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Torpor in the Patagonian opossum (*Lestodelphys halli*): implications for the evolution of daily torpor and hibernation

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Abstract Hibernation and daily torpor are two distinct forms of torpor, and although they are related, it is not known how and in which sequence they evolved. As the pattern of torpor expressed by the oldest marsupial order the opossums (Didelphimorphia) may provide insights into the evolution of torpor, we aimed to provide the first quantitative data on the thermal biology and torpor expression of the rare Patagonian opossum (*Lestodelphys halli*). It is the opossum with the southernmost distribution, has a propensity of autumnal fattening, and therefore, is likely to hibernate. We captured two male *Lestodelphys*, which while in captivity displayed strong daily fluctuations of body temperatures (T_b) measured with implanted miniature data loggers even when they remained normothermic. In autumn and early winter, torpor was expressed occasionally when food was available, but cold exposure and food withdrawal increased torpor use. The mean T_b throughout the study was 32.2 ± 1.4 °C, the minimum T_b measured in torpid *Lestodelphys* was 7.7 °C, average torpor bout duration was 10.3 h, and the maximum torpor bout duration was 42.5 h. Thus, the pattern of torpor expressed by *Lestodelphys* was intermediate between that of daily heterotherms and hibernators suggesting that it may represent an ancestral opportunistic torpor pattern from which the derived patterns of daily torpor and seasonal hibernation diverged.

Keywords Daily torpor · Evolution · Hibernation · Mammals · Opossums

Abbreviations

T_a	Ambient temperature
T_b	Body temperature
BMR	Basal metabolic rate
TBD	Torpor bout duration

Introduction

Opossums (order Didelphimorphia) form the ancestral group of the mammalian subclass Marsupialia (Bininda-Emonds et al. 2007). They are found over much of South and Middle America, but a single species (the Virginian opossum, *Didelphis virginiana*) now extends far into North America. The other six extant marsupial orders, including those living in Australia and adjacent islands, are derived from opossum ancestors, which diversified at ca. 65–62 million years ago (Luo et al. 2003; O’Leary et al. 2013).

Because opossums are small and therefore have high energy demands during activity, some are heterothermic and use torpor for energy and water conservation (Morrison and McNab 1962; McNab 1978; Douglas and Nicol 1993; Opazo et al. 1999; Silva-Duran and Bozinovic 1999; Bozinovic et al. 2005; Ribiero and Bicudo 2007; Cooper and Geiser 2008; Cooper et al. 2009). Torpor is characterized by temporal, controlled reductions of metabolic rate and body temperature (T_b) and other physiological functions (Boyer and Barnes 1999). Interestingly, all opossum species that have been investigated to date appear to be daily heterotherms (i.e., use daily torpor exclusively) and reduce metabolism during torpor to ~20–40 % of the basal metabolic rate (BMR). The T_b in known heterothermic opossums is lowered from ~35 °C during normothermia to between ~25 and 15 °C

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during torpor, which usually was entered during the rest phase and lasted only for a few hours (Morrison and McNab 1962; Opazo et al. 1999; Silva-Duran and Bozinovic 1999; Bozinovic et al. 2005; Cooper et al. 2009), typical for other avian and mammalian daily heterotherms (Geiser and Ruf 1995).

The pattern of torpor observed in opossums clearly differs from that observed in mammalian hibernators, which can express a sequence of deep, multiday torpor bouts lasting a few days to weeks during a prolonged hibernation season and have very low T_b minima (often between 0 and 10 °C) and metabolic rates (Geiser and Ruf 1995). The only South American marsupial known to hibernate and express deep, multiday torpor bouts is the monito del monte (*Dromiciops gliroides*) from southern Chile and Argentina, the only living species of the order Microbiotheria (Martin 2010). This species can remain torpid for up to 5 days with a low T_b (<10 °C) and a metabolic rate that is only ~4 % of the BMR (Grant and Temple-Smith 1987; Bozinovic et al. 2004; Nespolo et al. 2010; Franco et al. 2012; Withers et al. 2012). Hibernation in *Dromiciops* is similar to hibernation in many placental mammals and also the pygmy possums (Burramyidae) and feathertail gliders (Acrobatidae) both belonging to the Australian marsupial order Diprotodontia (Geiser and Ruf 1995; Geiser and Körtner 2010). Thus, as in placental mammals, daily torpor and hibernation appear to be distinct expressions of torpor used by different marsupial taxa, and although the evolution of the two torpor patterns must be linked, it is not known how and in which sequence they have evolved.

The opossum with the southernmost distribution in Argentina is the rare Patagonian opossum (*Lestodelphys halli*) extending from about 34 to 50 ° south (Marshall 1977; Martin 2005). It is mainly found in extreme xeric and cold environments (Martin and Udrizar Sauthier 2011). Most of the records on the species from the field are derived from owl pellets (Martin 2005), but there is some limited information on behavior from a few live-trapped individuals (Martin and Udrizar Sauthier 2011). The species is small (about 50 g), carnivorous/insectivorous, and appears to be largely terrestrial. It fattens in autumn, and its tail becomes incrassate (Plate 1). Although it has been observed to enter torpor (Pearson 2007; Martin and Udrizar Sauthier 2011), thermal biology and variables and patterns of torpor have not been quantified. We therefore aimed to provide the first quantitative data on torpor use and patterns of torpor in the Patagonian opossum. We hypothesized that because of its distribution, diet, and seasonal fattening, the species is the most likely opossum to display deep and prolonged torpor. This knowledge is important since the type of torpor expressed by the Patagonian opossum has the potential to shed light on the evolution of daily torpor and hibernation in mammals because of the phylogenetic position of the Didelphimorphia.



Plate 1 Patagonian opossum (*Lestodelphys halli*). Head-body length 14 cm

Methods

Two male *L. halli* were captured at Nahuel Pan (42°58'21.1"S, 71°09'10.7"W) near the city of Esquel, Chubut Province (Argentina) at an elevation of 745 m in April 2011 using 92 Sherman and 75 Tomahawk traps. Permits for the work were provided by the University of New England Animal Ethics Committee and by Dirección de Fauna y Flora Silvestre, Ministerio de Industria, Agricultura y Ganadería, Provincia del Chubut, Argentina. The mean minimum and maximum ambient temperature (T_a) in Esquel is −2.9 and 6.3 °C during the coldest month (July), 7.6 and 21.0 °C during the warmest month (January), and 2.2 and 14.8 °C during the month we trapped (April). Opossum 1 (Lh1, a calm and bold individual) was captured on 7 April, opossum 2 (Lh2, a shy and timid individual) on 13 April. A total of >4,000 trap nights were required to catch the two opossums. Animals were transported to a cabin and held individually in a glass terrarium (50×20×30 cm) provided with wood shavings and a nesting box. The photoperiod in the holding room was natural, and the T_a was not controlled, but was buffered from external extremes. Animals were fed a mixture of Whiskas “Carne” and “Pollo” cat food and minced meat. Banana was offered initially, but because animals did not eat it after a few days in captivity, it was later discontinued. Food and water were provided daily ad libitum if not otherwise specified. Food offered and food consumed was weighed to the nearest 0.1 g with an electronic balance, and daily food consumption was estimated. Body mass was measured regularly to the nearest 0.1 g; testes and tail width was measured with calipers.

After animals had been in captivity for 10 days, they were surgically implanted with iButtons (DS1922L Maxim USA, programmed to read at a resolution of 0.06 °C) to measure

core T_b in 30 min intervals over time. Prior to implantation, the iButtons were waxed (Elvax, Minimitter) and calibrated to the nearest 0.2 °C in a water bath. Waxed iButtons weighed 3.7 g well below the recommended weight for transmitters or loggers implanted into small terrestrial mammals (<10 % of body mass; Rojas et al. 2010). Waxed iButtons were placed in 70 % alcohol before implantation. Surgery was conducted under general anesthesia with 4 mg Ketamine under supervision of a veterinarian. Waxed iButtons were inserted through a small abdominal incision that was sutured as described by Rojas et al. (2010). Xylocaine (10 %, AstraZeneca, North Ryde, Australia) was used for local anesthesia and Children's Panadol (Glaxo Smith Kline, Ermington Australia) was provided for 3 days post-surgery.

Animals were allowed to recover from surgery for 18 days in the holding room. Feeding and experimental procedures were altered thereafter to induce torpor. This included exposure to low T_a in a controlled temperature cabinet for several days and withdrawal of food. Animals were weighed after several days of food withdrawal (1 to 6 days) at low T_a (~7 to 10 °C) to ensure they would not run out of energy. To not prematurely disrupt prolonged torpor bouts during times of cold exposure and food withdrawal, animals were weighed when they were normothermic. Body mass remained well above capture mass throughout measurements (Fig. 1). The T_a was also measured at 30 min intervals with calibrated iButtons in each animal cage throughout the time of measurements. Continuous data on T_b and time were obtained over 68 days (Lh1) and 57 days (Lh2), after which measurements were discontinued.

Numerical values are reported as means \pm 1 SD, N =number of measurements. Torpor was defined as times with $T_b < 30.0$ °C (Körtner and Geiser 2000). T_b measurement were used to obtain mean and extreme T_b s in normothermic and torpid animals, torpor bout duration (TBD), and maximum cooling and rewarming rates over 30 min in torpor bouts lasting >1 h. Differences between means were tested using t tests. Regressions were fitted by the least squares method. Analysis of covariance (ANCOVA) was used to compare slopes and intercepts of regressions. The Q_{10} values for torpor bout duration were calculated as $Q_{10} = \text{TBD at } T_b1 / \text{TBD at } T_b1 + 10$ °C.

Results

Body mass at capture was 48.0 ± 1.3 g, tail width was 13.8 ± 0.4 mm, and testes width 5.0 mm in both opossums. Body mass increased substantially soon after capture, stabilized or fell somewhat after implantation of iButtons, and then increased again (Fig. 1). The maximum mass reached after extensive feeding was 80.6 ± 2.1 g. Tail width also increased after 10 days in captivity to 17.0 ± 1.4 mm, whereas testes width remained at 5.0 mm. Both opossums rapidly increased body mass when food was provided, and lost mass at a similar

rate when food was withheld for torpor induction (Fig. 1). The mean body mass of both opossums throughout measurements was 67.3 ± 2.0 g. Food consumption on days food provided was 22.2 ± 9.4 g/day in Lh1 and 19.2 ± 7.1 g/day in Lh2.

Even on days torpor was not expressed (Fig. 2), daily fluctuations of T_b were pronounced (4 to 5 °C) in both individuals. During activity at night, T_b ranged from about 37 to 39 °C and the T_b maxima observed were 38.7 °C (Lh1) and 38.9 °C (Lh2). During the rest phase, when animals remained normothermic, T_b fell to about 33 °C.

Both individuals entered spontaneous (food ad libitum) and induced torpor (food withheld) in the holding room, where T_a ranged from ~10 to 20 °C (Fig. 2). Food withdrawal and exposure to low T_a increased torpor use. Overall, 21 torpor bouts were observed in both opossum over 68 days of measurements in Lh1 and over 57 days in Lh2. The mean minimum T_b during torpor was statistically indistinguishable (13.7 ± 6.1 °C, Lh1; 15.7 ± 6.7 °C, Lh2; t test), and the absolute minimum T_b observed was 7.7 °C (Lh1) and 9.6 °C (Lh2). Even when the T_b and T_a were below 10 °C, the $T_b - T_a$ differential was small (often <1.0 °C) suggesting that both opossums were thermo-conforming and had not reached their regulated T_b minima (Fig. 2). The mean T_b over all entire torpor bouts (i.e., during the entire time T_b was <30 °C) was 17.4 ± 6.1 °C (Lh1) and 20.7 ± 5.2 °C (Lh2), and in both opossums, the minimum T_b during torpor and mean T_b during entire torpor bouts were strongly correlated ($p < 0.0001$, $r^2 = 0.96$, Lh1; $p < 0.0001$, $r^2 = 0.94$, Lh2; not shown). The overall mean T_b throughout the period of measurements, including bouts of torpor and activity, was 31.2 ± 8.9 °C (Lh1, $N = 3,225$) and 33.2 ± 5.8 °C (Lh2, $N = 2,925$).

Torpor bout duration ranged from brief bouts of 30 min to a maximum of 42.5 h. The mean torpor bout duration was 13.9 ± 11.7 h (Lh1) and 6.6 ± 4.2 h (Lh2) and differed between individuals (t test, $p = 0.011$). The duration of torpor bouts was strongly correlated ($r^2 > 0.90$) with the mean and minimum T_b of both individuals, and the response in both individuals was similar and showed a linear response after \log_{10} transformation of torpor bout duration (Fig. 3). Responses of individuals were indistinguishable for slope and intercept of mean T_b ; slopes differed between individuals for minimum T_b (ANCOVA, $p = 0.001$). In Lh1, the slope for the relationship between torpor bout duration and mean and minimum T_b was statistically indistinguishable (ANCOVA, $p = 0.949$), whereas the intercept differed (ANCOVA, $p < 0.0001$). In Lh2, both the slope (ANCOVA, $p = 0.022$) and intercept (ANCOVA, $p < 0.0001$) differed for the relationship between mean and minimum T_b and the duration of torpor bouts. The duration of torpor bouts also was correlated with the minimum $T_b - T_a$ differential ($p = 0.001$; $r^2 = 0.68$). In <1 h torpor bouts, the minimum $T_b - T_a$ differential was around 10 °C; this decreased with bout duration until during torpor bouts of >20 h; the $T_b - T_a$ differential was <1.0 °C (mean 0.5 ± 0.2 °C).

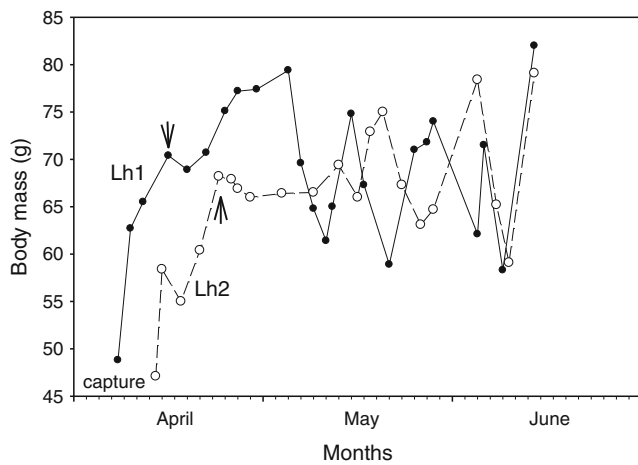


Fig. 1 Body mass of two male *L. halli* during their time in captivity. Increases in body mass indicate times of feeding and decreases times of food withdrawal. Arrows indicate times of iButton implants

Mean maximum cooling rates over 30 min during torpor entry were $0.15 \pm 0.03 \text{ } ^\circ\text{C min}^{-1}$ (Lh1, $N=19$) and $0.14 \pm 0.03 \text{ } ^\circ\text{C min}^{-1}$ (Lh2, $N=18$). Mean maximum rewarming rates over 30 min were $0.35 \pm 0.06 \text{ } ^\circ\text{C min}^{-1}$ (Lh1, $N=19$) and $0.36 \pm 0.08 \text{ } ^\circ\text{C min}^{-1}$ (Lh2, $N=18$), more than twice as fast as cooling rates, and for both rates, the means for the two individuals were almost identical. The maximum measured rewarming rate was $0.49 \text{ } ^\circ\text{C min}^{-1}$ in both individuals.

Discussion

Our study provides the first quantitative data on thermal biology and variables of torpor in the Patagonian opossum. It shows that the species can enter deep and prolonged torpor. However, although it has the capacity of extensive fattening, it does not exhibit a prolonged hibernation season with predictable

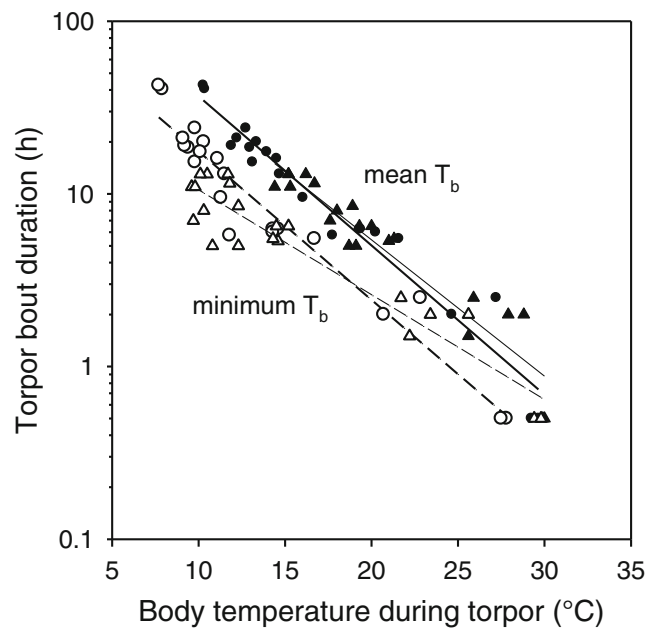


Fig. 3 Torpor bout duration (TBD) as a function of body temperatures (T_b , means and minima) during torpor. Equations: Lh1 (black-filled circle) $\log_{10} \text{ TBD (h)} = 2.431 - 0.0864 \text{ mean } T_b \text{ (} ^\circ\text{C)}$, $r^2 = 0.95$, $p < 0.0001$. Lh1 (white-filled circles) $\log_{10} \text{ TBD (h)} = 2.106 - 0.0864 \text{ minimum } T_b \text{ (} ^\circ\text{C)}$, $r^2 = 0.94$, $p < 0.0001$. Lh2 (black up-pointing triangles) $\log_{10} \text{ TBD (h)} = 2.313 - 0.0789 \text{ mean } T_b \text{ (} ^\circ\text{C)}$, $r^2 = 0.90$, $p < 0.0001$. Lh2 (white up-pointing triangles) $\log_{10} \text{ TBD (h)} = 1.63 - 0.0607 \text{ minimum } T_b \text{ (} ^\circ\text{C)}$, $r^2 = 0.90$, $p < 0.0001$

multiday torpor bouts interrupted by brief periodic arousals as in many mammalian hibernators. It appears that this largely carnivorous species uses torpor ranging from several hours to almost 2 days to minimize energy expenditure during times of low food availability and cold exposure, but continues foraging between torpor bouts to replenish stored resources. This pattern is intermediate between that expressed by daily heterotherms and hibernators, and therefore, only partly supports our hypothesis.

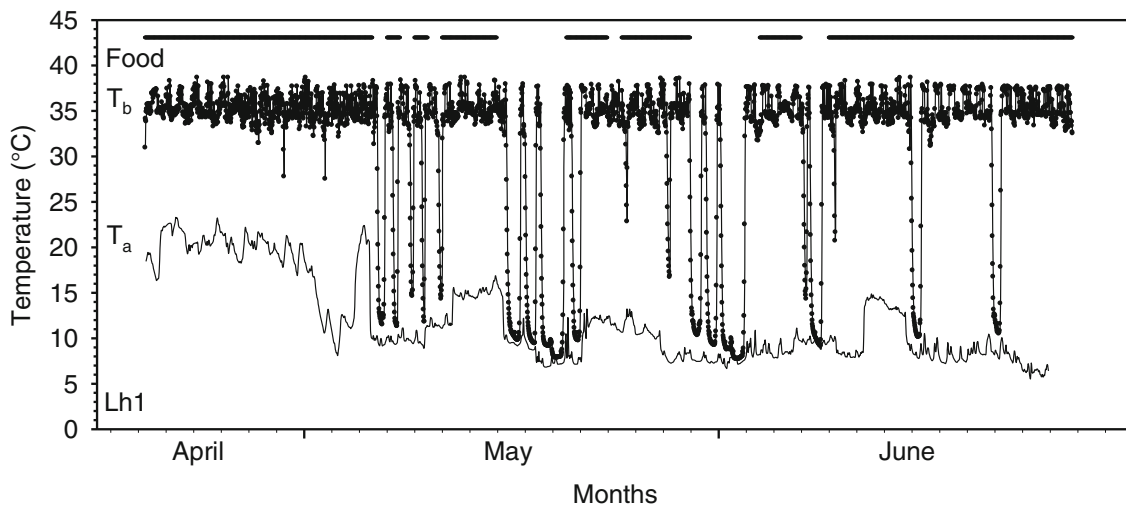


Fig. 2 Body temperature (T_b) and ambient temperature (T_a) as a function of time in *L. halli* Lh1 in autumn and early winter. Times when food was available are shown as black horizontal bars at the top of the graph, gaps indicate times when food was withheld

Lestodelphys lives in arid/semiarid cool temperate habitats that likely explain its frequent use of torpor to some extent. The group of Australian marsupials that thrive in deserts are the carnivorous/insectivorous dasyurids (order Dasyuromorphia), and it has been suggested that their success is related to their extensive use of torpor. However, unlike *Lestodelphys*, all dasyurids known to use torpor are strictly daily heterotherms with a duration of torpor bouts typically lasting for a few hours and minimum $T_b > 10^\circ\text{C}$ (Cooper and Geiser 2008; Geiser and Körtner 2010; Munn et al. 2010). These desert dasyurids range in latitude from ~ 14 to 38°S , and therefore, are exposed to much higher T_a than *Lestodelphys* with a more southerly distribution. Other known heterothermic opossums also use daily torpor exclusively with T_b minima $> 14^\circ\text{C}$, but, like the dasyurids, they are found in warmer habitats than *Lestodelphys* (Morrison and McNab 1962; McNab 1978; Douglas and Nicol 1993; Opazo et al. 1999; Silva-Duran and Bozinovic 1999; Bozinovic et al. 2005; Cooper et al. 2009). Perhaps, differences in climate can explain some of the different values especially in the T_b minima between species and groups despite their similar sizes and diets.

Although our data are restricted to two males, they are precise, extensive, and continuous measurements of core T_b over about 2 months. We therefore argue that they are representative for the species for several reasons. First, the number of torpor bouts expressed by the two individuals was similar over a similar time and treatment period. Second, although the maximum duration of torpor bouts differed between individuals, the T_b minima and cooling and rewarming rates were similar, and maximum rewarming rates ($0.49^\circ\text{C min}^{-1}$) were similar to those predicted for marsupials of similar body mass (Geiser and Baudinette 1990). Third, although it is known that patterns of torpor during the nonreproductive season can differ between sexes, such differences are pronounced only in strictly daily heterotherms (Geiser 1988), whereas in species capable of multiday torpor bouts, known gender differences are smaller (French 1982; Batavia et al. 2013), although the timing of the hibernation season may differ between sexes (Barnes and Ritter 1993). Thus, it is likely that we trapped only male opossums because males have larger home ranges and typically are easier to trap than females, and not because females were hibernating. As large numbers of rodents were captured during our field work, potential prey was equally available for both sexes (see Martin and Udrizar Sauthier 2011). Finally, although patterns of torpor are known to differ between the laboratory and the field, such differences, as for differences between sexes, are often more pronounced in daily heterotherms than in species capable of multiday torpor (Geiser et al. 2000).

The duration of torpor bouts in *Lestodelphys* was strongly affected by temperature as a characteristic of many heterothermic species (Twente and Twente 1965; Geiser and Kenagy 1988; Buck and Barnes 2000; Malan 2010). However, cause and effect between T_b and torpor bout duration are often disputed. Some argue that T_b must be a function of torpor bout duration because

it takes time for the body to cool. While this is correct during torpor entry or short torpor bouts, this will obviously not be the case during long torpor bouts when a steady state T_b is reached and T_b no longer is changing. Nevertheless, T_b and torpor bout duration continue to be correlated during long torpor bouts and consequently cause and effect must be reversed. Although the evidence that T_b affects the duration of torpor bouts is strong (i.e., over the T_b range torpid animals are thermo-conforming, torpor bout duration typically is a logarithmic function of T_b as in Fig. 3), the mechanisms governing periodic arousals remain controversial. It has been suggested that the duration of torpor bouts, which increase with decreasing T_b during torpor over a wide range of T_a , are caused by a combination of the temperature-dependent and low T_b and low metabolic rates during torpor (Geiser and Kenagy 1988). However, the Q_{10} values calculated for torpor bout duration as a function of T_b in *Lestodelphys* (Fig. 3) were 7.3 for both mean and minimum T_b in Lh1 and 6.2 (mean T_b) and 4.1 (minimum T_b) in Lh2 well above those typically observed for biological processes (usually Q_{10} is 2 to 3). In thermo-conforming hibernating ground squirrels, the Q_{10} for torpor bout duration is between about 2 and 4 on the high side for typical biochemical processes and on the low side in comparison to *Lestodelphys* (Twente and Twente 1965; Geiser and Kenagy 1988; Buck and Barnes 2000). The overall change in torpor bout duration over the entire T_b range measured here also was pronounced (85-fold, Lh1; 26-fold, Lh2) well above the range predicted by non-temperature-compensated biological clocks (Malan 2010). Clearly, the issue of periodic rewarming from torpor is still not resolved and perhaps needs the consideration of multiple rather than single factors.

The maximum torpor bout duration (42.5 h) measured here in *Lestodelphys* is well above reported averages for daily heterotherms and below those of hibernators, whereas the minimum T_b during torpor (7.7°C) is $\sim 10^\circ\text{C}$ below published averages in daily heterotherms (Geiser and Ruf 1995). The mean maximum torpor bout duration in marsupial daily heterotherms is 11.3 h, which is shorter than even the mean torpor bout duration of Lh1 (13.9 h). For Lh2, the timid individual, the maximum torpor bout duration of 13 h was still above the mean maximum for marsupial (11.3 h) and other daily heterotherms (11.2 h). Thus, both the minimum T_b and torpor bout duration of *Lestodelphys* fall between those expressed by daily heterotherms and hibernators (Geiser and Ruf 1995).

What does this tell us about the evolution of torpor patterns? It has been proposed recently, using a phylogenetic approach, that torpor in mammals is monophyletic in agreement with the traditional view (Lovegrove 2012). In contrast, developmental data suggest that torpor has evolved independently in birds and mammals and also is polyphyletic in different mammalian taxa (Geiser 2008). The latter interpretation is supported by the rather ambiguous phylogenetic signals for functional variables in some heterothermic endotherms (Cooper and Geiser 2008;

Riek and Geiser 2013). Expression of an intermediate torpor pattern with T_b below 10 °C and torpor bouts of up to almost 2 days in *Lestodelphys*, a member of the most ancestral marsupial order, suggests that this approach might have been a torpor pattern expressed by ancestral mammals. As such intermediate patterns of torpor derived from long-term studies like ours are rare (Geiser and Ruf 1995), this interpretation is supported by data on elephant shrews that exhibit astonishingly similar torpor patterns as *Lestodelphys* and are the only group currently known to do so (Lovegrove et al. 1999; Geiser and Mzilikazi 2011; McKechnie and Mzilikazi 2011). Elephant shrews (Macroscelidea) represent a very old group of Afrotherian placental mammals of similar age as the opossum ancestors (O'Leary et al. 2013). Consequently, this opportunistic intermediate pattern of torpor with low T_b , but not highly predictable multiday torpor in these two ancient mammalian orders, may represent the ancestral form of torpor. One plausible interpretation therefore is that daily torpor in the daily heterotherms and deep, multiday torpor in the hibernators were derived from this ancestral torpor pattern in all mammals. However, because marsupials and placentals diverged about 150 million years ago and developmental data suggest a polyphyletic derivation of torpor in mammals, the other possible interpretation is that the two derived patterns of torpor have evolved independently in the two mammalian subclasses.

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