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Seasonal effects on thermoregulatory abilities of the Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) in KwaZulu-Natal, South Africa

C.T. Downs*, M.M. Zungu, M. Brown

School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X 01, Scottsville 3209, Pietermaritzburg, South Africa

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ABSTRACT

Seasonal variations in ambient temperature (T_a) require changes in thermoregulatory responses of endotherms. These responses vary according to several factors including taxon and energy constraints. Despite a plethora of studies on chiropteran variations in thermoregulation, few have examined African species. In this study, we used the Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*, body mass \approx 115 g) to determine how the thermoregulatory abilities of an Afrotropical chiropteran respond to seasonal changes in T_a . Mass specific Resting Metabolic Rates (RMR_{Ta}) and basal metabolic rate (BMR) were significantly higher in winter than in summer. Furthermore, winter body mass was significantly higher than summer body mass. A broad thermoneutral zone (TNZ) was observed in winter (15–35 °C) compared with summer (25–30 °C). This species exhibited heterothermy (rectal and core body temperature) during the photophase (bats' rest-phase) particularly at lower T_a s and had a low tolerance of high T_a s. Overall, there was a significant seasonal variation in the thermoregulatory abilities of *E. wahlbergi*. The relative paucity of data relating to the seasonal thermoregulatory abilities of Afrotropical bats suggest further work is needed for comparison and possible effects of climate change, particularly extreme hot days.

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1. Introduction

Seasonal variation in climatic conditions occurs in most habitats with the most pronounced variations occurring in temperate and/or arctic regions (Stawski and Geiser, 2010). In the latter the variations are more predictable whereas in more tropical areas the variations are often unpredictable (Holmgren et al., 2001; Landman and Goddard, 2010). A consequence of this is seasonal fluctuations in primary productivity of the environment, subsequently resulting in different physiological demands on animals (Stawski and Geiser, 2010). Similarly unpredictable adverse weather conditions may affect food availability and impact negatively on an endotherm's energy balance. Endotherms have the ability to adapt morphologically, physiologically and behaviorally to their thermal environment in order to obtain thermal homeostasis in a changing thermal environment (Simeone et al., 2004; Brown and Downs, 2003; Brown and Downs, 2005, 2007; Lindsay et al., 2009a,b). One of these adaptations is energy conservation with the ability to enter a physiological state of reduced metabolic requirements and allow body temperature (T_b) to decrease and so exhibit heterothermy, particularly torpor (Downs

and Brown, 2002; Matheson et al., 2010). During this period, the T_b is maintained at a reduced set-point, usually several degrees below normal T_b , which helps in reducing heat loss and subsequently energy requirements (Geiser, 2004). Seasonal changes in torpor patterns are a characteristic of many mammals found in areas with cold climates or energetic stress (Geiser, 2004; Stawski, 2010). Usually torpor is more pronounced in winter with some species not exhibiting it during summer with others using it regularly irrespective of season (Turbill et al., 2003; Geiser, 2004; Stawski, 2010; Stawski and Geiser, 2010).

Another endothermic adaptation in response to different seasonal ambient temperatures (T_a) is change in basal metabolic rate (BMR) (Coburn and Geiser, 1998; Saarela et al., 1995; Bush et al., 2008; Nzama et al., 2010; Wilson et al., 2011). Although BMR and metabolic rate (MR) were considered specific for a particular T_a , seasonal variations in both of these physiological parameters have been documented in a number of avian species (Hart, 1962; Dawson, 2003; McKechnie, 2008; Wilson et al., 2011) as well as several mammals (Geiser and Baudinette, 1987; Feist and White, 1989; Arnold et al., 2006). Bats are an ecologically and taxonomically diverse group of flying mammals with a broad range in body mass (Bishop, 2008) belonging to the order Chiroptera which was previously subdivided into two sub-orders, the Microchiroptera (insectivorous bats) and Megachiroptera (fruit/nectar eating bats) (Taylor, 2005). However, recent molecular evidence

* Corresponding author. Tel.: +27 33 2605127; fax: +27 33 2605105.
E-mail address: downs@ukzn.ac.za (C.T. Downs).

(Hutcheon and Kirsch, 2006) has shown that there is a close alliance between Old World fruit bats (Pteropodidae) and certain families belonging to the Microchiroptera. Therefore this suborder has been named Pterododiformes with Vespertilioniformes suborder applying to accommodate the remaining Microchiropteran families (Monadjem et al., 2010).

One of the earliest reviews on bat thermal physiology (Hock, 1951) concluded that bats differ from other endotherms as T_b at rest, irrespective of season, approximates that of the environment thereby minimizing energy expenditure. Since then there have been a plethora of laboratory and field studies on thermoregulatory ability of a range of bat families from temperate, subtropical and tropical regions (Herreid and Schmidt-Nielsen, 1966; Licht and Leitner, 1967; McNab, 1969; Lyman, 1970; Studier and Wilson, 1970, 1979; Holyoak and Stones, 1971; Studier and O'Farrell, 1972; Kurta and Kunz, 1988, Audet and Fenton, 1988; Genoud et al., 1990; Genoud, 1993; Rodríguez-Durán, 1995; Webb et al., 1995; Hosken and Withers, 1997, 1999; Choi et al., 1998; Ochoa-Acuña and Kunz, 1999; Cryan and Wolf, 2003; Turbill et al., 2003; Geiser, 2004; Willis et al., 2005; Marom et al., 2006; Solick and Barclay, 2007; Wojciechowski et al., 2007; Stawski, 2010; Stawski and Geiser, 2010; Storm and Boyles, 2011). Most of these studies documented changes in bats' T_b . In response to cold or unfavorable conditions, most insectivorous bats decrease T_b with the use of heterothermy, particularly torpor, to conserve energy (Herreid and Schmidt-Nielsen, 1966; Lyman, 1982; Marom et al., 2006). There is usually a concomitant reduction in MR reducing energy expenditure (Geiser and Ruf, 1995). Bats lose heat rapidly at low T_a s because of their large surface area to volume ratios (Bartels et al., 1998). This, coupled with periods of food scarcity, highly energy-expensive flight and low internal energy stores (Bartels et al., 1998), suggests they avoid costly energy requirements to maintain constant T_b . In contrast to Microchiroptera, the former sub-order Megachiroptera in the past was thought to be homeothermic (Ransome, 1990). Due to their relatively large sizes, and that they are restricted to tropical and subtropical regions where the fluctuations in food availability are less severe than in temperate regions, it was believed they had no need for heterothermy (Bartels et al., 1998). However, studies on Australasian fruit- and blossom-eating bats of various body sizes have shown that they are indeed heterothermic irrespective of season and particularly if weather is unpredictable (Bartholomew et al., 1964; 1970; Geiser et al., 1996; Bonaccorso and McNab, 1997; Ochoa-Acuña and Kunz, 1999; Coburn and Geiser, 1998; Bartels et al., 1998; McNab and Armstrong, 2001; McNab and Bonaccorso, 2001; Geiser et al., 2005; Riek et al., 2010). Relatively little is known about the thermoregulatory abilities, particularly plasticity in energetics, of Chiroptera from Africa, with most published work on insectivores (Stegeman, 1989; Bronner et al., 1999; Maloney et al., 1999; Jacobs et al., 2007; Vivier and van der Merwe, 2007; Cory Toussaint et al., 2010).

To establish how physiological variables are affected by seasonal changes in temperature in an Afrotropical chiropteran, we investigated seasonal thermoregulatory abilities of the Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*, Sundevall, 1846). It is a nocturnal Old World species restricted to the continent of Africa (Taylor, 2005). In the southern African region, this species is confined to eastern parts, penetrating westwards into the drier areas up river valleys such as Zambezi and Limpopo (Taylor, 2005). Since this region is largely affected by El Niño Southern Oscillations (ENSO) (Jury and Nkosi, 2000), the rainfall patterns of this regions; and subsequently primary production of the environment, remain highly unpredictable.

The aim of this study was to investigate the effect of season on the MR of *E. wahlbergi*. The objectives were to determine oxygen

consumption (VO_2) at various T_a s in both seasons (summer and winter) and to examine changes in the Resting Metabolic Rate (RMR), BMR and the thermoneutral zone (TNZ) between seasons. There has been debate in the literature regarding the definition of RMR. The most widely accepted definition of this term is that RMR is the metabolic rate of a resting and post-absorptive endotherm measured within its thermoneutral zone, and when this is in the thermoneutral zone is called BMR (Withers, 1992; Hill et al., 2004). Another definition which has been suggested is that RMR is the metabolic rate of an endotherm in its thermoneutral zone but not in a post-absorptive state (IUPS Thermal Physiology Terms, 2001). For this study, we refer to RMR as the metabolic rate of an endotherm in a post-absorptive state and measured at a specific T_a (RMR_{T_a}). We further investigated whether *E. wahlbergi* regulates its T_b or is heterothermic. We predicted that BMR and RMR would be higher in winter compared with summer. Furthermore, since an increase in the range of TNZ is coupled with a decrease in conductance (Cooper and Gessaman, 2004), we predicted the TNZ to be broader in winter compared with summer.

2. Materials and methods

2.1. Study animals, capture and maintenance

Ten adult *E. wahlbergi* (5 males, 5 females) captured in Pietermaritzburg, KwaZulu-Natal (KZN) (29°37'0"S; 30°23'0"E) during September 2009 under the permit from Ezemvelo KZN Wildlife were used for this study. Directly after capture, bats were transferred to the Animal House of the University of KwaZulu-Natal, Pietermaritzburg, at an altitude of 660 m, where they were housed in outdoor aviaries (2.4 × 4.1 × 2.0 m³) separated according to gender. Bats were fed a maintenance diet each day consisting of chopped up mixed fruits including bananas, apples, pears, pawpaw and guavas with a supplement (AviPlus Lorikeet Special; Aviproducts, Waterfall, KZN), with water or sugar solution provided ad lib.

2.2. Metabolic rate measurement

During summer (February 2010) and winter (late July–early August 2010) *E. wahlbergi* metabolic measurements during the photophase (bats' rest phase) were indirectly made by measuring VO_2 using the open-flow respirometry system described in Lindsay et al. (2009a). Measurements in each season were at seven respective T_a s (5, 10, 15, 20, 25, 30 and 35 °C) in random order and only one T_a per day. Bats were only measured on alternate days. Bats were caught with sweep nets in the morning and placed in separate respirometers (35 × 20 × 25 cm³) in a Conviron[®] (Winnipeg, Manitoba, Canada) at 07h15. They were removed from their respirometers at 15h00, except at 35 °C when they were removed at 12h00. Body mass and rectal T_b s were measured before and after each trial. Rectal T_b was measured using a digital thermometer (Yu Fing Electronics; range –50 to 1300 °C), with a thermocouple inserted ± 0.4 mm into the rectum of each bat.

An oxygen analyzer (model S-3A/1, Ametek, Pittsburgh, PA, USA) was used to determine the fractional concentration of O₂ in dry air samples (Lindsay et al., 2009a). Air flow was controlled using a computerized open-flow-through system. Atmospheric air was pumped in and dried using a silica gel column before reaching the temperature control cabinet Conviron[®]. Flow rate was maintained at a level ensuring < 1% change in oxygen consumption (Lindsay et al., 2009a) and varied between 0.5 and 0.9 L min⁻¹. Flow rate of each chamber was measured using Brooks thermal

mass flow meter (Model 580E: Hatfield, PA, USA) factory calibrated to standard temperature and pressure (STP). Solenoid valves and a separate pump for each chamber were used to take simultaneous measurements of six chambers (five experimental and one control chamber) (Lindsay et al., 2009a). Excurrent air passed through a water condenser to remove most of the water vapor, then a silica gel column to remove any residual water, and soda lime to remove CO₂ before the oxygen analyzer. Water vapor extracted by the condenser was used as an indirect measure of evaporative water loss (EWL) for each bat at each temperature during summer and winter respectively. Measurements of various parameters for each chamber (T_a , flow rate and fractional O₂ concentrations) were recorded as described in Lindsay et al. (2009a). Air from each chamber was allowed to stabilize for 45 s before measurement. The first 2 h (before 09h00) of data recorded were excluded from analyses so bats were post-absorptive and resting. The lowest hourly mean VO₂ during the day for each individual was taken as its RMR_{T_a}.

2.3. Core body temperature

Early in June 2010, each *E. wahlbergi* had a calibrated data logger *i-Buttons*[®] (Model DS 1922 L ± 0.06 °C, Dallas semiconductor, USA), covered with paraffin wax, surgically implanted into the peritoneal cavity under anesthetic by a veterinarian. These recorded core T_{bs} every 20 min while bats were in their outdoor aviary. The first 2 day of data were ignored and regarded as recovery time.

2.4. Data analysis

Statistical analyses were performed using STATISTICA (Statsoft Inc., version 7, Tulsa, USA). As seven metabolic measurements were performed on each individual bat in a particular season, Generalized Linear Models (GLM) Repeated Measures of ANOVA (RMANOVA) was used to analyze RMR_{T_a}s to determine change with T_a . Post hoc Tukey's HSD tests were used to determine significant differences in RMR_{T_a} at various T_a s. These results were used to determine the width of the TNZ in both summer and winter (Lindsay et al., 2009a,b). Body mass and EWL were also analyzed in a similar way. Data obtained are presented as means ± standard error.

3. Results

3.1. Body mass

Body mass of *E. wahlbergi* ranged from 86.42 to 144.51 g (mean 115.61 ± 17.79 g) in both seasons. As individuals varied in body mass metabolic measurements were expressed as specific values. Generally males were heavier than females. Body mass was significantly higher in winter than in summer at different T_a s (RMANOVA, $F_{(6, 54)}=3.487$, $P=0.006$, Fig. 1). However, within seasons, no differences in body mass were observed (Post hoc Tukey's HSD test, $P>0.05$). Furthermore, body mass before each trial was significantly higher than body mass after each trial for both summer and winter respectively (RMANOVA, $F_{(6, 54)}=2.362$, $P=0.042$).

3.2. Metabolic measurements

There was a significant difference in RMR_{T_a} at various T_a s for *E. wahlbergi* between summer and winter (RMANOVA, $F_{(6, 24)}=5.113$, $P=0.002$, Fig. 2a). In winter, there was a significant difference in metabolic rate between 5 °C and 10 °C (Post hoc Tukey's HSD test,

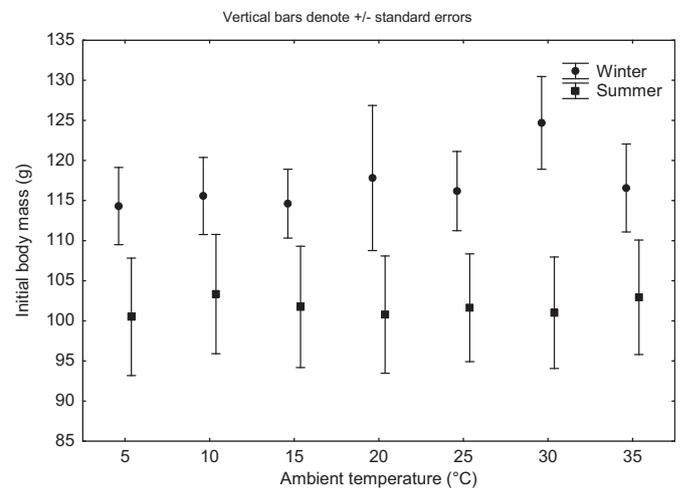


Fig. 1. Seasonal variation in initial body mass of Wahlberg's epauletted fruit bats at various ambient temperatures in winter and summer.

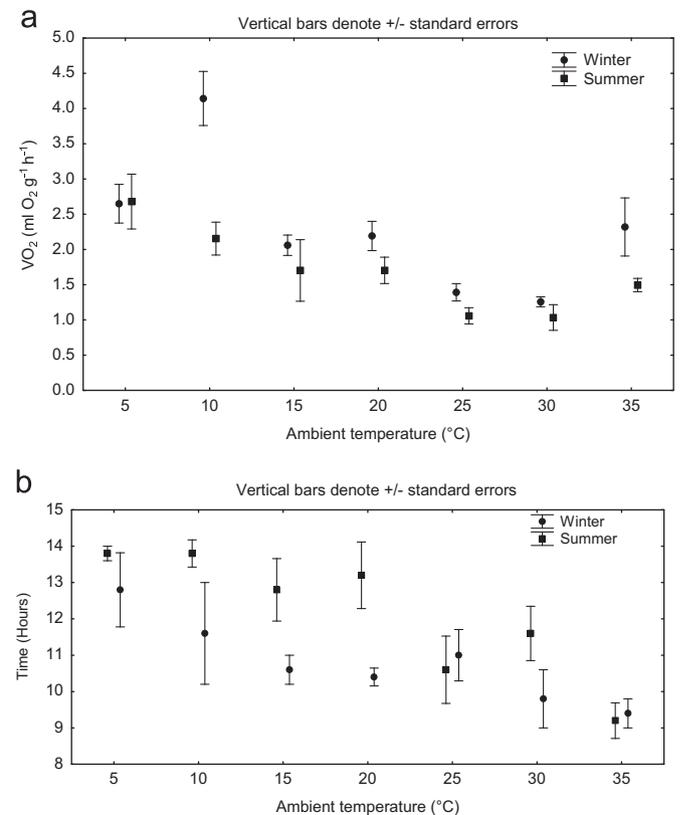


Fig. 2. (a) Oxygen consumption (RMR_{T_a}, VO₂ ml g⁻¹ h⁻¹) of Wahlberg's epauletted fruit bats and (b) time when this was reached at various ambient temperatures in winter and summer.

$P<0.05$), and between 10 °C and 15 °C (Post hoc Tukey's HSD test, $P=0.0004$), but not between 15 °C and 20 °C (Post hoc Tukey's HSD test, $P>0.05$). In summer, a significant difference in metabolic rate was observed between 20 °C and 25 °C (Post hoc HSD test, $P<0.05$). The TNZ was broad in winter, ranging from 15 to 35 °C while in summer it was narrower from 25 to 30 °C (Fig. 2a). Minimum metabolic rate in the TNZ which was taken as BMR was recorded at 30 °C for both seasons. The winter BMR (1.260 ± 0.070 ml O₂ g⁻¹ h⁻¹) was significantly higher than the summer BMR (1.034 ± 0.182 ml O₂ g⁻¹ h⁻¹) (summer BMR was 82.1% of winter BMR) (T -test, $df=9$, $t=5.312$, $P=0.013$). At the

various T_a s in both seasons, the time when RMR_{Ta} was reached for *E. wahlbergi* did not differ significantly (RMANOVA, $F_{(6, 24)}=1.838$, $P=0.134$, Fig. 2b). However, there was individual variation and the time for 35 °C was significantly earlier in both seasons compared with other ambient temperatures (Post hoc HSD test, $P < 0.05$; Fig. 2b). The time to reach RMR_{Ta} at 10 °C may have affected the value in winter (Fig. 2a and b) as it appears that the bats increased MR possibly to defend T_b .

3.3. Body temperature

There was no significant difference in final rectal T_b of *E. wahlbergi* between both summer and winter at various T_a s (RMANOVA, $F_{(6, 54)}=1.948$, $P=0.090$, Fig. 3). Rectal T_b was strongly correlated with T_a particularly in summer (summer $r^2=0.98$, $P=0.00$; winter $r^2=0.93$, $P=0.004$; with fitted linear lines summer $Y=32.24+0.89x$; winter $Y=31.48+0.93x$; Fig. 3). Core T_b of *E. wahlbergi* during winter showed that the bats exhibited heterothermy but not torpor (Figs. 4 and 5). Individual variation was evident but all had the lowest core T_b s during the rest-phase photophase (Fig. 5b) with lowest recorded 31.99 °C

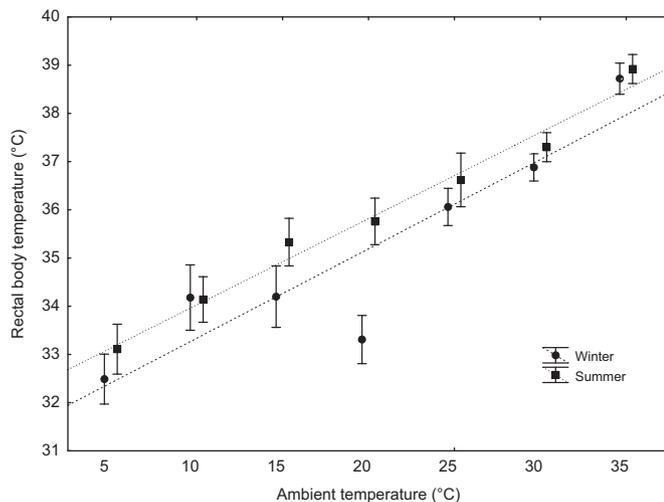


Fig. 3. Rectal body temperature of Wahlberg's epauletted fruit bats at different ambient temperatures in summer and winter. Dotted lines indicate regression lines.

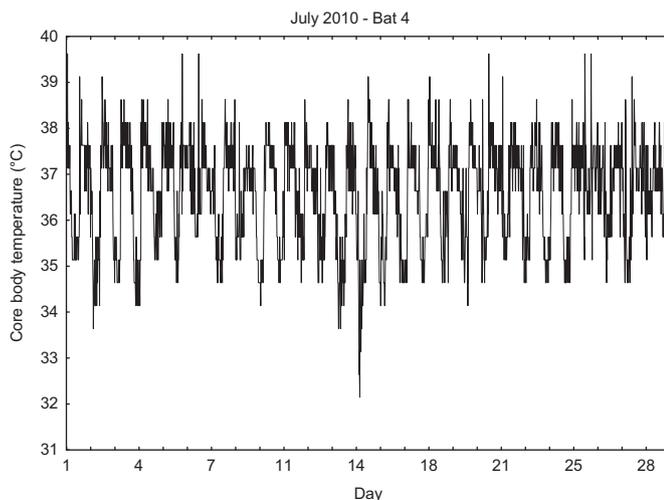


Fig. 4. Core body temperature of a Wahlberg's epauletted fruit bat during winter (July) when in an outdoor aviary.

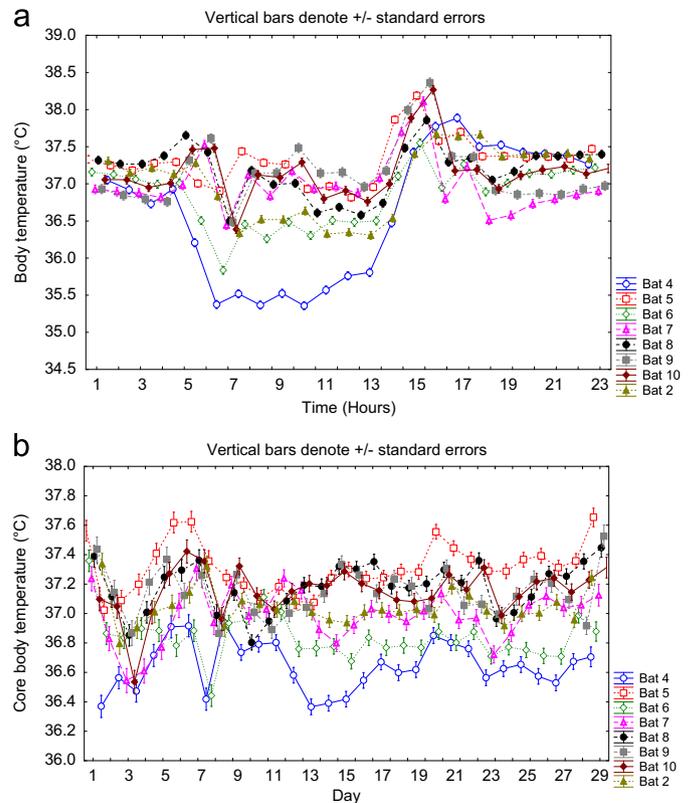


Fig. 5. Individual variation in hourly mean core body temperature of Wahlberg's epauletted fruit bats during winter (June–July) where (a) is with time ($n=31$ day) and (b) is with day ($n=31$ day).

and maximum 41.78 °C during the June–July winter period (Fig. 5). In contrast T_a s showed far greater variation during this period (June 2010 lowest daily mean \pm SD 8.66 \pm 5.93 °C, highest daily mean 22.05 \pm 5.10 °C, lowest minimum 0.20 °C, highest maximum 31.60 °C; July 2010 lowest daily mean 11.00 \pm 2.55 °C, highest daily mean 18.00 \pm 5.44 °C, lowest minimum 2.60 °C, highest maximum 28.00 °C; (Wilson et al., 2011, South African Weather Service). For one individual core body temperature was recorded from June to September (Mean \pm SD, 36.57 \pm 1.17 °C; Min 29.65 °C, Max 41.12 °C).

3.4. Evaporative water loss

There was a significant difference in EWL between T_a s in the two seasons (RMANOVA $F_{(6, 36)}=4.638$, $P=0.0014$). In winter there were significant differences in EWL of *E. wahlbergi* between various T_a s (RMANOVA, $F_{(6, 54)}=24.340$, $P=0.0005$; Fig. 6). EWL at 5 °C and 10 °C were significantly lower than at any other T_a s (Post hoc Tukey's HSD test, $P < 0.05$). Similarly in summer there were significant differences in EWL of *E. wahlbergi* between various T_a s (RMANOVA, $F_{(6, 52)}=22.060$, $P=0.0005$; Fig. 6). EWL in summer at 25 °C, 30 °C and 35 °C were significantly higher than the other T_a s (Post hoc Tukey's HSD test, $P < 0.05$). At 35 °C in both summer and winter, the bats were removed earlier from the respirometer as a result of salivation and dehydration.

4. Discussion

Afrotropical regions, including South Africa, are rendered unpredictable by ENSO (Landman and Goddard, 2010). Animals inhabiting regions rendered unpredictable by ENSO should have a lower BMR in comparison to regions with predictable environments in

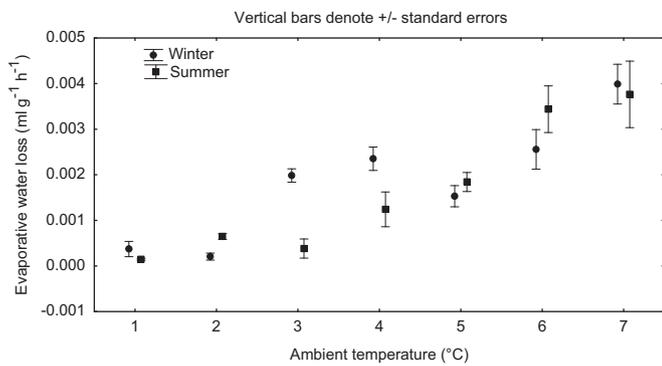


Fig. 6. Evaporative water loss of Wahlberg's epauletted fruit bats at various ambient temperatures in summer and winter.

order to offset the effects of low resource availability (Lovegrove, 2000). In this study, the mass-specific BMR of *E. wahlbergi* was found to be 137% in winter and 106% of that predicted by allometric scaling for a mammal of its size using the Chiropteran equation (Hayssen and Lacy, 1985). This unexpectedly suggests winter upregulation rather than summer down-regulation of BMR. This differs to Smit and McKechnie's (2010) assertion that Afro-tropical endotherms (in particular birds) should show down-regulation of BMR in winter as a consequence of the unpredictable environment, but is similar to data from red-winged starlings *Onychognathus morio* (Chamane and Downs, 2009). The greater vasa parrot *Caracopsis vasa* showed summer upregulation of BMR, which also differed with this assertion (Lovegrove et al., 2011). It also questions the use of allometric scaling to predict mammalian BMR, as it has been argued in many previous studies that a single allometric relationship cannot sufficiently predict the BMR for all mammals (McNab, 1988; Lovegrove, 2000), particularly if the value used for a species was for a particular season.

A recent study (Almeida and Cruz-Neto, 2011) examined the phenotypic capacity of three species of fruit-eating phyllostomid bats from Brazil and found no variation in BMR between seasons. Environmental conditions, rather than season, determine torpor use and temperature selection in large mouse-eared bats (*Myotis myotis*) (Wojciechowski et al., 2007), and in a relatively small subtropical blossom-bat (*Syconycteris australis*) in Australia (Geiser et al., 2005). In contrast, our *E. wahlbergi* data show that thermal energetics of Afro-tropical fruit-eating bats may be more affected by season.

Winter BMR of *E. wahlbergi* was higher than summer BMR, consistent with our prediction that BMR would be elevated in winter compared with summer. These results differ to a number of studies which have found no seasonal differences in BMR for mammal species (Geiser and Baudinette, 1987; Feist and White, 1989; Coburn and Geiser, 1998). Interestingly, the latter study found *S. australis* enter torpor with a higher frequency in summer suggesting this is the season when they experience the greatest pressure in maintaining a constant T_b due to energy and ecological constraints including unpredictable climate and food supply (Coburn and Geiser, 1998).

According to Hill et al. (2004), species experiencing a high seasonal variability in ambient conditions are predicted to show a great seasonal variation in physiological parameters such as MR and BMR. Furthermore, the South East Africa regions, the area where *E. wahlbergi* occur, show the highest degree of seasonal variation in T_a across the whole of the Afro-tropical region (Jury and Nkosi, 2000). The increase in BMR during winter in *E. wahlbergi* appears to be a metabolic process that helps this species overcome heat loss during winter.

Winter body mass of *E. wahlbergi* was significantly higher than the summer body mass. An animal's body mass is governed by

several factors such as ambient temperatures, physiological status and food availability (Zheng et al., 2008). Seasonal thermoregulatory responses in small mammals (< 500 g) are centered more on increasing the thermogenic capacity through an increase in non-shivering thermogenesis (NST) capacity and large reductions in conductance (Lovegrove, 2005). However, bats are known to have a labile body mass, with the greatest variation in body mass over a 24 h period recorded for any mammal species (Studier et al., 1970). Furthermore, the body mass of bats is largely dependent upon the nutritive status of an individual (i.e. a hungry bat weighs far less than a well-fed bat) (McNab, 1982). Therefore the seasonal increase in body mass of *E. wahlbergi* may not be as a result of increased fat deposits for insulation or metabolizing tissues as observed in other endotherms (Zheng et al., 2008), but since it coincides with an increase in BMR, it may occur as a result of excessive eating as a result of increased metabolic costs associated with an increase in BMR. Of interest, is the elevated RMR_{Ta} at 10 °C in winter, which we speculate could be an attempt to defend T_b at low $T_{a,s}$ in winter when resources are not limiting.

The TNZ of *E. wahlbergi* showed a significant seasonal shift from a narrow TNZ in summer to a very broad TNZ in winter, which was consistent with our predictions. A broad TNZ can serve as an energy saving mechanism, allowing an organism to tolerate a wide range of temperatures without having to increase its metabolism (Hill et al., 2004). Furthermore, since an increase in TNZ is coupled with a decrease in conductance and an increase in insulation (Hill et al., 2004), this further reduces the energy expenditure by an organism (Cooper and Gessaman, 2004). Therefore an increase in TNZ during winter is advantageous, as it allows maintenance of a minimal normothermic MR over a wide range of ambient temperatures (Hill et al., 2004).

Although no evidence of torpor (see Geiser, 2004 for definition) was observed in this study, *E. wahlbergi* was heterothermic. Individuals generally lowered core T_b by only a few degrees during their daytime rest-phase despite much lower $T_{a,s}$ in winter. In both winter and summer, rectal T_b of the bats decreased linearly with $T_{a,s}$. These results correspond with a number of studies conducted on fruit- and blossom-eating chiropterans (Bartholomew et al., 1964; 1970; McNab, 1989; Genoud et al., 1990; Geiser et al., 1996; Bonaccorso and McNab, 1997; Ochoa-Acuña and Kunz, 1999; Coburn and Geiser, 1998; Bartels et al., 1998; McNab and Armstrong, 2001; McNab and Bonaccorso, 2001; Geiser et al., 2005; Riek et al., 2010). This shows that these chiropterans adopt the energy saving strategy of heterothermy particularly during their rest-phase, and with decreased T_a or food scarcity irrespective of body size. Furthermore, *E. wahlbergi* is significantly bigger than many fruit- and blossom-eating bats, making it less likely to rely on torpor, but rather some degree of heterothermy as a means of conserving energy.

There was a significant increase in EWL in *E. wahlbergi* with an increase in T_a in summer and winter. Although there was such a high rate of EWL at high $T_{a,s}$, no significant increase in metabolic rate was observed. At low $T_{a,s}$, EWL occurs as a by-product of ventilation since the mammalian skin is not perfectly impermeable to water (Maloney et al., 1999). EWL during the hottest part of the day poses a considerable dehydration stress on this species since at 35 °C, excessive salivation was observed in this species. Furthermore, in another similar study, when this species was placed in a respirometer at 40 °C, one of the bats died, and some deaths of bats were observed in outside aviaries on extreme hot days (> 40 °C) (M.M. Zungu, Downs, C.T. pers. obs.). Furthermore, bats do not have sweat glands, and thus depend on less-efficient means of dissipating excess heat such as salivation, panting, body licking and wing fanning (McNab, 1982). This provides further support that this species is intolerant of high $T_{a,s}$ as a result of ineffective means of offloading excess heat.

In conclusion, the *E. wahlbergi* increased their RMR_{Ta} and BMR during winter. This increase is important for winter survival as it leads to an increase in metabolically-produced heat. The increase in *E. wahlbergi*'s TNZ range during winter is also important for their winter survival, as they use less energy to keep warm when T_a drops. The observation of heterothermy in *E. wahlbergi* confirmed the results of previous studies which have shown that the former sub-order Megachiroptera are indeed heterothermic, particularly during the rest-phase. The ability of *E. wahlbergi* to use heterothermy is important as it spends less energy maintaining elevated T_b s. This study also showed that *E. wahlbergi* is intolerant of high T_{as} , as at high T_{as} , excessive salivation was observed, and may lead to death if T_{as} go higher. The intolerance of high T_{as} by *E. wahlbergi* have significant implications about the influence global warming would have on this species, as it suggests that it is likely to be impacted. Furthermore, this study shows the importance of microclimate on roost selection during daytime rest phase period by the species (Boyles, 2007), improving our understanding of the ecology of this species. Lack of data on the energetics and seasonal variation of physiological parameters for Afrotropical bats in general suggest that more work is required for comparison with results of those in other regions and improve our understanding of the ecophysiology, particularly energetics, of fruit and nectar feeding bats, particularly given the climate change scenarios.

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