J Comp Physiol B (2001) 171: 1–10

ORIGINAL PAPER

B. G. Lovegrove · J. Raman · M. R. Perrin

Heterothermy in elephant shrews, *Elephantulus* spp. (Macroscelidea): daily torpor or hibernation?

Accepted: 26 July 2000

Abstract The physiological parameters of heterothermy (e.g. minimum body temperature and oxygen consumption, percentage metabolic reduction, and bout length) were measured in two species of *Elephantulus* elephant shrews (*Elephantulus myurus* and *Elephantulus rozeti*; Macroscelidea) as a function of ambient temperature. Both species displayed deep torpor whereby the body temperatures of ca. 5 °C and oxygen consumption as low as 2% of basal metabolic rate were attained. Torpor bout length ($n = 57$ bouts) never exceeded 24 h. These data are characteristic of both hibernation (minimum body temperature and metabolism) and daily torpor (bout length), and argue that these two physiological responses may not necessarily have separate evolutionary origins.

Key words Torpor · Heterothermy · Elephant shrews · Elephantulus · Macroscelidea

Abbreviations *EE* energy expenditure · *HR* rate of heating · T_a ambient temperature · T_b body temperature · T_{lc} thermoneutrality · VO_2 oxygen consumption

Introduction

Geiser and Ruf (1995) have defined the limits and ranges of physiological parameters associated with heterothermy in birds and mammals. When minimum oxygen consumption (VO_2) and body temperature (T_b) decrease below normothermic levels for periods not exceeding 24 h, the proximate physiological response is termed 'daily torpor' and the animal a 'daily heterotherm'. When hypothermia lasts more than 24 h, the proximate physiological response is termed 'hibernation' and the animal a 'hibernator'.

Geiser and Ruf's (1995) analyses showed that, although maximum bout length clearly differentiated hibernation (96–1,080 h) from daily torpor (1.5–22 h), there was some overlap, albeit marginal, in minimum T_b and VO_2, and metabolic reduction. Generally, mean minimum T_b is lower in hibernators than in daily heterotherms (5.8 °C vs. 17.4 °C), as is mean minimum VO_2 (0.037 ml O_2^{-1} g^{-1} h^{-1} vs. 0.535 ml O_2^{-1} g^{-1} h^{-1}) and mean metabolic reduction (5.1% vs. 29.5% of BMR; Geiser and Ruf 1995). Nevertheless, despite some overlap, the analyses are convenient because they aid in the differentiation between hibernation and daily torpor in most endotherms that routinely display non-pathological hypothermia under laboratory conditions.

The physiological distinction between hibernation and daily torpor argues for the independent evolution of these two proximate physiological responses (Geiser 1998). However, there are three possible routes that independent evolution of heterothermy could have followed (see Geiser 1998). First, one response (e.g. hibernation) may be derived from an ancestral state (e.g. daily torpor); thus we should see lineage-specific representation of the two heterothermic states. However, as discussed by Geiser (1998), this alternative is unlikely because several extant mammalian orders (Diprodontia, Didelphiformes, Chiroptera, Rodentia, Insectivora and Primates) display both traits. A second alternative is that a derived state (e.g. hibernation) evolved from the ancestral state (e.g. daily torpor) independently several times. This polyphyletic origin of hibernation is favoured by Geiser (1998), and is thought to explain the lack of heterothermy in older avian lineages as well as the existence of both daily torpor and hibernation within specific mammalian orders. The third alternative is that hibernation and daily torpor are not physiologically distinct, but merely represent components of a physiological gradient of hypothermia in which ecological and

---

Communicated by G. Heldmaier

B. G. Lovegrove (✉) · J. Raman · M. R. Perrin
School of Botany and Zoology, University of Natal,
Private Bag X01 Scottsville 3209, South Africa
e-mail: lovegrove@nu.ac.za
Tel.: +27-33-2605113; Fax: +27-33-2605105

energetic criteria favour two regions of the gradient that currently characterize daily torpor and hibernation. Wilz and Helmaier (2000) recently reached this conclusion in a comparison of hibernation, aestivation and daily torpor in the edible dormouse, *Glis glis*.

In this paper we show that elephant shrews (Macroscelidea) display characteristics of both hibernation and daily torpor that lend further support to the idea of a physiological gradient of heterothermy. Specifically, our data show that bout length may not be as distinct between daily torpor and hibernation as previously thought.

Elephant shrews belong to an ancient, African superordinal eutherian clade that includes elephants, dugongs, hyraxes, golden moles, and the aardvark (Porter et al. 1996; Stanhope et al. 1996 ; Springer et al. 1997). Observations of torpor in two species of elephant shrew, *Macroscelides proboscideus* (Lovegrove et al. 1999) and *Elephantulus rozeti* (Seguignes 1983) and in various golden moles (Kuyper 1979; Fielden et al. 1990; Bennett and Spinks 1995), confirm a pleisiomorphic (ancestral) origin of daily heterothermy in mammals (Geiser and Ruf 1995; Lovegrove et al. 1999).

In *M. proboscideus*, body temperature (T_b) was monitored by telemetry for several weeks under various ambient temperature (T_a) and food deprivation regimes (Lovegrove et al. 1999). Daily torpor could be induced by food deprivation, but the animals did not spontaneously enter torpor in response to low T_as (Lovegrove et al. 1999). The lowest T_b measured was ca. 10 °C at a T_a of ca. 10 °C (Lovegrove et al. 1999). Oxygen consumption was not measured during torpor.

The only non-Afrotropical macroscelid, *E. rozeti* from Morocco, also employs torpor (Seguignes 1983). These observations were based upon rectal T_b, the lowest of which was 11 °C measured at a T_a of 11 °C (Seguignes 1983).

In both studies the depth of torpor, i.e. minimum torpor T_b, seemed to be limited by T_a. Hence, because T_b has not been measured at T_as below 10 °C, we do not know whether elephant shrews are capable of controlling a minimum torpor T_b below 10 °C. This is important information because T_bs below 10 °C during hypothermia are more characteristic of hibernators than daily heterotherms (Geiser and Ruf 1995). Therefore the objectives of this study were to quantify the parameters that characterize torpor in *E. myurus* and *E. rozeti*.

Materials and methods

Study animals

E. myurus were trapped with aluminium Sherman traps in April 1998 in KwaZulu-Natal, South Africa, whereas *E. rozeti* were captured by hand by local village children near Skour, Rehamna, Morocco in July 1998. Both species were housed in Pietermaritzburg, South Africa, in a constant environment room at a T_a of 18 ± 1 °C and relative humidity of 70%. All plastic holding cages were provided with wood shavings, water ad libitum, and a wooden nest box. An 8L:16D photoperiod was used throughout all experiments. Animals were acclimated to the above conditions for 3 weeks prior to data measurement.

The animals were fed Pronutro (a commercial high protein cereal: 22% protein, 59% carbohydrate and 6% fat) mixed with water. This staple diet was supplemented daily with fresh lettuce and sliced apple, and weekly with live mealworms. Food was replenished every evening 1–2 h preceding the scotophase, i.e. between 1400–1500 hours.

Physiological measurements

T_b was measured using calibrated temperature-sensitive telemeters (Minimitter, Model XM; weight: 1.3 g; accuracy: 0.1 °C) surgically implanted into the intraperitoneal cavity under inhalation anaesthesia (2–3% isoflorane in oxygen for induction and maintenance). The transmitters were calibrated in a water bath at temperatures of 2–45 °C. Transmitter pulse intervals and water-bath temperatures were $\log_{10}$-transformed and quadratic equations fitted to the data. These regressions gave coefficients of determination >0.99, and provided a better fit to the data than linear models. T_b was recorded simultaneously with VO_2 every 6 min by a microcomputer linked to radio receivers (McKechnie and Lovegrove 1999). T_bs could be monitored continuously on a computer monitor to observe the progress of hypothermia without disturbing the animals.

Metabolic rate was measured by indirect calorimetry from oxygen consumption measured in a six-channel flow-through negative-pressure system. The animals were placed in perspex respirometers within a 1-m^3 temperature-controlled chamber fitted with an air-circulation fan. Outside air that had been partially dried with silica gel to attain a relative humidity of ca. 50% was pumped into the temperature chamber at a flow rate that exceeded all air flows extracted from the chamber thus ensuring a positive air pressure within the temperature chamber. From experience, we have found that an incurrent relative humidity of 50% maintains a relative humidity in the respirometer of 70–90% (with the addition of respiratory water vapour) and prevents water vapour saturation and condensation in the respirometer. The photoperiod of the chamber was matched to that of the constant environment rooms in which the animals were housed. The temperature within each respirometer was measured with a thermistor probe calibrated in the chamber with a mercury thermometer (0.05 °C) at T_as from −20 °C to 50 °C.

Air was drawn through the six respirometers (one control, five experimental) by six pumps individually plumbed with CO_2-proof tubing. The air vented into three-way solenoid valves after passing through a dew-point water condenser to remove water vapour from each air line. Under computer control, each solenoid valve was activated for 1 min every 6 min (or less depending upon the number of channels being utilized) during which time the experimental air from the respirometer was diverted for analysis. Non-activated solenoid values vented expired air from the respirometers into the room to avoid hypoxia within the respirometers and to maintain a constant air flow through each respirometer. The expired air from activated solenoid valves was passed through a thermal mass-flow meter (Brooks, Model 5810) and vented into a 50-ml syringe casing. Air was sub-sampled from the syringe casing at a flow rate lower than that passing through the respirometers to ensure a constant positive pressure within the syringe casing. The sub-sampled air was passed through an oxygen sensor (Ametek N-22 M) attached to an oxygen analyser (Ametek S-3A/l, accuracy 0.001% O_2) to determine the fractional concentration of oxygen in the dry air. Eq. 3a (Withers 1977) was used to calculate VO_2. We assumed an RQ value of 0.85 in the equation which can generate a maximum error in VO_2 of $\pm 3\%$ if the RQ is actually 1.0 or 0.7 (Withers 1977). Mass-specific VO_2 data were corrected for mass loss during data measurement by assuming a linear reduction in mass between the starting body mass and the final body mass.

Analogue outputs from the oxygen analyser, mass-flow meter, telemeter frequency-to-voltage converter (telemeter pulse intervals), and thermistor probes were digitized with a 48-channel A/D converter and recorded on a microcomputer.

The length of tubing between the solenoid valves and the sub-sampling syringe casing, as well as the length of the sub-sampling tubing to the oxygen sensor, was minimized (< 20 cm) to ensure adequate flushing of air from the previous channel. Oxygen consumption was measured at the end of each minute to ensure that a steady-state output from the oxygen analyser had been attained. Steady-state oxygen consumption could be attained within 1 min provided that the air flow through the respirometers was not less than ca. 200 ml min^{-1}. Generally, the flow rate through each respirometer was determined by T_a and the associated percentage O_2 depletion (never more than 1% O_2) within the respirometers when animals were normothermic, usually between 300–600 ml min^{-1}.

The first respirometer was always employed as a control and measured first within each measurement cycle. The percentage O_2 within the five experimental respirometers was then subtracted from that of the control channel to give the percentage O_2 utilized by the animals. This procedure overcame the problem of electronic baseline drift inherent in most analysers and allowed long-term data collection without the subsequent need for baseline drift corrections.

The animals were fed several hours prior to the commencement of the scotophase and then placed in perspex respirometers (2100 cm^3) where they remained for 15–24 h depending upon their state of hypothermia. They were not provided with either food or water in the respirometers. We initially placed a slice of apple in each respirometer as a source of water, but the animals did not eat the apple and the procedure was discontinued. Oxygen consumption and T_b were measured at T_as ranging from 2–36 °C.

Data analysis

Elephant shrews were considered to have entered torpor if T_b decreased below the lowest limits of the frequency distribution of normothermic T_bs measured over a 24-h period at $T_a = 25$ °C (Fig. 1). Although the lowest normothermic T_b was not less than 34 °C for both species, we took $T_b = 33$ °C as the T_b below which animals were deemed to be in a torpid state.

Torpor bout duration (h) was determined as the total time during which T_b was maintained below $T_b = 33$ °C. Within each torpor bout, the minimum T_b, the VO_2 associated with the minimum T_b, respirometer temperature (T_a), and the real time of entry and arousal from torpor were determined. In addition, average normothermic VO_2 and associated T_b values were determined over a period of 30 min prior to the onset of VO_2 and T_b reduction leading to entry into torpor. These data often proved to be the only normothermic data that could be obtained for these species at lower T_as because of their propensity for torpor.

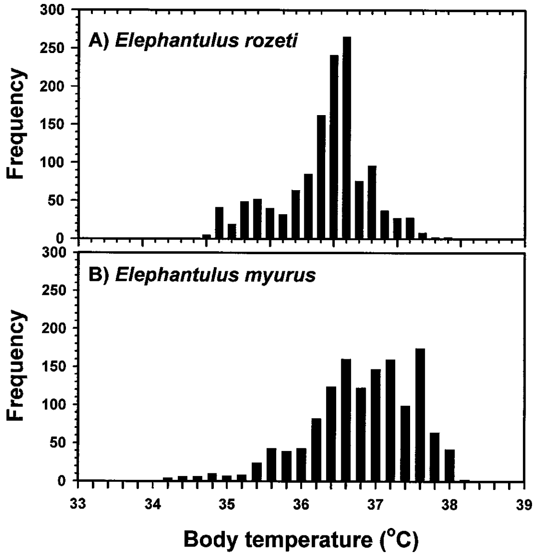


Fig. 1 Frequency distributions of normothermic body temperatures (T_b) measured every 6 min over a 24-h period at ambient temperature (T_a) = 25 °C in **A** *Elephantulus rozeti* ($n = 6$) and **B** *Elephantulus myurus* ($n = 6$). These data were used to determine the T_b below which animals were deemed to be torpid ($T_b = 33$ °C)

At certain T_as in which the onset of heat production during arousal was sufficiently distinct for the inflection to be statistically discernible (Yeager and Ultsch 1989), the rate of heating of T_b was determined. We approximated the rate of heating (°C min^{-1}) with the slope of linear models fitted to the data from the point of inflection until T_b reached steady-state normothermia. Hence the slope of the regression is an average rate of heating from the onset of arousal to the attainment of normothermy. Where possible, the inflection of VO_2 at the onset of arousal was also determined this way (Yeager and Ultsch 1989) and used to identify the end of the maintenance phase and the onset of arousal. The energetic expenditure (kJ) during entry and maintenance, as well as during arousal, was calculated from the energy equivalence of VO_2 data integrated over the total time period of the respective components of the torpor bout. The energy equivalence was assumed to be 20.08 kJ l^{-1} O_2 (Schmidt-Nielsen 1983). Mean values are reported ± 1 SE.

Results

General observations

The elephant shrews readily entered torpor in the respirometers at all $T_a \leq 25$ °C. When torpid, both species adopted a crouched position with the snout resting on the ground. This body posture was not dissimilar to that described and illustrated by Rathbun (1979) for *Elephantulus rufescens* from East Africa when sleeping under low bushes. Our animals did not attempt to reduce surface areas by rolling into a ball like many small mammalian heterotherms (Lyman et al. 1982). The eyes remained slightly open during torpor, again similar to that described for sleeping *E. rufescens* (Rathbun 1979). The only visible sign of hypothermia was obvious piloerection at all T_as.

With the exception of a few *E. myurus* at $T_a = 5$ °C, all animals were capable of self- arousal from torpor. However, at $T_a = 5$ °C we interrupted torpor after 15–19 h in three *E. myurus* and one *E. rozeti* and removed the torpid animals from the respirometers. All were successfully reheated to normothermy with an artificial heat source within several hours. In retrospect, our concern for the welfare of these animals was possibly unfounded, but we were concerned that a sustained $T_b < 5$ °C and a virtually undetectable oxygen consumption were indicative of pathological hypothermia. One animal actually toppled over onto its side where it remained rigid for several hours before being removed and reheated successfully to normothermia.

Body mass

At the commencement of torpor measurements, the mean body masses of *E. rozeti* and *E. myurus* were 45.31 ± 1.36 g ($n = 7$) and 62.97 ± 1.78 g ($n = 7$), respectively. By the end of data measurement 1 month later, *E. rozeti* had significantly increased body mass to 53.07 ± 2.40 g (ANOVA; $F_{1,12} = 7.94$; $P < 0.05$), whereas *E. myurus* maintained its mass at 61.01 ± 1.34 g (ANOVA; $F_{1,12} = 0.77$; $P = 0.41$).

The mean percentage mass loss per measurement episode in *E. rozeti* was 9.90 ± 0.47%. When torpor occurred during the measurement period, the mean percentage mass loss (9.62 ± 0.54%; $n = 36$) was lower than when the measurement period lacked torpor (12.45 ± 0.56%; $n = 4$), but this difference was not significant (ANOVA; $F_{1,38} = 2.94$; $P = 0.09$). Moreover, irrespective of whether torpor occurred or not, linear regressions of proportional mass loss and T_a did not reveal significant correlations ($P > 0.05$).

On average, *E. myurus* lost 12.56 ± 0.65% of body mass during each data measurement episode. Although mass loss in the absence of torpor (15.83 ± 2.42%) was higher than that when torpor occurred (8.53 ± 2.79%), this difference was not significant (ANOVA; $F = 2.06$; $P = 0.25$). Again, linear regressions revealed that mass loss was not significantly correlated with T_a when the measurement period either included or excluded torpor ($P > 0.05$).

Normothermic T_bs

At $T_a = 25$ °C, normothermic T_bs for *E. myurus* and *E. rozeti* ($n = 6$) over 24 h (i.e. 240 measures per animal) were 36.73 ± 0.02 °C and 36.78 ± 0.02 °C, respectively (Fig. 1). These data showed a unimodal distribution, despite the influence of a light-dark cycle during data measurement. The maximum range of normothermic T_bs was 4.2 °C and 3.9 °C for *E. myurus* and *E. rozeti*, respectively, indicating fairly high lability of normothermic T_bs independent of a light-dark cycle.

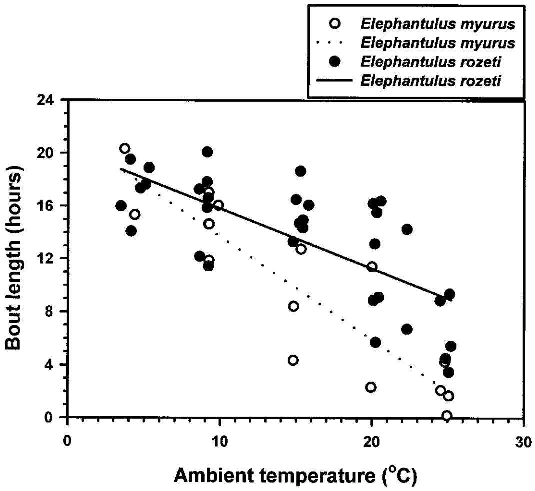


Fig. 2 Torpor bout lengths (h) of *E. rozeti* (*dots and solid line*) and *E. myurus* (*circles* and *dotted line*). The data exclude bout lengths for animals that were reheated to normothermy with exogenous heat

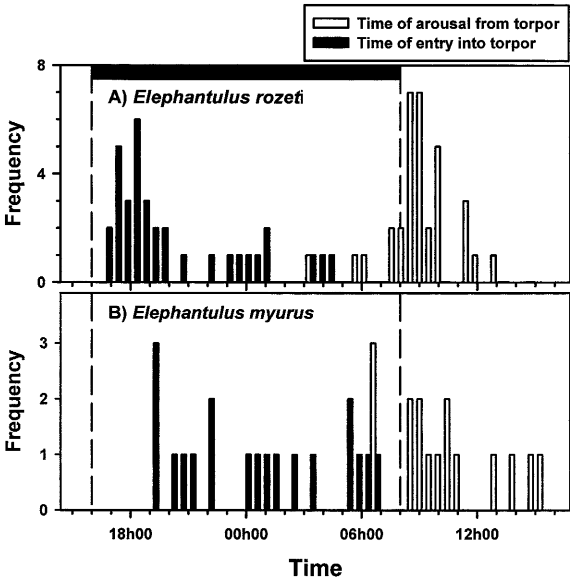


Fig. 3 The real times of entry (*filled bars*) and arousal (*clear bars*) from torpor in **A** *E. rozeti* and **B** *E. myurus*. The *vertical dotted lines* and the *black bar* at the top of the upper graph indicate the scotophase (dark hours)

Torpor bout length and timing

A linear increase in torpor bout length was significantly correlated with decreasing T_a in both *E. rozeti* ($r = 0.71$, $F = 32.7$; $P < 0.001$) and *E. myurus* ($r = 0.90$; $F = 57.2$; $P < 0.001$; Fig. 2). The mean bout length of *E. rozeti* was 13.58 ± 0.79 h ($n = 34$; range: minimum 3.5 h at $T_a = 25.1$ °C, maximum 20.1 h at $T_a = 9.1$ °C), significantly longer (ANOVA; $F_{1,47} = 7.87$; $P < 0.05$) than that of *E. myurus* (9.85 ± 1.62 h; $n = 12$; range: minimum 0.2 h at $T_a = 25$ °C, maximum 20.3 h at $T_a = 3.7$ °C). At $T_a > 10$ °C (Fig. 2), for example, the average torpor bout lengths of *E. rozeti* (11.8 h) were 2.2-times longer than those of *E. myurus* (5.3 h).

In *E. rozeti* the mean real time of arousal occurred at 0851 hours, shortly after the end of the scotophase at 0800 hours (Fig. 3). The mean real time of entry into torpor occurred at 1958 hours, although the distribution was strongly right-skewed around this mean time. For example, the earliest entries occurred at the onset of the scotophase, whereas the latest entries occurred at ca. 0400 hours. Plots of T_b and VO_2 of one individual *E. rozeti* illustrate that the arousal times are fairly closely coupled to the onset of the photophase, except when long bout lengths and slow heating rates at the lowest ambient temperatures delay arousal (Fig. 4).

In *E. myurus*, the mean time of arousal was 1008 hours, although the latest arousals occurred at ca. 1400 hours. The mean time of entry into torpor was 0017 hours. This distribution showed a large variability in the time of entry into torpor: the earliest entries occurred at ca. 1900 hours and the latest between 0600 hours and 0700 hours (Fig. 3).

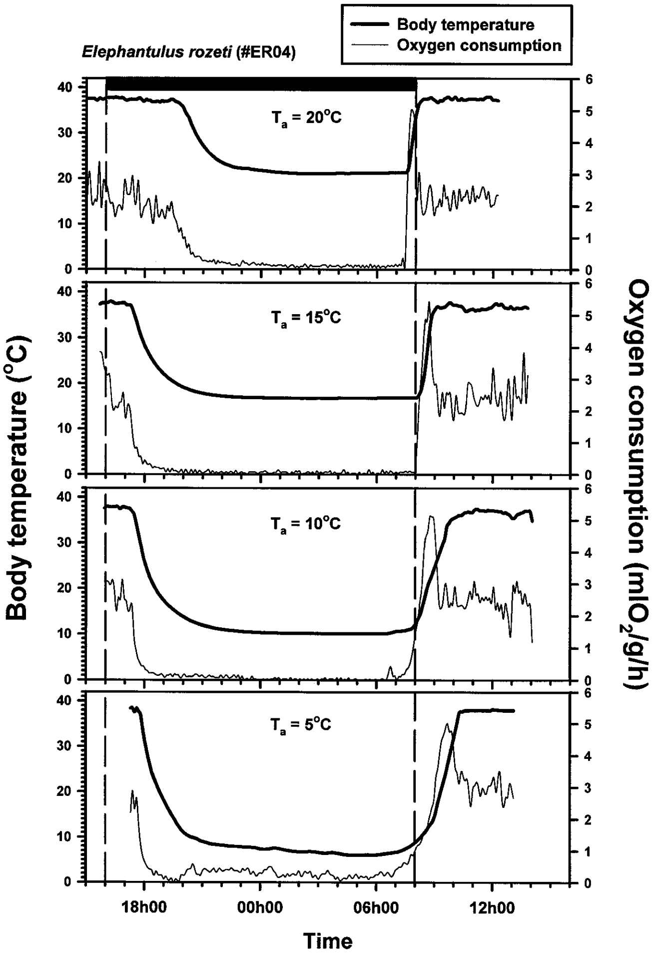


Fig. 4 Plots of body temperature (*thick lines*) and oxygen consumption (*thin lines*) of an individual *E. rozeti* (#ER04) measured at various ambient temperatures

Oxygen consumption and T_b

In normothermic animals, VO_2 increased linearly with decreasing T_a (Fig. 5a, c). For both individual animals and the combined data set, we could not detect significant inflections in the data using the method of Yeager and Ultsch (1989) to determine the lower limit of thermoneutrality (T_{lc}). We hence assumed T_{lc} to be > 25 °C, i.e. we assumed a linear physiological response of VO_2 to decreasing T_a below $T_a = 25$ °C, and calculated the slope and intercept of regressions of the metabolic response to T_a in individual animals at $T_a < 25$ °C. In *E. myurus* all analyses revealed significant linear responses ($P < 0.05$) with mean slopes and intercepts of –0.056 ± 0.004 ml O_2 g^{-1} h^{-1} $°C^{-1}$ and 3.012 ± 0.145 ml O_2 g^{-1} h^{-1}, respectively. In *E. rozeti*, regressions were also significant ($P < 0.05$). Compared with *E. myurus*, the slopes (–0.067 ± 0.006 ml O_2 g^{-1} h^{-1} $°C^{-1}$; $n = 7$) were not significantly different (ANOVA; $F_{1,12} = 2.36$; $P = 0.15$), whereas the intercepts (3.521 ± 0.133 ml O_2 g^{-1} h^{-1}; $n = 7$) were significantly higher (ANOVA; $F_{1,12} = 6.68$; $P = 0.024$).

We estimated the basal metabolic rate (BMR) of each species as the lowest VO_2 recorded in each animal at any $T_a > 25$ °C. The choice of this temperature was based upon visual examination of where the lowest normothermic VO_2 values occurred. For *E. rozeti*, the mean BMR was 1.055 ± 0.054 ml O_2 g^{-1} h^{-1} ($n = 7$) and occurred at a mean T_a of 35.39 ± 0.32 °C. The BMR of *E. myurus* was 1.053 ± 0.034 ml O_2 g^{-1} h^{-1} ($n = 7$) at a mean T_a of 30.97 ± 0.71 °C.

In both species, torpid animals showed a linear decrease in minimum T_b with T_a, whereas normothermic T_b remained stable at 37.06 ± 0.08 °C ($n = 82$) and 36.86 ± 0.09 °C ($n = 94$) for *E. rozeti* and *E. myurus*, respectively (Fig. 5b, d). The lowest torpor T_b recorded in *E. rozeti* was 5.1 °C at $T_a = 4.1$ °C, whereas the lowest in *E. myurus* was 4.9 °C at $T_a = 3.0$ °C. However, this latter animal was removed from the respirometer because of suspected pathological hypothermia after 16 h in torpor. It was reheated successfully to normothermy within several hours with an artificial heat source. The lowest T_b attained during torpor by a *E. myurus* that was capable of self-arousal after 20.3 h in torpor was 5.5 °C at a $T_a = 3.7$ °C.

The mean temperature gradient between T_b and T_a in torpid *E. rozeti* was 1.22 ± 0.19 °C ($n = 33$), which was significantly 1.6 °C lower (ANOVA; $F_{1,51} = 16.21$; $P < 0.001$) than that in *E. myurus* (2.84 ± 40 °C; $n = 20$). Five of the *E. rozeti* T_b–T_a calculations were negative (the largest was −1.6 °C) indicating a T_b lower than the respirometer temperature (Fig. 5b). Other than telemeter drift, we have no immediate explanation for these observations, despite having investigated every possible source of likely measurement error. Identical equipment was used to measure T_b in *E. myurus* in which anomalous T_b data did not occur.

The relationship of the minimum oxygen consumption with the minimum torpor T_b was exponential in both species (Fig. 6). The pattern was better approximated with an exponential model than a linear model. In each instance, we regressed the residuals calculated by best-fit exponential and linear models with the dependent values predicted by each curve respectively. For *E. rozeti* we excluded data at $T_a < 6$ °C from the regressions because these data indicated evidence of heat production in defence of a torpor set point T_b (Fig. 6a). For the balance of the data, an exponential fit ($VO_2 = 0.0074e^{0.135T_b}$; $F = 332$; $r^2 = 0.93$; $P < 0.0001$) provided a stronger linear regression of observed torpor VO_2 as a function of predicted exponential values ($r = 0.97$) than did the linear model ($r = 0.90$; Fig 6a). Similarly, in *E. myurus*, the exponential fit ($VO_2 = 0.034e^{0.085T_b}$; $F = 74.98$; $P < 0.0001$) provided a stronger linear regression of predicted versus observed torpor VO_2 values ($r = 0.90$) than the linear model ($r = 0.81$; Fig. 6b).

The mean of the lowest VO_2 recorded ($n = 7$) during torpor in each animal was 0.023 ± 0.006 ml O_2 g^{-1} h^{-1} for *E. rozeti*, and 0.078 ± 0.019 ml O_2 g^{-1} h^{-1} for *E. myurus*.

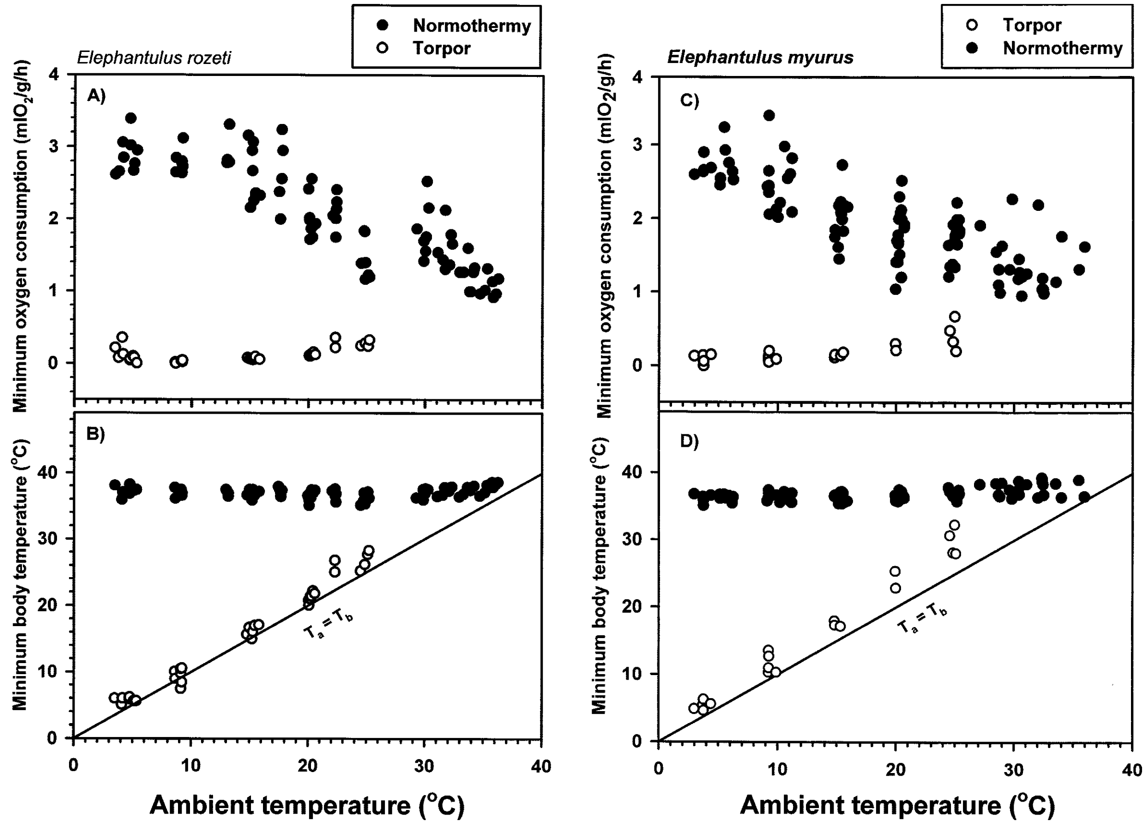


Fig. 5 The minimum T_b and oxygen consumption during torpor (*circles*) and normothermy (*dots*) for *E. rozeti* (**A** and **B**) and *E. myurus* (**C** and **D**). In graphs B and D the *diagonal solid line* represents the $T_a = T_b$ line

Heating rates

In *E. rozeti*, the rate of heating (HR; °C min^{-1}) during arousal from torpor showed a bell-shaped relationship with minimum torpor T_b (Fig. 7a). The HR increased with decreasing minimum torpor T_b until an asymptote was attained, but then decreased at the lowest minimum torpor T_bs (Fig. 7a). These data were better described by a quadratic polynomial equation ($r = 0.68$; $F = 12.31$; $P < 0.001$) than by a linear model ($r = 0.40$; $F = 5.66$; $P = 0.02$). The quadratic equation predicted a mean maximum heating rate of 0.39 °C min^{-1} at a minimum torpor T_b of 17.7 °C at the asymptote. The mean for all observations was 0.30 ± 0.02 °C min^{-1} ($n = 34$) irrespective of minimum torpor T_b or T_a. There was a similar quadratic relationship of HR as a function of T_a ($r = 0.68$; $F = 12.39$; $P < 0.001$).

Similarly, in *E. myurus*, a polynomial equation fitted to the HR data as a function of minimum torpor T_b ($r = 0.74$; $F = 8.05$; $P < 0.01$) provided a better fit to the data than a linear model which was not significant ($r = 0.15$; $F = 0.31$; $P = 0.59$; Fig. 7b). The polynomial equation predicted a maximum HR of 0.30 °C min^{-1} at a minimum torpor T_b of 18.9 °C. The mean HR for all *E. myurus* data was 0.19 ± 0.03 °C min^{-1} ($n = 16$).

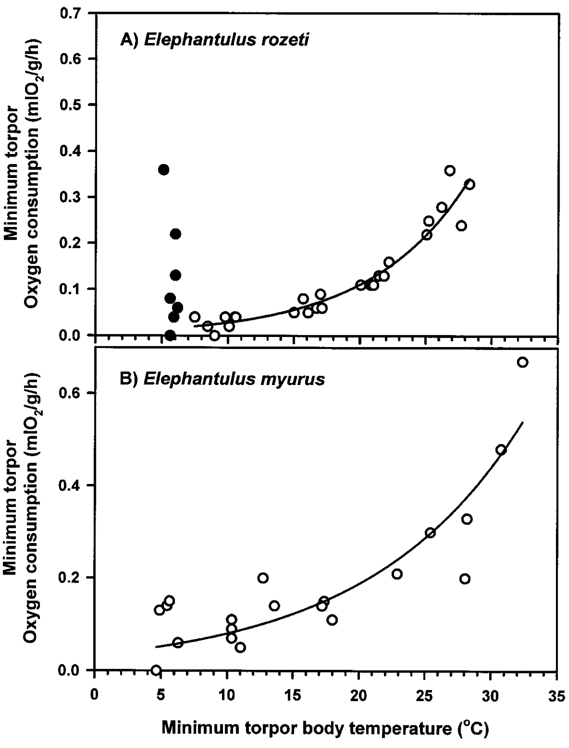


Fig. 6 The minimum oxygen consumption during torpor as a function of the corresponding minimum T_b attained in **A** *E. rozeti*, and **B** E. *myurus*. The *dots* in graph **A** for *E. rozeti* illustrate thermoregulatory heat production at $T_a < 8$ °C in some individuals. These data were excluded from the exponential functions fitted to the data (*solid lines*)

Again, a polynomial equation of HR as a function of T_a also provided a reasonable fit to the data ($r = 0.62$; $F = 4.12$; $P = 0.042$).

Energy expenditure (EE): costs and savings

The cost of arousal per torpor bout increased linearly with decreasing T_a in *E. rozeti* (Fig. 8a) from ca. 40% of the total energy expenditure during the bout at $T_a = 25$ °C, to ca. 90% of the bout EE at $T_a = 10$ °C (Fig. 8a *inset*). However, at $T_a < 10$ °C the cost of arousal was the highest in absolute terms, but represented a reduced percentage (70%) of the total bout cost because of thermogenesis during maintenance in defence of the torpor set-point T_b at the lowest T_as (Fig. 8a). Generally, the combined EE of entry and maintenance decreased with decreasing T_a from ca. 60% at

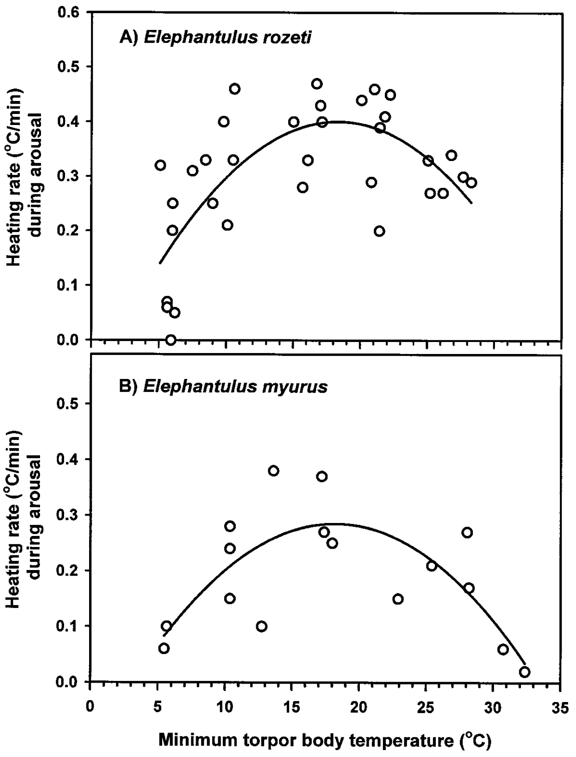
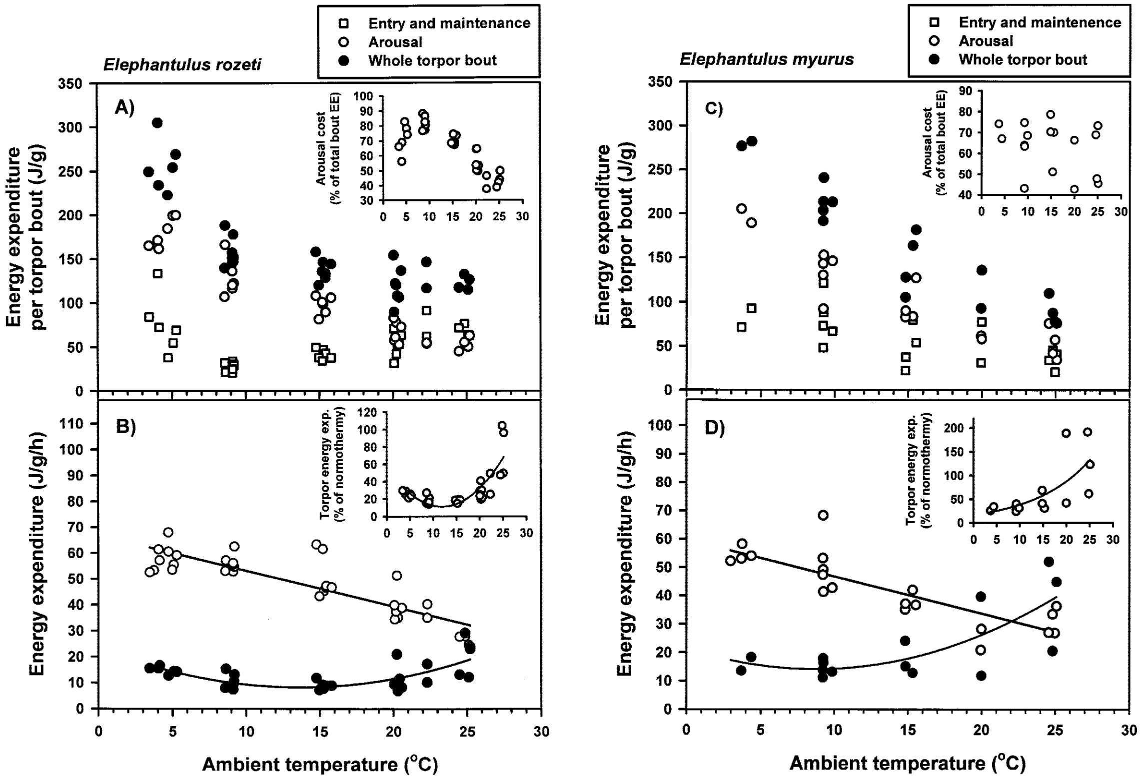


Fig. 7 The rate of heating (°C min^{-1}) during arousal from torpor for **A** *E. rozeti* and **B** *E. myurus*. Polynomial functions (*solid lines*) have been fitted to the data to illustrate slower heating rates at the lowest and highest T_as

Fig. 8 The total energy expenditure during entry and maintenance (*squares*), arousal (*circles*) and of complete torpor bouts (*dots*) in **A** *E. rozeti* and **C** *E. myurus*, as a function of T_a. These data were calculated by integrating the energetic equivalence of metabolic rate over the respective time intervals representing the various phases of the torpor bout. The inset graphs in **A** and **C** show the energy expenditure of arousal plotted as percentage of the energy expenditure of complete torpor bouts. The average energy expenditure during normothermy (*circles*) and torpor (*dots*) in **B** *E. rozeti* and **D** *E. myurus* have been represented with linear and polynomial functions (*solid lines*), respectively. The inset graphs in **B** and **D** show the average energy expenditure during torpor plotted as a function of the average normothermic energy expenditure



$T_a = 25$ °C to ca. 10% at $T_a = 10$ °C, until the onset of torpor heat production at $T_a < 6$ °C (Fig. 8a).

Relative to the linear cost of normothermy with decreasing T_a, torpor EE in *E. rozeti* showed a curvilinear response (Fig. 8b). A polynomial quadratic equation fitted to the data ($r = 0.67$; $F = 12.43$; $P < 0.001$) gave a minimum torpor EE of 8.52 J g^{-1} h^{-1} at $T_a = 13.7$ °C (Fig. 8b). When expressed as a percentage of normothermy, a polynomial quadratic equation ($r = 0.83$; $F = 32.00$; $P < 0.001$) gave a minimum torpor EE that represented 10.9% of the cost of normothermy at $T_a = 19.9$ °C (Fig. 8b *inset*).

In *E. myurus*, the cost of arousal expressed as a percentage of the total bout EE also generally increased with decreasing T_a (Fig. 8c) from 45–70% of the total bout EE at $T_a = 25$ °C, to ca. 80% at $T_a = 5$–10 °C (Fig. 8c *inset*). However, in contrast to *E. rozeti*, entry and maintenance EE in *E. myurus* increased linearly with decreasing T_a (Fig. 8c).

The cost of normothermy in *E. myurus* also increased linearly with decreasing T_a, whereas the EE in torpid animals was also curvilinear (Fig. 8d). A polynomial quadratic equation fitted to the torpor EE data ($r = 0.78$; $F = 8.54$; $P < 0.01$) gave a minimum EE of 14.18 J g^{-1} h^{-1} at $T_a = 8.7$ °C (Fig. 8d). Expressed as a percentage of normothermy, a polynomial fitted to the data ($r = 0.75$; $F = 6.94$; $P < 0.05$) gave a minimum torpor EE that represented 23.9% of normothermy at $T_a = 2.6$ °C (Fig. 8d *inset*).

Discussion

Both species of elephant shrew were capable of controlled heterothermy, although it is not possible to classify the response as either daily torpor or hibernation by contemporary definition. The values of several physiological variables were consistent with those observed in hibernators (minimum torpor T_b and VO_2, and the magnitude of BMR reduction), whereas others, such as bout length, were entirely consistent with values expected for daily heterotherms.

Heat production at the lowest T_as in *E. rozeti* confirms defence of a torpor set-point T_b of ca. 6 °C (Fig. 6a). However, we cannot be certain whether *E. myurus* also defends a torpor T_b. If this species does indeed possess a torpor T_b set-point it must occur below 5 °C because our animals showed no obvious attempt to maintain a constant torpor T_b above this temperature through endogenous heat production (Fig. 6b).

The lowest torpor T_bs we have measured in *E. rozeti* and *E. myurus* (ca. 5 °C) are the lowest yet measured in eutherian daily heterotherms, but were consistent with the range reported for larger-sized hibernators (Geiser and Ruf 1995). The minimum torpor T_b of mammalian and avian heterotherms ranges from 5 °C to 29 °C (median: 16.7 °C), whereas the range for hibernators is −2.9 °C to 32.3 °C (median: 4.7 °C) (Geiser and Ruf 1995). Although the arctic ground squirrel maintains sub-zero T_bs during hibernation (Barnes 1989), and several hibernators routinely maintain a minimum T_b only a few degrees above freezing (Geiser and Ruf 1995), as far as we are aware, no eutherian daily heterotherm is capable of a minimum T_b lower than 10 °C during daily torpor. The tiny (10 g) marsupial honey possum, *Tarsipes rostratus,* is the only non-placental mammalian daily heterotherm known to attain a minimum torpor T_b below 10 °C (Withers et al. 1990).

The lowest torpor VO_2 recorded in *E. rozeti* was also three-times lower than the lowest VO_2 yet recorded in a marsupial (0.07 ml O_2 g^{-1} h^{-1}; *Petaurus breviceps*) and 6.5-times lower than that measured in a eutherian (0.15 ml O_2 g^{-1} h^{-1}; *Perognathus* spp. daily heterotherm (Geiser and Ruf 1995). Indeed, the lowest torpor VO_2 for *E. myurus* was also lower than anything previously measured in eutherian daily heterotherms (Geiser and Ruf 1995).

When expressed as a percentage of BMR, the lowest torpor VO_2 of *E. myurus* was 7.4% of BMR using our BMR estimate, and ca. 6.6% of BMR using published BMR estimates of 1.20 ml O_2 g^{-1} h^{-1} and 1.17 ml O_2 g^{-1} h^{-1} (Leon et al. 1983; Du Toit 1993). For *E. rozeti*, the minimum torpor VO_2 represented 2.2% of our BMR estimate. Again, these very low values fall within the range characteristic of hibernators (Geiser and Ruf 1995). The mean torpor VO_2 value for all daily heterotherms was 29.5% of BMR (Geiser and Ruf 1995). In fact, no eutherian daily heterotherm has yet been shown to display a torpor VO_2 less than 10% of its BMR (Geiser and Ruf 1995).

The marked difference in minimum VO_2 between the two *Elephantulus* species can account for: (a) the 1.6 °C difference in the minimum gradient between T_b and T_a maintained during torpor, and (b) the comparative energy expenditure of torpor relative to normothermy. Notwithstanding the five spurious negative T_b–T_a observations, in *E. rozeti* the gradient is obviously smaller than that seen in any other marsupial or eutherian daily heterotherm. Again, a minimum torpor T_b close to that of T_a is more characteristic of hibernators than daily heterotherms (Geiser and Ruf 1995).

Wilz and Heldmaier (2000) suggest that the higher torpor T_b and metabolic rate of daily heterotherms relative to hibernators is a consequence of insufficient time during the comparatively shorter length of daily torpor bouts for animals to attain minimum steady-states of these variables. They argue that, during entrance into hibernation and daily torpor, *Glis glis* cooled at the same rate but that steady-state minimum T_b and metabolic rate were determined by the total time in dormancy. They estimated that dormice require between 30–40 h to attain minimum steady-state T_bs. Our data do not support this idea. For example, our analysis of 387 torpor bouts at $T_a = 18$ °C show that both *Elephantulus* species attained steady-state minimum body temperatures within 7 h of the onset of torpor (see Fig. 9 in Lovegrove et al. 2000).

The mean maximum rates of rewarming from torpor in both species of *Elephantulus* were 15–25% lower than those predicted by the allometric equation for daily heterotherms (Geiser and Baudinette 1990). The decrease in rewarming rates at the lowest T_as we observed has also been reported in marsupials (Geiser and Baudinette 1990). Our lower average rewarming rates were a consequence of extremely slow initial rewarming rates when T_b was ca. <10 °C. However, the rewarming rate increased dramatically once T_b had been elevated above ca. 15 °C. Nevertheless, despite a slightly lower-than-expected average rewarming rate, our data illustrate a capacity for thermogenesis in *Elephantulus* at body temperatures ranging from 5–25 °C that is more typical of hibernators than daily heterotherms.

On the other hand, the range of torpor bout lengths of both *Elephantulus* species fall comfortably within the range of 1.5–22 h characteristic of daily heterotherms (Geiser and Ruf 1995). Although much of the physiological evidence presented thus far would argue that the two *Elephantulus* species may be hibernators, current bout length data do not support this because torpor bouts lengths longer than 24 h have yet to be recorded in these species. Bouts longer than 24 h were lacking in this study, in which we recorded a total of 57 torpor bouts, as well as in a second study in which T_b was measured in these same animals continuously for three months (Lovegrove et al. 2000). In this latter study, a total of 315 torpor bouts were recorded in both species at $T_a = 18$ °C under short photoperiods (8:16 L:D) and most were induced by food reduction. On the other hand, we cannot be certain that the four animals which we "rescued" from hypothermia may not have continued to complete a normal self-arousal after more than 24 h.

One factor that may have prevented our animals from maintaining torpor bouts longer than 24-h in their cages was the regular feeding regime. We opted to feed the animals at a time of the day (1–2 h prior to the scotophase) that we predicted would have the lowest probability of disturbing torpid animals. Thus animals could have become entrained to these feeding times which could, theoretically, influence torpor bout length.

The lack of long torpor bouts in *Elephantulus* is an important observation, because bout length is the physiological parameter that best differentiates hibernation from daily heterothermy – there is no quantitative overlap between these two hypothermic states (Geiser and Ruf 1995). However, behavioural, physiological and ecological data for *Elephantulus* lend poor support for typical hibernation.

First, no species of *Elephantulus* is known to build or use insulated nests either in captivity or in the wild. For example, during a 3-year study in Kenya on free-ranging *Elephantulus rufescens*, the animals never once used a burrow or nest for shelter and sleeping (Rathbun 1979). Their resting places consisted merely of a leafy, shallow scraping under a low thorn bush. Moreover, in six species of elephant shrews we have kept in captivity at various times, none showed any inclination towards nest building even when provided with nesting material. Hence, although the significance of nest-building behaviour remains speculative, we would tend to argue that the lack of nest-building behaviour is rare among small hibernators, and indeed in daily heterotherms as well.

Second, free-ranging *E. myurus*, at least, showed no seasonal changes in body mass (Woodall 1987). Generally, hibernators that store fat increase body mass in autumn prior to the hibernation season (Lyman et al. 1982; Heldmaier 1989). Hibernators that do not store fat may alternatively hoard food (Lyman et al. 1982), but we can find no evidence that any species of elephant shrew hoards food.

Third, all species of *Elephantulus* tend to occur in semi-arid and arid habitats, and in Africa arid-adapted hibernators are rare. The only semi-arid, small mammal hibernator (spectacled dormouse *Graphiurus ocularis*; bout lengths of ca. 2 weeks) of which we are aware is a montane species that may spend several months beneath a snow cover (B.G. Lovegrove, personal observation).

Last, there is no evidence of seasonal disappearance of elephant shrews. *E. myurus* were trapped in every month of the year for 18 consecutive months (Du Toit 1993). Low trapping success, i.e. temporary disappearance, was associated with local adverse weather (rain and wind), but not necessarily with seasonal climatic patterns (Du Toit 1993).

Although these data suggest that *Elephantulus* are unlikely to be typical seasonal hibernators, they do not rule out the likelihood of opportunistic, aseasonal hibernation. In other words we are not discounting the possibility of prolonged torpor for periods longer than 24 h in free-ranging *Elephantulus*. In the laboratory, the ability for aseasonal (summer), prolonged torpor, generally termed aestivation (Schmidt-Nielsen 1983), has been demonstrated in the Palearctic dormouse *Glis glis* (Wilz 1998), and the Australasian eastern pygmy possum *Cercartetus nanus* (G. Körtner, personal communication).

Sometimes animals that are thought to lack the capacity for heterothermy in the laboratory employ daily torpor or hibernation in the wild under the appropriate environmental conditions. For example, the lack of daily torpor has been reported for captive tawny frogmouths, *Podargus strigoides* (McNab and Bonaccorso 1995; Bech and Nicol 1999), yet data from implanted telemeters in free-ranging birds show clear evidence of daily torpor (Körtner et al. 2000).

Our data for *Elephantulus* thus strongly emphasize the urgent need to measure heterothermy in free-ranging animals. These data are vital because they should resolve the problem of whether or not elephant shrews stay torpid for longer than 24 h. For the present, though, we must accept that bout length may not be the only parameter in which no quantitative overlap occurs between daily heterotherms and hibernators. Thus we must also accept that, similar to the dormouse *Glis glis* (Wilz and Heldmaier 2000), a clear physiological distinction between hibernation and daily torpor is currently not possible for elephant shrews.

Comments on the energetics of torpor

Despite the fact that elephant shrews were able to lower their torpor T_bs to ca. 5 °C, in terms of energetic savings, the coldest T_as were not necessarily the most cost-effective in both species. In *E. rozeti*, the most cost-effective T_a for torpor in terms of the total energy expenditure of the bout was ca. 14 °C, closer to the average minimum torpor of ca. 17 °C for all daily heterotherms (Geiser and Ruf 1995). Moreover, although the cost of torpor maintenance in this species generally decreased with decreasing T_a, thermogenesis with respect to the torpor set-point T_b at the lowest T_as increased maintenance costs thus reducing the cost-effectiveness of the lowest T_as. On the other hand, the lack of thermogenesis at the coldest T_as in *E. myurus* rendered these the most cost-effective T_as for daily torpor. Unfortunately, in the absence of data for free-ranging animals, it is not possible to evaluate the significance of these data.

Acknowledgements We thank Gerhard Körtner, University of New England, Armidale, Australia, for his helpful comments on the draft manuscript. This study was financed by an FRD core-rolling grant and a University of Natal Research Grant to BGL and MRP. All research procedures reported here were evaluated by the University of Natal Ethics Committee and were conducted under the rules and regulations of The University of Natal Code of Animal Ethics.

References

Barnes B (1989) Freeze avoidance in a mammal: body temperatures below 0 °C in an Arctic hibernator. Science 244: 1593–1595

Bech C, Nicol SC (1999) Thermoregulation and ventilation in the tawny frogmouth, *Podargus strigoides*: a low-metabolic avian species. Aust J Zool 47: 143–153

Bennett NC, Spinks AC (1995) Thermoregulation and metabolism in the Cape golden mole (Insectivora: *Chrysochloris asiatica*). J Zool (Lond) 236: 521–529

Du Toit JS (1993) Ecophysiology and host status of the rock elephant shrew, *Elephantulus myurus* (Thomas and Schwann 1906). MSc Dissertation, University of the Orange Free State, South Africa

Fielden LJ, Waggoner JP, Perrin MR, Hickmann GC (1990) Thermoregulation in the Namib Desert Golden Mole, *Eremitalpa granti namibensis* (Chrysochloridae). J Arid Environ 18: 221–237

Geiser F (1998) Evolution of daily torpor and hibernation in birds and mammals: importance of body size. Clin Exp Pharmacol Physiol 25: 736–740

Geiser F, Baudinette RV (1990) The relationship between body mass and rate of rewarming from hibernation and daily torpor in mammals. J Exp Biol 151: 349–359

Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiol Zool 68: 935–966

Heldmaier G (1989) Seasonal acclimatization of energy requirements in mammals: functional significance of body weight control, hypothermia, torpor and hibernation. In: Wieser W, Gnaiger E (eds) Energy transformations in cells and organisms. Thieme, Stuttgart, pp 130–139

Körtner G, Brigham RM, Geiser F (2000) Winter torpor in a large bird. Nature 407: 318

Kuyper MA (1979) A biological study of the golden mole *Amblysomus hottentotus*. MSc dissertation, University of Natal, Durban

Leon B, Shkolnik A, Shkolnik T (1983) Temperature regulation and water metabolism in the elephant shrew *Elephantulus edwardi*. Comp Biochem Physiol A 74: 399–407

Lovegrove BG, Lawes MJ, Roxburgh L (1999) Confirmation of pleisiomorphic daily torpor in mammals: the round-eared elephant shrew *Macroscelides proboscideus* (Macroscelidea). J Comp Physiol B 169: 453–460

Lovegrove BG, Raman J, Perrin MP (2000) Daily torpor in elephant shrews (Macroscelidea: *Elephantulus* spp.) in response to food deprivation. J Comp Physiol B 171: 11–21

Lyman CP, Willis JS, Malan A, Wang LC-H (1982) Hibernation and torpor in mammals and birds. Academic Press, New York

McKechnie AE, Lovegrove BG (1999) Circadian metabolic responses to food deprivation in the black-shouldered kite. Condor 101: 426–432

McNab BK, Bonaccorso FJ (1995) The energetics of Australasian swifts, frogmouths, and nightjars. Physiol Zool 68: 245–261

Porter CA, Goodman M, Stanhope MJ (1996) Evidence on mammalian phylogeny from sequences of Exon 28 of the von Willebrand Factor Gene. Mol Phylogenet Evol 5: 89–101

Rathbun GB (1979) The social structure and ecology of elephant-shrews. Paul Parey, Berlin

Schmidt-Nielsen K (1983) Animal physiology: adaptation and environment. Cambridge University Press, Cambridge

Seguignes M (1983) La torpeur chez *Elephantulus rozeti* (Insectivora: Macroscelididae). Mammalia 47: 87–91

Springer MS, Cleven GC, Madsen O, Jong de WW, Waddell VG, Amrine HM, Stanhope MJ (1997) Endemic African mammals shake the phylogenetic tree. Nature 388: 61–64

Stanhope MJ, Smith MR, Waddell VG, Porter CA, Shivji MS, Goodman M (1996) Mammalian evolution and the interphotoreceptor retinoid binding protein (IRBP) gene: evidence for several superordinal clades. J Mol Evol 43: 83–92

Wilz M (1998) Hibernation, Aestivation und täglicher Torpor beim Siebenschläfer (*Glis glis*, L.). PhD dissertation, Philipps University, Marburg

Wilz M, Heldmaier G (2000) Comparison of hibernation, estivation and daily torpor in the edible dormouse, *Glis glis*. J Comp Physiol B 170: 511–521

Withers PC (1977) Measurement of VO_2, VCO_2, and evaporative water loss with a flow-through mask. J Appl Physiol 42: 120–123

Withers PC, Richardson KC, Wooller RD (1990) Metabolic physiology of euthermic and torpid honey possums, *Tarsipes rostratus*. Aust J Zool 37: 685–693

Woodall PF (1987) Digestive tract dimensions and body mass of elephant shrews (Macroscelidae) and the effects of seasons and habitat. Mammalia 51: 537–545

Yeager DP, Ultsch GR (1989) Physiological regulation and conformation: a BASIC program for the determination of critical points. Physiol Zool 62: 888–907