (Schmidt-Nielsen 1997, Willmer et al. 2005). For any heat dissipation to occur there needs to be at least a 1–2°C differential between the animal's skin and the wet-bulb temperature (Sherwood & Huber 2010). Thus, whereas mammals inhabiting higher latitudes usually encounter large water vapour pressure deficits that favour evaporative cooling (Walsberg 2000), the high relative humidity (RH) conditions in the tropics could potentially retard evaporative cooling and lead to fatal levels of heat storage (Mora et al. 2017). The rate at which animals store heat is size-dependent. Due to a high surface-area-to-volume ratio the rate of heat exchange is greater in small mammals (<1 kg). As a result, small mammals have low thermal inertia and store heat faster (Schmidt-Nielsen 1997, Tattersall et al. 2012). Based on the above, Lovegrove et al. (2014) argued that arboreal tropical small mammals have the highest risk of suffering heat stress due to global warming. Arboreality is a high-risk factor, as several arboreal mammals lead exposed lifestyles, and are thus susceptible to environmental perturbations (Bondarenco et al. 2014, Lovegrove et al. 2014).

Many tropical bats are small and roost in trees or other exposed sites (Kunz 1982, Kunz & Lumsden 2003, Santana et al. 2011), but are perceived to be less vulnerable to heat stress because they have the potential to migrate. Indeed, there is evidence of climate related range shifts by bats (Welbergen et al. 2008). Be that as it may, due to their nocturnal nature, bats are likely to endure daytime conditions rather than relocate (but see Bondarenco et al. 2014). As such, the vulnerability of tree-roosting species to pathological hyperthermia should not be disregarded (Kunz 1982, Welbergen et al. 2008). Case in

point, the mass die-offs that have been observed in flying-foxes *Pteropus* spp. during heatwaves (Welbergen et al. 2008, Sherwin et al. 2013). Due to climate change, these extreme-weather events are likely to increase in frequency and severity, even within the tropics (Rohini et al. 2016, Russo et al. 2016). It is therefore concerning that many tropical bats display $T_b \leq 34$°C (see McNab 1969, 1989, Soriano et al. 2002) and that tree-roosting is common among fruit bats (Family Pteropodidae) (Kunz & Lumsden 2003, Santana et al. 2011). From an economic perspective, the monetary value of all ecosystem services rendered by bats is estimated to be upwards of US$250 billion, with several $100 million stemming from revenue linked to pollination and seed dispersal services of tropical fruit bats alone (Fujita & Tuttle 1991, Kunz et al. 2011, Kasso & Balakrishnan 2013). From an ecological perspective, nectivorous and frugivorous bats play a vital role in maintaining and restoring plant communities by facilitating plant gene flow and aiding in seedling recruitment (Mello et al. 2011, Lewanzik & Voigt 2014, Preciado-Benítez et al. 2015, Abedi-Lartey et al. 2016). Given the significance of these bats, evaluating their chances of survival as well as the ecological consequences of a population collapse or a migratory exodus should be a priority.

Bat–fruit networks are more robust than bird–fruit networks because they have a large overlap between interacting species (Fleming et al. 2009, Mello et al. 2011). However, as argued above, many fruit bats are susceptible to hyperthermia, and it is not yet clear how they will respond to global warming or climate change at large (Sherwin et al. 2013, O'Shea et al. 2016). Generalist species are expected to be less affected by climate change (Gilman et al. 2010, Hof et al. 2012, Gough et al. 2015, Afonso Silva et al. 2017) and are more likely to survive and persist within their current habitats. Thus, one potential outcome could be that generalist bats, although they are not the preferred plant companion, would serve as a safeguard in maintaining ecosystem integrity. Here, we focus on the lesser dog-faced fruit bat *Cynopterus brachyotis*, a species that is likely to fulfil the role of a safeguard. *C. brachyotis* is a foliage-roosting generalist frugivore that is widely distributed throughout Asia (Liat 1970, Abdullah 2003). These bats are important seed dispersers that also participate in pollination (Liat 1970, Boon & Corlett 1989, Tan et al. 1998). Thus, within their specific bat–fruit network, *C. brachyotis* could potentially substitute for specialists at either role. Relative to other bats, *C. brachyotis* has a high T_b (36.5°C; McNab 1989) and should

maintain a favourable ΔT for longer than their lower T_b counterparts. In addition, these bats are heterothermic (McNab 1989) and torpor would enable them to conserve energy and water, and make them more resilient to climate change (Geiser & Turbill 2009, Geiser et al. 2011, Geiser & Brigham 2012). Considering the potential significance of *C. brachyotis* as a safeguard of the ecosystem (i.e. through their dual role in pollination and seed dispersal), we wanted to confirm the thermoregulatory data reported by McNab (1989). With the aid of modern techniques, our objective was to determine the interplay between core T_b, resting metabolic rate (RMR) and evaporative heat loss (EHL) in freshly caught wild bats at T_a of 21–36°C. To afford the study animals the best opportunity to offload heat, especially at low ΔT, we conducted our experiments in a low humidity atmosphere. However, to gain insight about the bats' natural setting and provide context for the laboratory data, we also documented T_a and RH at capture sites.

2. MATERIALS AND METHODS

2.1. Study site and animal capture

The study included 27 adult *Cynopterus brachyotis* (16 males, 11 non-pregnant females) with a mean (±SE) body mass (M_b) of 31.9 ± 0.9 g at first capture. Bats were caught in mist nets during sampling periods between August–October 2014 and March–August 2015 at 4 sites within the Sarawak Province, Borneo, Malaysia. A total of 16 bats were caught at Mount Singai, 5 on the western slope (site 1: 1° 30′ 0″ N, 110° 09′ 22″ E; M_b = 28.2 ± 0.9 g) and 11 on the eastern slope (site 2: 1° 30′ 17″ N, 110° 10′ 35″ E; M_b = 29.7 ± 1 g). Six bats were caught at the Universiti Malaysia Sawarak (UNIMAS) campus (site 3: 1° 30′ 17″ N, 110° 10′ 35″ E; M_b = 34.8 ± 1.9 g) and the remaining 5 bats were caught at Sama Jaya Nature Reserve (site 4: 1° 30′ 17″ N, 110° 10′ 35″ E; M_b = 36.8 ± 2.1 g). Nets were periodically rotated between sites throughout trapping, and were placed across streams, near fruiting trees and along clearings between potential roosting areas. All nets were opened shortly before dusk at ca. 18:00 h and checked at regular intervals throughout the night. We used precalibrated HOBO temperature and relative humidity data loggers (Onset Computer Corporation; resolution: T_a = 0.02°C, RH = 0.05%) to record the T_a and RH between 18 February 2015 and 15 June 2015 at capture sites 2 and 3. The loggers were installed at a height of ca. 1.5 m above ground and set to record at 10 min intervals.

Captured individuals were sexed, and weighed using a Pesola spring scale (micro-line metric spring scale, model 20060, 60 g; resolution: 0.5 g). Morphometric measurements were also collected for use in a long-term monitoring program. To assess their pregnancy status, females were inspected for nipple swelling or vaginal perforation, and an abdominal palpation was conducted. Pregnant or lactating females were excluded from the study. After inspection, a temperature-sensitive passive integrated transponder (PIT) tag (Biomark HDX12; resolution: 0.1°C) was injected directly into each bat's interperitoneal cavity to facilitate T_b measurements and serve as a unique identification marker. They were then hydrated and kept in cloth bags without access to food for 6 h prior to respirometry measurements to ensure a post-absorptive status. Upon completion of respirometry measurements, bats were housed in a wire mesh cage and provided with a mixture of locally available fruits (apple, banana and/or pineapple) and water. All animals spent a maximum of 36 h in captivity.

2.2. Gas exchange measurements and experimental protocol

We used a flow-through respirometry system with an incurrent flow measurement design (Lighton 2008) to measure the rate of oxygen consumption ($\dot{V}O_2$), carbon dioxide production ($\dot{V}CO_2$) and EWL of bats exposed to T_a between 21–36°C. During respirometry measurements, bats were housed individually in sealed 1 l respirometers constructed from glass jars. The roof of each respirometer was modified to allow the bats to hang in a natural position. A 1 cm layer of vegetable oil was poured into the base of each respirometer to prevent evaporation from urine and faeces affecting the readings. High-vacuum grease (Dow Corning) was applied to all joints to ensure an air-tight seal, and respirometers were tested for leaks before every measurement. The O_2 concentration within the respirometers was kept >20% by flowing dry CO_2-free air past the animal at constant flow rates between 150–400 ml min^{-1}. Incurrent air was dried and scrubbed of CO_2 by drawing atmospheric air through a PC-4 Condensing Dryer (Sable Systems) and then columns of silica gel, indicating soda lime and indicating Drierite. Once dried, the airstream was split, and one stream was blown through the respirometer past the animal

while the other stream was used as a reference airstream. Separate pump and flow meter units (SS-4 sub-sampler; Sable Systems) were used for each airstream. We used a RM-8 Flow Multiplexer (Sable Systems) to sequentially select between the reference stream and the excurrent air from the respirometer, which was sub-sampled and flowed through a series of gas analysers. A RH-300 water vapour analyser (Sable Systems) unit was used to measure the water vapour content of the sub-sampled air and a field gas analysis system (Foxbox-C; Sable Systems) measured the fractional concentrations of CO_2 and O_2. Water vapour and CO_2 were removed from the air once they had been measured and dry CO_2-free air flowed through the O_2 analyser. The digital outputs of the instruments were recorded on a personal laptop at 1 s intervals using the Sable System's data acquisition software, Expedata (v.1.7.22), and all gas-exchange traces were synchronized before any calculations were made.

We used the equations in Withers (2001) to calculate $\dot{V}O_2$, $\dot{V}CO_2$ and EWL from steady-state traces corresponding to the most level continuous 10 min section of the $\dot{V}O_2$ trace. The associated M_b was calculated from a regression of the animals' M_b at the start and end of respirometry measurements. We calculated the respiratory exchange ratio as $\dot{V}CO_2$:$\dot{V}O_2$, and converted RMR from gas exchange measurements to a measure of energy (Watts) using the thermal equivalence data in Table 4.2 of Withers (1992). We also converted EWL to a measure of evaporative heat loss (Watts) using the standard conversion factor of 2.26 J mg H_2O^{-1}. Thereafter, we calculated the amount of metabolic heat dissipated through evaporation as the ratio between EHL and the metabolic heat produced (MHP) through resting metabolism (i.e. EHL/MHP).

All measurements were conducted during the rest phase (06:00–18:00 h) and bats were exposed to a single T_a for 4–6 h at $T_a < 34°C$. Following the death of a bat at $T_a = 35°C$, the duration of exposure was reduced to 3 h at $T_a \geq 34°C$. Data from the dead bat were not used in calculations. Similarly, we excluded 4 potentially erroneous measurements of EWL (and thus EHL/MHP) from calculations. The T_a within respirometers was recorded using iButtons (DS1922L, Thermochron; resolution: 0.0625°C) that were attached to the underside of the lids and side walls. A Biomark HPR Plus reader and antennae was used to read the PIT tags and record T_b at 30 s intervals throughout the experiment. All iButtons and PIT tags were calibrated against a mercury thermometer to the nearest 0.1°C. The CO_2 and water vapour analy-

sers were calibrated monthly and the O_2 analyser was spanned before every measurement. The CO_2 analyser was calibrated using commercially available compressed gas and the water vapour analyser was calibrated using a bubbler flask and water bath to generate humid air of a known dew point temperature.

2.3. Data analyses

We adopted the statistical approach and techniques used by Levesque et al. (2014). Briefly, we performed a piecewise regression analysis in R v.3.0.2 (R Core Team 2017) using the package 'segmented' (Muggeo 2008) to identify any changes in the slope (i.e. points of inflection) along the respective thermoregulatory profiles of T_a versus RMR, T_b, EWL and EHL/MHP in non-torpid bats. Each segment of data identified through the analysis was treated as independent, and we used simple linear regression analyses to determine the relationship between the physiological variable and T_a. We used mass-specific data to account for the effect of M_b on metabolism when conducting regression analyses. However, we also determined the relative importance of T_a, M_b, sex and capture site on each physiological variable using mixed-effect models in the R package 'nlme' (Pinheiro et al. 2016). To account for repeated measurements, we included individual ID as a random factor in all models. We determined the model of best fit by comparing Akaike's information criterion values corrected for small sample size (AIC_c and AIC_cWt; Burnham & Anderson 2003) using the R package 'AICcmodavg' (Mazerolle 2015). Model assumptions were verified using QQ-plots and histograms of the residuals. All values are reported as mean ± SE unless stated otherwise.

All experimental protocols and permission to capture the bats were approved by the Sarawak Forestry Department (permit number: NCCD.907.4.4(9)-223, NCCD.907.4.4(13)-277). All experimental and animal care procedures were also reported to and approved by the University of Kwazulu-Natal Animal Ethics Committee (116/13/Animal).

3. RESULTS

RMR displayed a point of inflection at $T_a = 30.2 \pm 3.0°C$ (±95 % CI) (Fig. 1a) and had a positive relationship with T_a above the inflection ($F_{1,35} = 26.17$, p < 0.01, $r^2 = 0.44$; Table 1), but a negative relationship
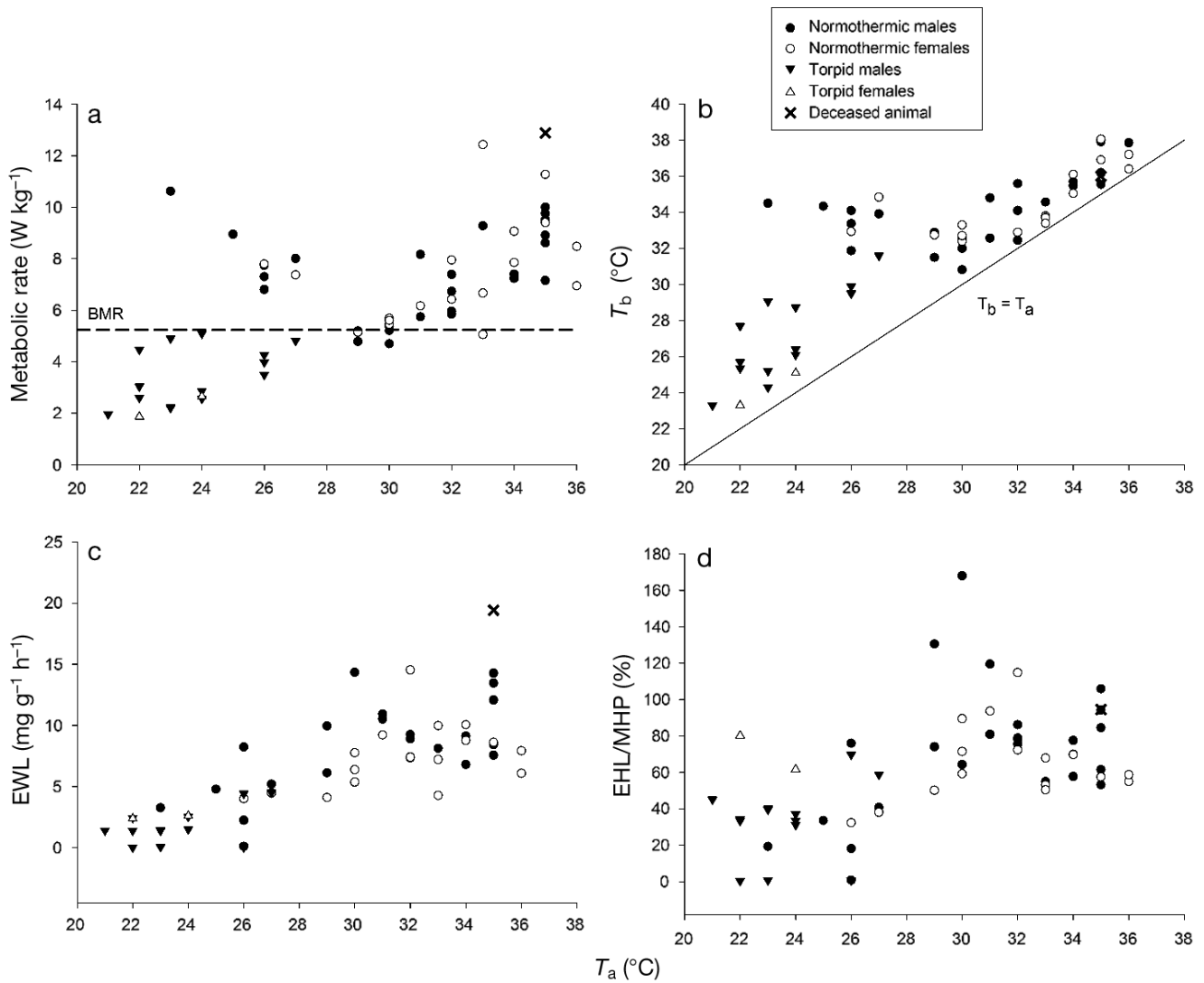
Fig. 1. Thermoregulatory profile of *Cynopterus brachyotis*. (a) Effect of ambient temperature (T_a) on resting metabolic rate. Dashed line: basal metabolic rate (BMR). (b) Effect of T_a on core body temperature (T_b). Diagonal line: where body temperature equals ambient temperature ($T_b = T_a$). (c) Effect of T_a on the rate of evaporative water loss (EWL). (d) Effect of T_a on the amount of metabolic heat dissipated through evaporative cooling, i.e. the ratio of evaporative heat loss (EHL) to metabolic heat produced (MHP)

Table 1. Relationship between ambient temperature (T_a) and mass-specific resting metabolic rate (RMR), body temperature (T_b), rate of evaporative water loss (EWL) and amount of metabolic heat dissipated through evaporative cooling (EHL/MHP) in non-torpid *Cynopterus brachyotis*. **$p < 0.01$

Parameter	T_a (°C)	Measures included	Regression equation
Mass-specific RMR	< 28	Normothermic only	RMR = 28.873 − 0.808 × T_a**
	≥30	All	RMR = 0.671 × T_a − 14.496**
T_b	23–36	Normothermic only	T_b = 0.3679 × T_a + 22.919**
EWL	23–36	Normothermic only	EWL = 0.6197 × T_a − 11.2893**
EHL/MHP	≤30	Normothermic only	EHL/MHP = 12.67323 × T_a − 290.493**

with T_a below the inflection ($F_{1,7} = 16.98$, p < 0.01, $r^2 = 0.74$; Table 1). The model of best fit for RMR above the inflection included T_a as the only fixed factor (Akaike weight = 0.51; Table 2) whereas the model of

best fit below the inflection included all fixed effect factors except sex (Akaike weight = 1; Table 2). To determine the thermoneutral zone (TNZ), we used an analysis of variance (ANOVA) to test if there was a

difference between the minimum non-torpid RMR observed at T_a = 29°C and those observed at T_a = 30–32°C. The ANOVA determined that there was a difference in RMR ($F_{1,16}$ = 16.29, p < 0.01), and using a Tukey's HSD post hoc test we found that RMR at T_a = 29°C differed from those at T_a = 32°C (p = 0.03), but not those at T_a = 30–31°C (p = 0.93–0.06). Thus, we determined TNZ to be 29–31°C and used the data therein to calculate a basal metabolic rate (BMR) of 5.60 ± 0.26 W kg^{-1} (1.01 ± 0.05 ml O$_2$ g^{-1} h^{-1}). Because we did not have data at T_a = 28°C, we attempted to resolve the lower limit of TNZ by determining the T_a at which BMR intersected the line describing the relationship between T_a and RMR at T_a < 28°C. The intersection occurred at T_a = 29.3°C and supports our initial estimate of TNZ.

Table 2. Best fitting linear mixed-effect models evaluating the influence of ambient temperature (T_a), body mass (M_b), sex and capture site on resting metabolic rate (RMR), body temperature (T_b), rate of evaporative water loss (EWL) and amount of metabolic heat dissipated through evaporative cooling (EHL/MHP) in non-torpid *Cynopterus brachyotis*. k: no. of parameters for each model; AIC$_c$: Akaike's information criterion values corrected for small sample size. Only models with Akaike weights > 0.01 are presented

Fixed factors	Random factor	k	AIC$_c$	Akaike weights
RMR (T_a > 30°C)				
T_a	~1|ID	4	−138.29	0.51
T_a + M_b	~1|ID	5	−136.52	0.21
T_a + sex	~1|ID	5	−136.41	0.20
T_a + M_b + sex	~1|ID	6	−134.42	0.07
T_a + capture site	~1|ID	6	−129.78	0.01
RMR (T_a < 28°C)				
T_a + M_b + capture site	~1|ID	8	−189.34	1
T_b				
T_a + capture site	~1|ID	7	169.02	0.40
T_a + M_b + capture site	~1|ID	8	170.27	0.21
T_a	~1|ID	4	171.51	0.12
T_a + sex + capture site	~1|ID	8	171.95	0.09
T_a + M_b	~1|ID	5	172.68	0.06
T_a + M_b + sex + capture site	~1|ID	9	173.39	0.05
T_a + sex	~1|ID	5	173.69	0.04
T_a + M_b + sex	~1|ID	6	174.12	0.03
EWL				
T_a + M_b	~1|ID	5	209.37	0.63
T_a + M_b + sex	~1|ID	6	211.41	0.23
T_a + capture site	~1|ID	7	214.71	0.04
T_a + M_b + capture site	~1|ID	8	214.96	0.04
T_a + M_b + sex + capture site	~1|ID	9	215.65	0.03
T_a + sex + capture site	~1|ID	8	215.69	0.03
EHL/MHP (≤30°C)				
T_a	~1|ID	4	167.17	0.55
T_a + sex	~1|ID	5	168.36	0.30
T_a + M_b	~1|ID	5	170.11	0.13
T_a + M_b + sex	~1|ID	6	173.67	0.02

Both T_b ($F_{1,43}$ = 31.100, p < 0.01, r^2 = 0.42; Fig. 1b, Table 1) and EWL ($F_{1,40}$ = 19.13, p < 0.01, r^2 = 0.32; Fig. 1c, Table 1) had a positive relationship with T_a and there were no inflection points in either variable. The model of best fit for T_b included T_a and capture site as the only fixed effect factors (Akaike weight = 0.40; Table 2), whereas the model of best fit for EWL included T_a and M_b as the only fixed effect factors (Akaike weight = 0.63; Table 2). Due to the thermolabile nature of the bats, we determined a normothermic T_b of 32.5 ± 0.3°C from bats measured within the TNZ.

EHL/MHP displayed a single point of inflection at T_a = 30.1 ± 1.8°C (±95% CI), and had a positive relationship with T_a until the point of inflection ($F_{1,15}$ = 10.57613, p < 0.01, r^2 = 0.43; Table 1), but there was no relationship with T_a thereafter. The model of best fit for EHL/MHP included T_a as the only fixed effect factor (Akaike weight = 0.55; Table 2).

T_a at capture sites displayed a unimodal right skewed distribution (Fig. 2). The overall range in T_a at capture site 2 was 21.4–30.0°C and the modal T_a was 24.1°C. The overall range in T_a at capture site 3 was 21.6–31.2°C and the modal T_a was 24.3°C. Only ca. 1 h 25 min and ca. 6 h 22 min of the 118 d of recording at capture site 2 and 3 respectively was spent at T_a ≥ 30°C. By contrast, the RH at both sites remained high throughout the recorded period, with RH ≈ 100% observed for 90% of the time at capture site 2 and for 68% of the time at capture site 3. The lowest RH recorded at capture site 2 was 77.8% and the lowest RH at capture site 3 was 58.6%.

4. DISCUSSION

Our results contradict those of McNab (1989), and suggest that *Cynopterus brachyotis* (at least the individuals studied here) are physiologically more susceptible to hyperthermia than previously thought. Whereas McNab (1989) measured rectal temperature as a proxy measure for core T_b, we measured core T_b directly. We found that normothermic bats typically maintained a T_b that was ca. 3.1°C lower than the T_b reported previously. Accordingly, because T_b and BMR are correlated (Lovegrove 2003, 2005, Clarke et al. 2010), our observation that bats maintained a BMR that was ca. 79% of the BMR reported previously provides corroborating support. Due to their low T_b, the ability of *C. brachyotis* to defend normothermia was compromised at seemingly
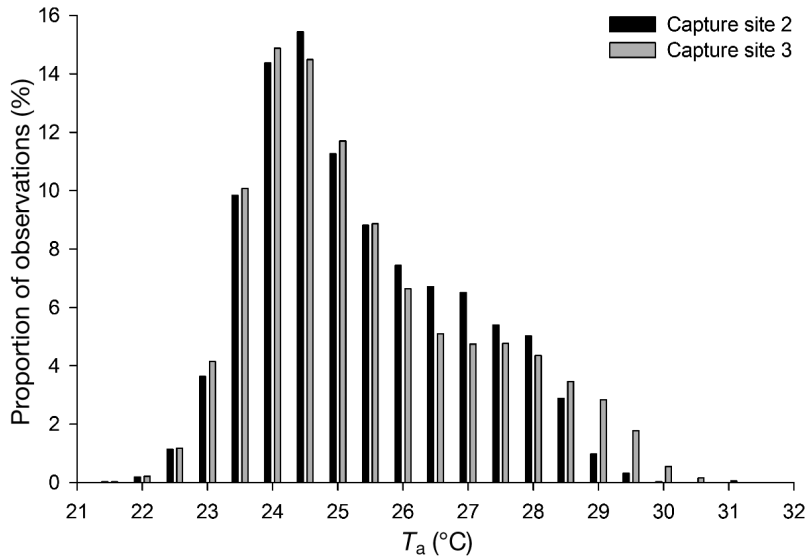
Fig. 2. Ambient temperature (T_a) recorded at capture sites between 18 February 2015 and 15 June 2015. Capture site 2: eastern slope of Mount Singai; capture site 3: Universiti Malaysia Sarawak campus. Data are presented as a percentage of the total number of recordings

moderate T_a, and heat storage occurred at $T_a \geq 31°C$. As expected, the bats displayed a thermoregulatory increase in evaporative cooling as T_a increased, and could dissipate ca. 98% of their resting MHP through evaporation at $\Delta T = 1°C$. Metabolic processes are temperature sensitive (Withers 1992, Tattersall et al. 2012), and it appears that once $T_a \approx T_b$, the increase in MHP due to Arrhenius effects overcame their capacity for evaporative cooling, despite any increase in EWL.

The inability of the bats to defend normothermia beyond $\Delta T = 1°C$ within a dry atmosphere is concerning. Due to the high humidity in the field, the results suggest that heat storage is likely to develop even before $T_a = 31°C$. Fortunately, capture sites remained cool and forest T_a seldom exceeded 30°C. *C. brachyotis* are primarily foliage-roosting tent-making bats (Campbell et al. 2006), and recent work suggests that tent shelters may not be as effective at buffering high T_a as they are at buffering low T_a (Rodríguez-Herrera et al. 2016). Tents that are constructed in open areas are hotter and are more variable because they are exposed to solar radiation (Rodríguez-Herrera et al. 2016). Thankfully, the cooler conditions closer to the ground afford the bats the option to exploit roosts that are less exposed and more stable in temperature. In addition to lowering their risk of hyperthermia, exploiting thermally stable roosts would reduce their daily energy expenditure (Rodríguez-Herrera et al. 2016) and bolster the benefits gained through torpor.

As mentioned earlier, torpor is a highly effective mechanism of energy and water conservation, and significantly improves the survivability of mammals and delay fetal development during periods of unfavorable environmental conditions (Geiser & Turbill 2009, Geiser & Stawski 2011, Stawski et al. 2014, Bondarenco et al. 2016). It lowers the risk of extinction in bats because it reduces their risk of predation and increases their reproductive success by enabling them to manipulate pregnancy and delay fetal development during periods of unfavorable environmental conditions (Geiser & Brigham 2012, Stawski et al. 2014). In addition, recent work suggests that torpor may also afford bats greater resiliency to heat stress. Bondarenco et al. (2014) reported that one little broad-nosed bat *Scotorepens greyii* and 2 inland freetail bats (*Mormopterus* species 3), both of which are heterotherms, managed to survive the extreme T_a during a desert heat wave. The authors noted that the bats thermoconformed at high T_a and argued that by doing so, they could reduce their water loss and prevent dehydration. Here, we observed that *C. brachyotis* had a similar ability to thermoconform at high T_a, and it is possible that they did so to prevent dehydration, but we add that torpor likely also reduced the bats' heat stress by lowering the contribution of MHP to the overall heat budget. Evidence of torpor use at high T_a is growing, and has been reported in eastern pygmy-possums *Cercartetus nanus* (Song et al. 1997), spiny mice *Acomys russatus* (Grimpo et al. 2013) and grey short-tailed opossums *Monodelphis domestica* (Busse et al. 2014). Given the benefits of torpor, it seems that heterothermic species have a pre-adaptive advantage over their homeothermic counterparts when dealing with climate change.

We acknowledge that phenotypic plasticity may have contributed to some of the physiological differences observed between bats in our study and those in McNab (1989). In this regard, there are attempts to determine the influence of phenotypic plasticity on species responses to climate change (Canale & Henry 2010, Chevin et al. 2010, Boyles et al. 2011). However, given that physiological tolerances limit adaptability (Sherwood & Huber 2010) and our limited understanding of torpor at high T_a, we argue that *C. brachyotis*, at least the bats in our study area, are physiologically susceptible to heat stress. Bats are already threatened by climate change (Sherwin et al.

2013), and plant–animal interactions are severely threatened by a range of anthropogenic related activities such as land use changes, species eradication and phenological mismatches due to climate change (Garrett et al. 2006, Abrol 2012, Sherwin et al. 2013). For example, land use changes have been extensive throughout the tropics. Within the southeast Asian region, much of the natural vegetation has been converted to industrial plantations, particularly for use as oil palm plantations (Miettinen et al. 2016). The land use change on the Island of Borneo has been particularly aggressive (Reynolds et al. 2011) and there are concerns about the effect that it may have on atmospheric composition (Pyle et al. 2011, Warwick et al. 2013). It is estimated that 76% of Borneo was covered by old-growth forests in 1973, but that 34% of this land had been cleared by 2015 (Gaveau et al. 2016). The island is shared by 3 sovereign states, namely Indonesia, Malaysia and Brunei, and the majority of the deforestation occurred in Indonesian Borneo, followed by Malaysian Borneo and comparatively little in Brunei (Gaveau et al. 2016). In addition to reducing the available area for animals to live in, deforestation increases habitat fragmentation, which significantly alters the climate within forests and could make them less hospitable (Turner & Corlett 1996, Laurance 2004, Tuff et al. 2016). Therefore, it is crucial, especially in situations where the land is shared, to preemptively earmark suitable areas for conservation and protect thermal refugia (Struebig et al. 2010, Morelli et al. 2016). Even though bat–fruit networks are robust, the consequences of a population collapse or a migratory mass exodus of bats to distant, more suitable areas, could bear significant consequences on the ecosystem.

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