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## Does torpor of elephant shrews differ from that of other heterothermic mammals?

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Torpor bouts of elephant shrews are intermediate in duration to those of daily heterotherms and hibernating mammals, but their body temperatures ( $T_b$ s) and metabolic rates are very low and similar to those of hibernating mammals. We quantified the thermal physiology of the Cape rock elephant shrew (*Elephantulus edwardii*), a species endemic to high-altitude regions of South Africa, where winters are cold and wet, and tested whether it displays multiday torpor characteristic of hibernators at low ambient temperature ( $T_a$ ). *E. edwardii* regularly displayed torpor over a wide range of  $T_a$ s. Occurrence of torpor and duration of torpor bouts increased with decreasing  $T_a$ . Whereas normothermic  $T_b$  was stable,  $T_b$  in torpid individuals fell with  $T_a$ . The mean  $T_b - T_a$  differential at the minimum  $T_b$  was  $0.7^\circ\text{C}$ , and the mean minimum  $T_b$  at  $T_a 8.9^\circ\text{C}$  was  $9.3^\circ\text{C}$ . Duration of torpor bouts ranged from 6.5 to 44 h and was correlated negatively with  $T_a$  and  $T_b$  during torpor. Time required for the reduction of  $T_b$  to a  $T_b - T_a$  differential of  $<2.0^\circ\text{C}$  was faster for  $>1$ -day torpor bouts than those lasting  $\leq 1$  day, suggesting that the duration of a bout might be determined at the beginning, not during, a bout. The nature of heterothermy in *E. edwardii* seems qualitatively similar to that of other elephant shrews, although torpor is somewhat deeper and longer in this species. Temporal patterns of torpor in *E. edwardii* differ from those of most cold-climate hibernators, likely for ecological rather than physiological reasons.

Key words: body temperature, cooling and rewarming rates, Macroscelidea, torpor occurrence and duration

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Torpor is used by diverse mammals belonging to  $>50\%$  of all mammalian orders. Because torpor is characterized by pronounced reductions in body temperature ( $T_b$ ) and metabolic rate, it is the most effective strategy for energy conservation available to mammals (Boyer and Barnes 1999; Geiser 2004; Merritt 2010). In contrast to homeothermic mammals, which are incapable of using torpor, species using torpor are often referred to as heterotherms, and most of these appear to belong to 2 distinct groups, the hibernators—species capable of employing prolonged, multiday torpor—and the daily heterotherms—species capable of daily torpor usually lasting only part of a day (Geiser and Ruf 1995).

Hibernation in many species consists of a sequence of multiday torpor bouts (often 1–3 weeks) interrupted by periodic rewarming and brief (hours) normothermic periods when high  $T_b$ s are maintained. Hibernation often is seasonal, usually lasts from late summer–autumn to late winter–spring, and occurs especially, but not exclusively, at low ambient temperature ( $T_a$ ). The duration of torpor bouts generally increases with decreasing  $T_a$  over a wide range of  $T_a$ s, and

although torpor bouts can last for weeks at low  $T_a$ , at high  $T_a$  they can last only for hours and superficially might appear to be daily torpor (Geiser and Brigham 2000; Song et al. 1997). Torpid hibernators have extremely low  $T_b$  (often between  $0^\circ\text{C}$  and  $10^\circ\text{C}$ ), metabolic rates, and  $T_b - T_a$  differentials, which might explain why they are capable of multiday torpor bouts and does explain why they can survive for months on stored body fat (Bieber and Ruf 2009; Boyer and Barnes 1999; Song et al. 1997).

Daily heterotherms, in contrast to hibernators, are incapable of multiday torpor bouts. Daily torpor lasts only for hours and usually, but not always (Körtner and Geiser 2009), requires daily foraging and feeding (Geiser and Ruf 1995; McKechnie and Lovegrove 2002). Because during daily torpor  $T_b$ , metabolism, and the  $T_b - T_a$  differentials generally are substantially higher than in hibernators, daily heterotherms

have relatively higher energy requirements during torpor and apparently require regular uptake of food to maintain a balanced energy budget.

Whereas most variables in relation to torpor examined statistically show a strong bimodal distribution and place heterothermic mammals into 1 of these 2 groups, a few species apparently do not fit these general patterns. For example, some species of elephant shrews (Macroscelidea) show low  $T_b$  and metabolic rates similar to those of torpid hibernators (Lovegrove et al. 2001). However, their torpor bouts tend to be short and usually last for 8–10 h, with a maximum of 20.3 h in the laboratory and 39 h in the field (Lovegrove et al. 2001; Mzilikazi and Lovegrove 2004, 2005; Mzilikazi et al. 2002). Nevertheless, quantitative data on duration of torpor bouts as a function of  $T_a$  in elephant shrews are currently limited, and torpor has not been examined under conditions that often are used to examine hibernation; that is, at  $T_a < 10^\circ\text{C}$  when food is withheld.

The purpose of our study was to investigate whether torpor is expressed in the Cape rock elephant shrew (*Elephantulus edwardii*), which is endemic to South Africa. The species is restricted to relatively high altitudes but has not been shown to undergo torpor (Leon et al. 1983). If *E. edwardii* proved to be heterothermic, we were interested in quantifying how duration of torpor bouts is related to  $T_a$ . The duration of torpor bouts is affected strongly by  $T_a$  in other species (French 1985; Geiser and Kenagy 1988), and exposure to low  $T_a$  should reveal whether the species is capable of multiday torpor. *E. edwardii* seems to be particularly interesting in this regard because it lives in an area that experiences semiarid conditions for about half the year and especially during hot summers, whereas in winter it is exposed to cold and wet and occasionally snow. Because *E. edwardii* lives in a winter rainfall area, it is unlikely that it regularly uses exogenous heat uptake (basking) in winter, as does, for example, *E. myurus* from a summer rainfall area in which torpor bouts seem to be terminated by basking in the sun (Mzilikazi et al. 2002).

## MATERIALS AND METHODS

Rock elephant shrews (*E. edwardii*; 4 females and 3 males), were trapped at an altitude of approximately 700 m at Gamkaberg Nature Reserve (33°38'S, 21°59'E) near Oudtshoorn, South Africa, a winter rainfall area with mean annual precipitation of approximately 400 mm. The prevailing photoperiod in midwinter (July) is close to 10L:14D (sunrise at 0730 h and sunset at 1745 h), and the average minimum and maximum  $T_a$  are 9°C and 21°C, respectively (Gamkaberg Nature Reserve records). Animals were captured from 4 to 10 June 2008 (austral winter) in Sherman box traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) baited with peanut butter and rolled oats and checked in the early morning after 1 night of trapping. Animals were transferred to the Zoology Department, Nelson Mandela Metropolitan University, Port Elizabeth, where they were held individually in large terraria provided with wood shavings and nest boxes in a constant

temperature room at  $T_a$  20°C. Initially, animals were fed daily ad libitum, alternating between a mixture of ProNutro (Bokomo, South Africa) soaked in water (18% ProNutro powder, consisting of 22% protein, 59% carbohydrate, and 6% fat, soaked in 82% water) or canned dog food; water was provided ad libitum. To provide a continuous record of  $T_b$  temperature data loggers (iButtons DS 1922L, resolution 0.06°C; Maxim, Sunnyvale, California) were calibrated to the nearest 0.1°C, programmed to read  $T_b$  every 30 min, waxed (mass 3.3 g including wax), sterilized, and implanted intraperitoneally under sterile conditions. Oxygen-isoflurane was used for anesthesia. After surgery on 13 June animals were kept in a precisely controlled constant temperature room at  $T_a$  24.8°C ± 0.1°C for recovery for 4 days, which continued at 18.4°C because this  $T_a$  represents only a mild cold load. To mimic autumnal cooling  $T_a$  was reduced stepwise: on 17 June to  $T_a$  18.4°C ± 0.1°C, on 24 June to 15.4°C ± 0.1°C, on 1 July to 12.2°C ± 0.1°C, on 8 July to 8.9°C ± 0.1°C, and on 29 July to 18.4°C ± 0.1°C for the remainder of the measurements. We quantified  $T_b$  as a function of  $T_a$  in this experiment because our main aim was to determine whether the species can express multiday torpor, and this approach required only limited disturbance and handling. Metabolic measurements would have required frequent disturbance or handling, or both, which would have interfered with our aim and was unnecessary because it is well established that  $T_b$  and metabolic rate in thermo-conforming torpid mammals are closely correlated (Geiser 2004; Song et al. 1997).  $T_a$  was recorded in the constant temperature room with an iButton (DS 1922L) at 30-min intervals. Most animals ( $n = 6$ ) thrived in captivity, but 1 female, the lightest individual at capture, died after 2 weeks in captivity.

Food was provided ad libitum daily until 9 July ( $T_a$  8.9°C); from that date animals were fed every 2nd day to ensure torpid individuals were not disturbed daily and aroused prematurely from a torpor bout. At the end of measurements iButtons were removed under general anesthesia, as described above. Because 2 of the iButtons failed, data are reported for 4 individuals (2 females and 2 males).

Animals were considered torpid when their  $T_b$  fell below 30°C (see “Results”), and duration of torpor bouts was calculated from the time  $T_b$  remained below 30°C. Times of entries and arousals from torpor were examined by a Rayleigh test ( $Z$ ; Zar 1999) to determine whether times differed significantly from a random distribution. Maximum entry and arousal rates were calculated for the 30 min for which the most pronounced change of  $T_b$  was measured. To examine whether physiological variables are interrelated or related to  $T_a$ , linear regressions, fitted by the method of least squares, were used; residuals were examined for homoscedasticity. To test for differences between mean values of variables  $t$ -tests were used; the Kolmogorov-Smirnov test was used to test for normality. Statistical analyses were accomplished using StatistiXL (version 1.8; statistiXL, Nedlands, Western Australia, Australia). Numeric values are given as means ± 1 SD.

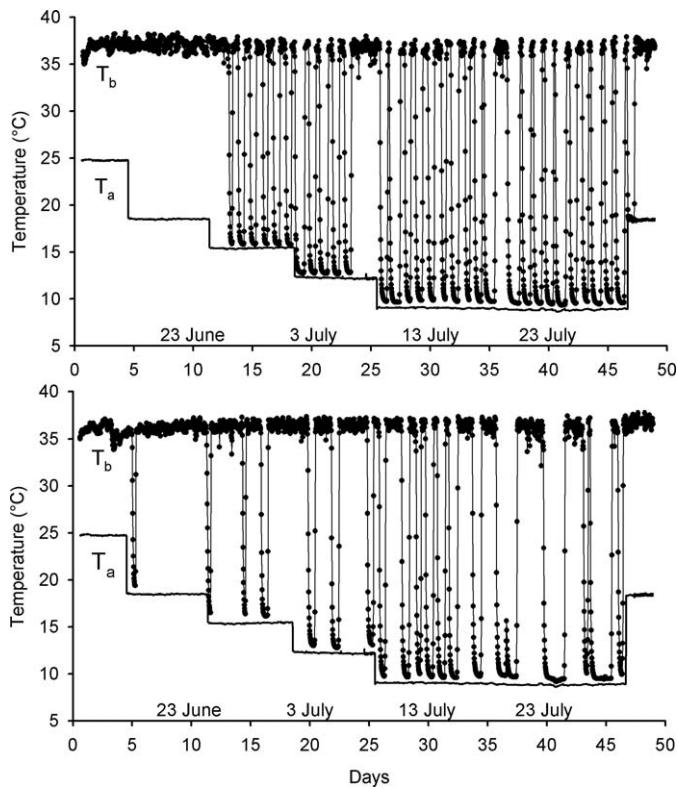


FIG. 1.—Body temperature ( $T_b$ ) fluctuations of 2 *Elephantulus edwardii* (top, male; bottom, female) exposed to different ambient temperatures ( $T_a$ ) as a function of time. Each point represents an individual reading of  $T_b$ .

Permits for animal experimentation were provided by the Animal Ethics Committee of the University of New England, the Nelson Mandela Metropolitan University, and the Cape Nature Conservation Board. Experimentation followed the guidelines of the American Society of Mammalogists (Gannon et al. 2007).

## RESULTS

Body mass of the 4 elephant shrews was  $47.5 \pm 4.7$  g before surgery when animals were fed ad libitum. One week after surgery body mass (without iButtons) had declined to  $41.9 \pm 4.2$  g; however, body mass over the next 2 weeks increased again to  $45.4 \pm 2.9$  g. When food was provided only every 2nd day at  $T_a$  8.9°C, body mass again declined to  $41.8 \pm 1.9$  g.

Elephant shrews frequently displayed torpor in the laboratory at  $T_a$ s of  $<24.8^\circ\text{C}$  (Fig. 1). Torpor was observed occasionally at  $T_a$  18.4°C, even though food was freely available, but torpor use increased with decreasing  $T_a$ . Although at  $T_a$  18.4°C and 15.4°C only 2 or 3 individuals used torpor, at  $T_a$  12.2°C and 8.9°C all 4 individuals expressed torpor. Occurrence of torpor (days torpid/days measured) was 32% at  $T_a$  15.4°C, 39% at 12.2°C, and 95% at 8.9°C. At  $T_a$  8.9°C, when food was withheld on every 2nd day, no difference in torpor use was observed between days with and without food because torpor occurred on almost all days. Torpor occurrence also did not appear to differ between sexes;

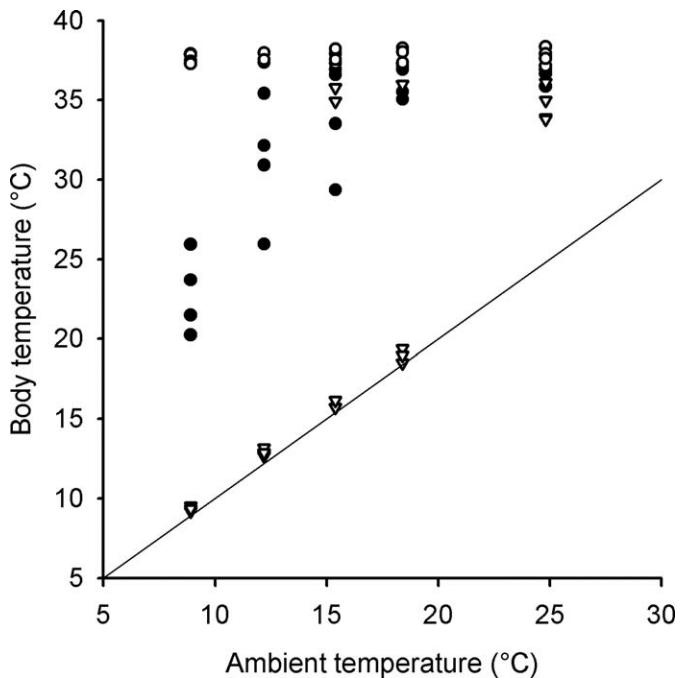


FIG. 2.—Body temperature ( $T_b$ ) as a function of ambient temperature ( $T_a$ ) in 4 *Elephantulus edwardii*. Maximum  $T_b$  (circles), mean  $T_b$  (dots), and minimum  $T_b$  (triangles) are shown. Each point represents the mean for an individual, and the diagonal line represents  $T_b = T_a$ .

females displayed a total of  $15.5 \pm 4.9$  bouts, males  $20.5 \pm 16.3$  bouts.

Torpor patterns were affected strongly by  $T_a$  (Fig. 1). Torpor bouts lasting for  $<24$  h were observed at all  $T_a$ s  $< 24.8^\circ\text{C}$ , but those lasting  $>24$  h were observed only at  $T_a$  8.9°C, the lowest  $T_a$  measured.

The maximum  $T_b$  during the active phase was not affected by  $T_a$  ( $r^2 = 0.01$ ,  $F_{1,18} = 0.18$ ,  $P = 0.676$ ) and was  $37.7^\circ\text{C} \pm 0.5^\circ\text{C}$  at  $T_a$  24.8°C and  $37.6^\circ\text{C} \pm 0.3^\circ\text{C}$  ( $n = 4$ ) at  $T_a$  8.9°C (Fig. 2). However, mean  $T_b$  declined significantly ( $y = 19.5 + 0.793x$ ,  $r^2 = 0.61$ ,  $F_{1,18} = 27.70$ ,  $P < 0.0001$ ) from  $36.6^\circ\text{C} \pm 0.5^\circ\text{C}$  at  $T_a$  24.8°C to  $22.8^\circ\text{C} \pm 2.5^\circ\text{C}$  at  $T_a$  8.9°C. The minimum  $T_b$  of torpid individuals also changed with  $T_a$  ( $y = -4.28 + 1.60x$ ,  $r^2 = 0.67$ ,  $F_{1,18} = 36.16$ ,  $P < 0.0001$ ) and fell close to  $T_a$  over the entire  $T_a$  range torpor was observed (Figs. 1 and 2). The mean minimum  $T_b$  at  $T_a$  8.9°C was  $9.3^\circ\text{C} \pm 0.1^\circ\text{C}$  ( $n = 4$ ), and the individual minimum  $T_b$  was  $9.2^\circ\text{C}$ . The  $T_b - T_a$  differential when  $T_b$  was minimal ranged between  $0.2^\circ\text{C}$  and  $1.2^\circ\text{C}$ , and the mean was  $0.7^\circ\text{C} \pm 0.2^\circ\text{C}$ . Over the  $T_a$  range from 18.4°C to 12.2°C the  $T_b - T_a$  differential was not affected by  $T_a$  ( $r^2 = 0.03$ ,  $F_{1,21} = 0.64$ ,  $P = 0.434$ ). However, when  $T_b - T_a$  differentials at  $T_a$  8.9°C were included in the linear regression, a weak but significant relationship was observed ( $T_b - T_a$  [°C] =  $1.03 - 0.029T_a$  [°C];  $r^2 = 0.13$ ,  $F_{1,70} = 10.74$ ,  $P = 0.002$ ), suggesting that at the lowest  $T_a$  measured the  $T_b - T_a$  differential was raised somewhat, perhaps from thermoregulation. Similarly, the relationship between duration of torpor bout and the  $T_b - T_a$  differential was not significant ( $r^2 = 0.04$ ,  $F_{1,70} = 2.63$ ,  $P$

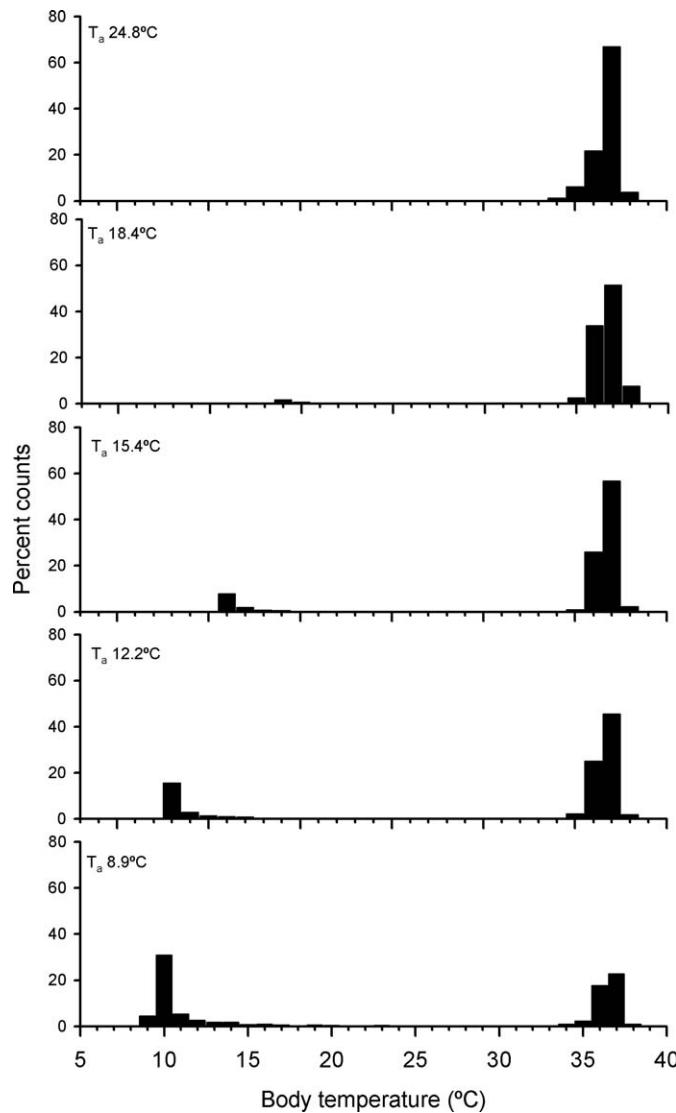


FIG. 3.—Frequency distribution of percent body temperature ( $T_b$ ) integers of 4 *Elephantulus edwardii* at the 5 ambient temperatures ( $T_a$ ) measured.

$= 0.11$ ) when all bouts over the entire  $T_a$  range where torpor was observed were regressed. However, when only bouts of  $<20$  h duration were regressed, the  $T_b - T_a$  differential was correlated negatively with torpor bout duration ( $T_b - T_a [^{\circ}\text{C}] = 1.37 - 0.39$  bout duration [h];  $r^2 = 0.35$ ,  $F_{1,39} = 22.50$ ,  $P < 0.001$ ). This regression intersected the mean  $T_b - T_a$  differential of  $0.7^{\circ}\text{C}$  at 17 h, suggesting that this bout duration is required for the species to reach its steady-state minimum  $T_b$ .

Although the mean maximum  $T_b$  was not affected significantly by  $T_a$ , the frequency distribution of integers of normothermic  $T_b$  changed with  $T_a$  (Fig. 3). Whereas  $T_b$   $36^{\circ}\text{C}$  and  $37^{\circ}\text{C}$  encompassed 21.7% and 67% of all  $T_b$ s measured at  $T_a$   $24.8^{\circ}\text{C}$ , these proportions changed and declined with decreasing  $T_a$ , and at  $T_a$   $8.9^{\circ}\text{C}$   $T_b$   $36^{\circ}\text{C}$  and  $37^{\circ}\text{C}$  made up only 17.7% and 22.8% of all  $T_b$ s, respectively. In contrast, the proportion of  $T_b$ s below  $20^{\circ}\text{C}$  increased with decreasing  $T_a$ ,

and at  $T_a$   $8.9^{\circ}\text{C}$   $T_b$   $10^{\circ}\text{C}$  represented the largest proportion (31%) of all  $T_b$ s measured.  $T_b$ s between  $33^{\circ}\text{C}$  and  $20^{\circ}\text{C}$  were represented by  $<0.6\%$  of all  $T_b$ s measured at the  $T_a$ s where torpor was observed.  $T_b$   $30^{\circ}\text{C}$  was represented on average over all  $T_a$ s by only 0.13% of  $T_b$ s measured; therefore it was the most transient of  $T_b$ s measured between normothermia and torpor and consequently seems most suitable as the threshold  $T_b$  for defining torpor in this species. Nevertheless, the other  $T_b$ s—for example,  $31$ – $33^{\circ}\text{C}$ —frequently used for defining  $T_b$  thresholds for torpor (Barclay et al. 2001; Willis and Brigham 2003) also were rarely observed (0.15–0.2% of all  $T_b$ s). Thus, any of these  $T_b$ s ( $30$ – $33^{\circ}\text{C}$ ) could be used safely for defining torpor without having any significant effect on other derived variables relying on a threshold  $T_b$ .

Torpor bouts lasted between 6.5 and 44 h, and the mean bout duration was  $17.3 \pm 8.3$  h. Overall, 9 of the total 72 torpor bouts observed lasted for  $>1$  day and were observed in 3 individuals (1 female and 2 males); the mean duration of these bouts was  $35.6 \pm 8.4$  h. The mean maximum duration of torpor bout for the 4 individuals was  $32.4 \pm 12.5$  h. Of the  $>1$ -day torpor bouts, those bouts that lasted for  $>40$  h (5 bouts in 1 female and 1 male) began on days no food was provided, but arousals also occurred on days when no food was provided. For  $>1$ -day bouts lasting  $<30$  h (4 bouts in 2 males) entry into torpor occurred on days food was provided, but all animals also aroused on days they were not fed, suggesting that all arousals from  $>1$ -day bouts were not caused by disturbance.

Torpor bout duration at  $T_a$   $18.4^{\circ}\text{C}$  and  $15.4^{\circ}\text{C}$  did not differ significantly ( $t_{10} = 0.51$ ;  $P > 0.66$ ); however, the duration of all torpor bouts was correlated negatively ( $r^2 = 0.15$ ,  $F_{1,67} = 11.81$ ,  $P = 0.001$ ) with  $T_a$  between  $15.4^{\circ}\text{C}$  and  $8.9^{\circ}\text{C}$ . Torpor bout duration ( $\log_{10}$ ) was strongly correlated with the minimum  $T_b$  over the entire range of  $T_a$ s measured ( $r^2 = 0.27$ ,  $F_{1,70} = 14.87$ ,  $P < 0.0001$ ; Fig. 4). At each separate  $T_a$  torpor bout duration and minimum  $T_b$  were correlated only at  $T_a$   $8.9^{\circ}\text{C}$  ( $r^2 = 0.17$ ,  $F_{1,47} = 9.49$ ,  $P = 0.003$ ) and  $T_a$   $12.2^{\circ}\text{C}$  ( $r^2 = 0.41$ ,  $F_{1,9} = 6.23$ ,  $P = 0.034$ ), but not correlated ( $T_a$   $15.4^{\circ}\text{C}$ :  $r^2 = 0.28$ ,  $F_{1,7} = 2.77$ ,  $P = 0.14$ ;  $T_a$   $18.4^{\circ}\text{C}$ :  $r^2 = 0.80$ ,  $F_{1,1} = 4.05$ ,  $P = 0.29$ ) at the other  $T_a$ s, likely because of the limited data. However, mean  $T_b$  during a torpor bout and duration of torpor bout at each of the 3 low  $T_a$ s examined showed strong negative linear relationships ( $r^2 \geq 0.57$ ,  $P < 0.01$ ) when plotted on logarithmic scales (Fig. 5).

Both torpor entries and arousals were nonrandom and occurred at specific times of day (entries:  $Z = 32.78$ ,  $P < 0.001$ ; arousals:  $Z = 52.77$ ,  $P < 0.001$ ; Fig. 6). Entry into torpor occurred at a mean angle of  $279.1^{\circ} \pm 50.8^{\circ}$  or  $1836 \pm 0323$  h (Rayleigh test), whereas arousals occurred at a mean angle of  $161.1^{\circ} \pm 31.9^{\circ}$  or  $1044 \pm 0207$  h. Although the mean time of torpor entry at  $T_a$   $8.9^{\circ}\text{C}$  between torpor bouts lasting  $<1$  day (entry time  $1840 \pm 0312$  h) and torpor bouts lasting  $>1$  day (entry time  $1530 \pm 0249$  h) was indistinguishable (95% confidence intervals [95% CIs] overlapped), in the 3 individuals that employed  $>1$ -day bouts the time of arousal differed significantly by about 3 h (<1 day:  $1029 \pm 0135$  h;

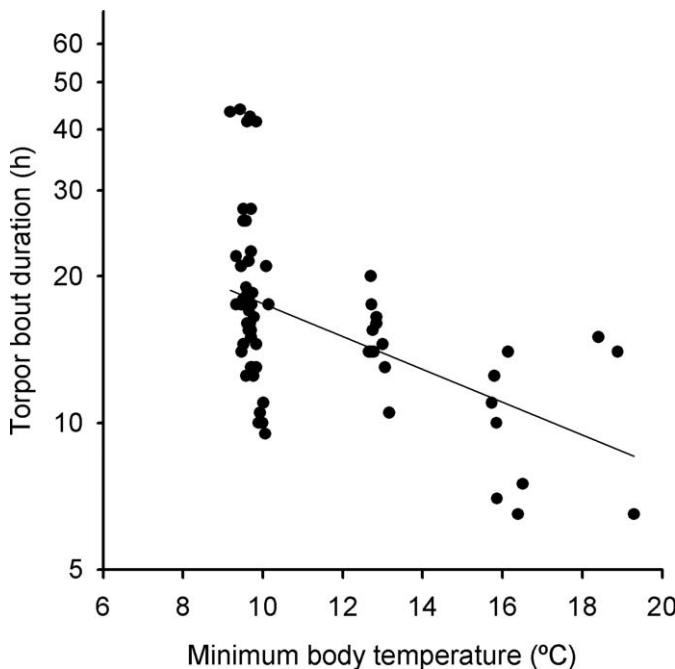


FIG. 4.—The duration of torpor bouts as a function of the minimum body temperature ( $T_b$ ) during a torpor bout in 4 *Elephantulus edwardii*. The regression equation was:  $\log_{10}y = 1.58 - 0.00337x$ ;  $r^2 = 0.27$ ,  $F_{1,70} = 14.87$ ,  $P < 0.0001$ .

>1 day:  $1324 \pm 0143$  h; no overlap and  $14.4^\circ$  or almost 1-h gap in 95% CI).

Maximum cooling rates during entry into torpor differed ( $T_a$   $15.4^\circ\text{C}$ :  $t_4 = 3.02$ ,  $P = 0.039$ ;  $T_a$   $12.2^\circ\text{C}$ :  $t_6 = 8.25$ ,  $P < 0.0001$ ;  $T_a$   $8.9^\circ\text{C}$ :  $t_6 = 6.54$ ,  $P = 0.001$ ) from maximum rewarming rates at all  $T_a$ s, with the exception of  $T_a$   $18.4^\circ\text{C}$ , where only limited data were available. Moreover, the overall individual means for maximum torpor entry rates at all  $T_a$ s ( $0.26 \pm 0.015^\circ\text{C}/\text{min}$ ) differed ( $t_6 = 5.14$ ,  $P < 0.01$ ) from the overall maximum rewarming rates ( $0.38 \pm 0.035^\circ\text{C}/\text{min}$ ). Further, the time required to reduce the  $T_b - T_a$  differential to  $<2.0^\circ\text{C}$  was significantly ( $t_4 = 2.65$ ,  $P < 0.05$ ) less for >1-day than <1-day bouts by  $38 \pm 4$  min in the 2 individuals that displayed multiple >1-day torpor bouts.

## DISCUSSION

Our study shows that *E. edwardii*, although described as homeothermic in a previous study (Leon et al. 1983), regularly displays torpor in the laboratory both when food is available and when it is restricted. Torpor bouts lasted for up to almost 2 days, which is longer than those reported in other elephant shrews. However, multiday torpor bouts lasting for up to several weeks as characteristic of many hibernators were not observed here, although the metabolic rates during torpor had to be extremely low to allow a  $T_b$  to approach within  $0.7^\circ\text{C}$  of  $T_a$  in ~45-g *E. edwardii*.

As in many other heterothermic species, occurrence of torpor in *E. edwardii* increased with decreasing  $T_a$ . At  $T_a$   $8.9^\circ\text{C}$  occurrence of torpor was 95%, similar to many

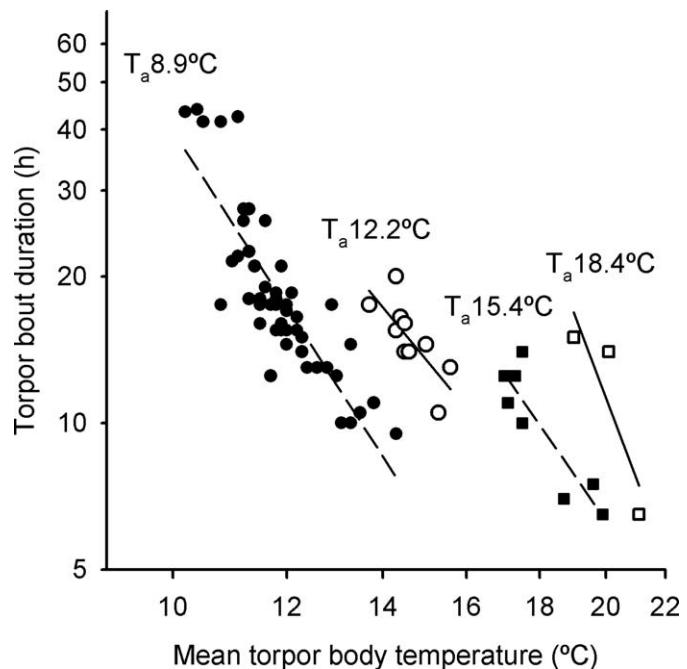


FIG. 5.—Duration of torpor bouts as a function of the mean body temperature ( $T_b$ ) during a torpor bout at different ambient temperatures ( $T_a$ ) of 4 *Elephantulus edwardii*. The regression equations were:

$$T_a 8.9^\circ\text{C} : \log_{10}y = 6.17 - 4.57 \log_{10}x; r^2 = 0.74, F_{1,47} = 133.20, P < 0.0001;$$

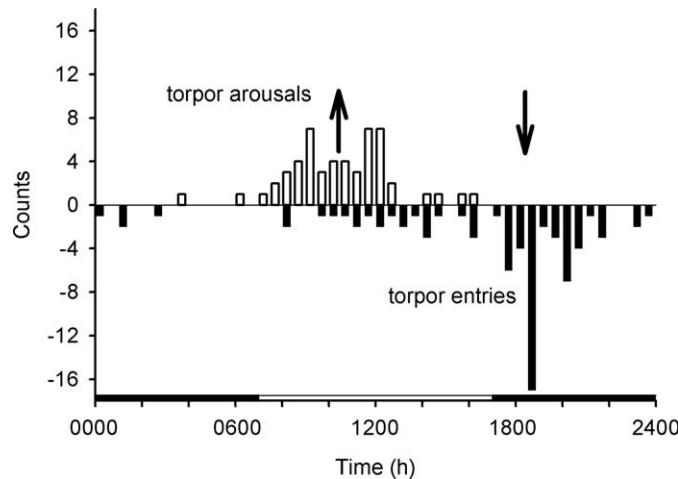
$$T_a 12.2^\circ\text{C} : \log_{10}y = 5.34 - 3.58 \log_{10}x; r^2 = 0.57, F_{1,9} = 11.77, P < 0.01;$$

$$T_a 15.4^\circ\text{C} : \log_{10}y = 6.35 - 4.27 \log_{10}x; r^2 = 0.81, F_{1,7} = 30.91, P < 0.002;$$

and

$$T_a 18.4^\circ\text{C} : \log_{10}y = 11.2 - 7.8 \log_{10}x; r^2 = 0.28, F_{1,1} = 3.49, P = 0.28.$$

hibernators and daily heterotherms in which occurrence of torpor at low  $T_a$  often approximates 100%, especially in the wild (Körtner et al. 2010; Stawski et al. 2009). Nevertheless, unlike in many hibernators, the torpor season in *E. edwardii* is not composed of a sequence of long torpor bouts interrupted by regular brief normothermic periods, but rather by frequent long or short torpor bouts that are interspersed by normothermic periods lasting from a few hours to >1 day (Fig. 1), likely in part for foraging. This pattern of torpor interspersed by activity seems appropriate for a species that lives in a region where it can forage and feed for prolonged periods (in contrast to, for example, one living in snow-covered alpine regions) and that relies on a diversity of invertebrates including ants and termites, some of which will be available all year (Lovegrove et al. 1999). Moreover, like other species of elephant shrews but unlike many hibernating species (Kenagy and Barnes 1988), *E. edwardii* does not show substantial



**FIG. 6.**—Timing of torpor entries (bottom) and arousals (top) in 4 *Elephantulus edwardii*. Arrows indicate average entry ( $\downarrow$ ) and arousal ( $\uparrow$ ) times as determined by Rayleigh tests. The bars at the bottom of the figure indicate the scotophase (dark) and photophase (light).

autumnal fattening (Mzilikazi et al. 2002). The absence of autumnal fattening should not limit multiday torpor bouts physiologically (Stawski et al. 2009), but an animal should forage regularly to ensure that limited body energy reserves are not depleted entirely.

The duration of torpor bouts of *E. edwardii* (overall mean 17.3 h, mean maximum 32.4 h, longest bout 44 h) was long for daily heterotherms measured in the laboratory (mean maximum bout duration 11.2 h) but short for hibernators (mean maximum 355 h, minimum 96 h—Geiser and Ruf 1995). The mean duration of torpor bouts of *E. edwardii* fell within the range of maximum torpor bouts in daily heterotherms, but the maximum bout duration (44 h) was 4-fold that of the mean maximum for daily heterotherms and about one-half as long as that of the shortest maximum bout (96 h) observed in hibernating species. Why does *E. edwardii*, despite its low  $T_b$  and  $T_b - T_a$  differential, not display longer torpor bouts? In several species torpor bouts are substantially longer in the field than in the laboratory (Körtner and Geiser 2009). Although this also might be possible in *E. edwardii*, it is likely that, even in the wild and in agreement with field data on other elephant shrews (Mzilikazi et al. 2002), it does not display the classic hibernation pattern of multiday bouts interspersed by brief normothermic periods for reasons related to climate, food, and fattening, as outlined above. Moreover, it is unlikely that *E. edwardii* experiences a prolonged hibernation season without foraging because we were able to trap it in winter.

Periodic rewarming from torpor has been observed in all heterothermic mammals studied to date, and although rewarming is usually energetically very costly and the reasons for its regular repetition are frequently discussed, currently no mechanism to explain its occurrence is widely recognized. Proposed explanations often infer some function that cannot

be accomplished at low  $T_b$  during torpor and requires a high  $T_b$  to be achieved (Körtner and Geiser 2000; Nemeth et al. 2010; Prendergast et al. 2002). Because, in many species duration of torpor bouts increases with decreasing  $T_a$ ,  $T_b$ , and metabolism over a wide range of  $T_a$ s (i.e., the  $T_a$  range in which torpid individuals are thermo-conforming), it is often assumed that torpor bout length is related to some metabolic process that is dependent on temperature (French 1985; Geiser and Kenagy 1988).

In our study the duration of torpor bouts was correlated with  $T_a$ , the minimum  $T_b$  during torpor, the mean  $T_b$  during torpor, and for bouts of  $<20$  h the  $T_b - T_a$  differential, supporting these interpretations to some extent. However, because low  $T_b$  is used for defining torpor and the  $T_b - T_a$  differential is at least partially a function of torpor bout duration—that is, it takes time for the body to cool—some of these apparent correlations can be based on circular reasoning. It is not surprising that the average  $T_b$ , for example, is related to torpor bout duration because the longer an animal is in torpor the lower its average  $T_b$  (and also average torpor metabolic rate) should be. However, this does not necessarily mean these variables are functionally linked. Although maximum cooling rate of *E. edwardii* did not differ, one of the significant differences between torpor bouts of  $<1$  day and those of  $>1$  day was that the time to reach a  $T_b - T_a$  differential of  $<2.0^{\circ}\text{C}$  was significantly shorter in the latter. Although this observation is based on limited data and requires verification from other species, the difference does suggest that the decision to enter a short or long torpor bout was determined at the time of entry into torpor because elephant shrews reduced  $T_b$  to near  $T_a$  faster before long bouts than before short ones. This interpretation also is supported by the observation that of the  $>1$ -day bouts,  $>40$ -h bouts began on days no food was provided, whereas  $<30$ -h bouts all began on days food was provided. This suggests that nutritional status at the beginning of a bout might be linked to its subsequent duration. This new observation in *E. edwardii* differs from previous hypotheses on determination of torpor bout duration because it suggests that the time an animal remains in torpor might be determined before or at entry into torpor, not during the event, as is usually assumed. This is especially interesting because the timing of torpor entry did not differ between short and long bouts, whereas the time of arousal did (i.e., a 3-h delay occurred on  $>1$ -day bouts).

Our study provides further evidence that many presumed homeothermic mammals are heterothermic. It emphasizes that superficial and short-term examination of thermoregulatory patterns does not necessarily reveal whether a species is able to use torpor. This is important because misclassification will result in wrong predictions about the biology and especially energy and foraging requirements of mammals in the wild. Our study adds another species to an increasing number of heterothermic mammals. Although in the past a widely held view was that torpor is rare and occurs only in a few cold-climate species, recent work has shown that torpor is employed widely in all climate zones (Dausmann 2008;

Körtner et al. 2010); for example, in Australia, some 43% of all terrestrial mammals are likely to be heterothermic (Geiser and Körtner 2010). Employment of torpor has enormous implications for increasing short-term survival because low energy and foraging requirements reduce exposure to predators (Stawski and Geiser 2010). Moreover, torpor is also important for long-term persistence of mammals that are exposed to anthropogenic destruction of habitat and introduction of competitors or predators (Geiser and Turbill 2009; Liow et al. 2009) and might help explain why *E. edwardii* is not threatened by extinction.

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