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ORIGINAL PAPER

White mouse pups can use torpor for energy conservation

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Abstract

White mice are ubiquitous laboratory animals and have been extensively studied. To reveal potential undiscovered traits, we tested the hypothesis that during development, when heat loss in mouse pups is high, they can use daily torpor for energy conservation. We determined at what age individual mouse pups are able to defend their body temperature at room temperature (ambient temperature, $T_a = 20$ °C) and whether they could use torpor from that time. Initially at 5/6 days (body mass, BM ~ 3 g), still naked mice cooled rapidly. In contrast, at ~ 14 days (BM ~ 6 g), they could maintain a high, constant body temperature and, therefore, had reached competent endothermy. These mouse pups at ~ 20% of adult BM were able to enter into and arouse from torpor as determined via the rate of oxygen consumption; this was the case for both individuals that were exposed to a cooling regime as well as those that were not. During torpor, metabolism fell by up to > 90% and torpor lasted for up to 12 h. As mice grew, torpor was still used but was less pronounced. Our study shows that although the physiology of laboratory mice has been widely examined, their functional capabilities have still not been fully revealed, which has implications for biomedicine. Our and other developmental data suggest that because torpor is so efficient in conserving energy, it is likely to be used during the growth phase by diverse mammals and birds to survive energetic and thermal challenges.

Keywords Daily torpor · Development · Ecology · Heterothermy · Medical implications · Mouse pups · *Mus musculus*

Introduction

At birth or hatching, most mammals and birds are naked and helpless, are only partially endothermic, and unable to produce enough heat internally to maintain a constant and high body temperature (T_b). Outside a protecting nest with their parent, the T_b of these altricial species cools rapidly to near ambient temperature (T_a) (Dawson and Evans 1960; Morrison and Petajan 1962; Hill 1976). However, as their body, fur and feathers grow, endothermic heat production increases, and their neural function and coordination improve, they develop the ability to maintain a high and constant T_b, i.e., animals become fully endothermic. Nevertheless, as this development typically occurs at between about 20 and 50% of adult body mass (BM), their relative large surface area results in substantial heat loss that must be compensated for by endogenous heat production fueled by ingested food if a constant T_b is to be maintained. Therefore, these young are highly vulnerable to heat loss and energy depletion, especially during cold exposure or at times when their parents are not able to supply enough food (Geiser et al. 2006).

One approach to deal with such energetic challenges would be to enter torpor, which is characterized by pronounced reductions of metabolic rate (MR) and T_b for effective energy conservation (Boyer and Barnes 1999; Kronfeld-Schor and Dayan 2013; Ruf and Geiser 2015; Dausmann and Warnecke 2016; Withers et al. 2016). It is now established that torpor has multiple functions (Geiser and Brigham 2012; Nowack et al. 2017; Barak et al. 2019) and that it is predominately used by species that are small as adults, including many diverse birds and mammals and also the house mouse, *Mus musculus* (Hudson and Scott 1979; Tomlinson et al. 2007; Swoap and Gutilla 2009; Schubert et al. 2010). Although torpor seems an obvious adaptation to enhance survival during development, only a very small proportion (< 0.1%) of the > 15,000 mammal and bird species

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have been investigated in this regard and juvenile house mice have not been studied (Boersma 1986; Geiser 2008; Eichhorn et al. 2011). Apart from permitting survival during development (Wacker et al. 2017; Geiser et al. 2019), torpor has other functions, as it can divert nutrients to enhance growth when food is limited (Giroud et al. 2014).

The purpose of our study was twofold. First, we aimed to determine at what age individual mouse pups are able to defend a constant high T_b when exposed to a mild T_a of 20.0 ± 1.0 °C, as often used as 'room temperature' for the maintenance of laboratory mice. Second, we tested the hypothesis that soon after endothermy is attained, mouse pups are able to enter and arouse from torpor and aimed to determine at what age and BM that occurs. Such data are important because they improve the understanding of the functional significance and diversity of torpor during development in endotherms. Moreover, as the physiology of heterothermic species (can use torpor) differs substantially from homeotherms (cannot use torpor) with regard to cardiac function, thermal and ischemic tolerance and muscle disuse atrophy (Carey et al. 2003), such findings have implications for biomedical research.

Material and methods

Four litters of Swiss albino laboratory mice (*Mus musculus*) bred in the animal house of the University of New England, Armidale, Australia were used in our study. Two litters (L1; L2) were used for cooling experiments during early development; the two other litters (C1; C2) were kept as controls and were left in the nest with their mothers for the first 2 weeks after birth, but all litters were used in the torpor experiments. The four litters contained 13 young on average and were kept with their mothers, except during the experiments. Each litter was held in a 47 × 26 × 20 cm rat cage, filled with ~ 3 cm of wood shavings plus some shredded paper as bedding material. Food (mouse cubes, Gordon's specialty feed, Yanderra, NSW, Australia) and water were provided ad libitum. The T_a was kept constant at 20.0 ± 1.0 °C and the photoperiod was LD 12:12, lights on from 06:00 to 18:00 h. At an age of 4 weeks, the litters were separated by sex to prevent mating; the mothers were kept with the females.

Cooling experiments in L1 and L2 began when mice were 5–6 days old. For these measurements, single mouse pups were randomly removed from the litter and ventral surface temperature (T_s) was measured immediately to the nearest 0.1 °C with an infrared thermometer (Digitech; QM-7218; CN287) and a thermal picture was taken (FLIR C2; Compact professional thermal imaging camera; emissivity 0.98; reflected temperature 20 °C; distance 0.2 m). The mouse pup was then placed into a cardboard beaker (250 ml), on a flat surface with a temperature of 20.0 ± 1.0 °C (measured in the beaker with the infrared thermometer and the thermal imaging camera). These non-invasive measurements of T_s are a good proxy for core T_b as they are within 0.5 °C of axillary T_b readings (Geiser et al. 2019). The animals were handled with a glove to minimize heat transfer from the hand. Measurements were repeated in 10-min intervals in $n = 10$ mice/litter over 30 min. Before mice were returned to their mother, they were weighed to the nearest 0.1 g with an electronic scale. Measurements of both experimental litters were conducted on every second day. Only non-invasive measurements were conducted for ethical considerations and because rectal core T_b measurements, that could have damaged mouse pups, were not needed for the purpose of this experiment.

The cooling experiments were performed on litters L1 and L2; litters C1 and C2 were not cooled and remained with their mothers. Cooling experiments continued until the mice were able to maintain a high, constant T_s and, therefore, T_b at T_a 20 °C.

From one day after the mice maintained a high and constant T_s (at ~ 14 days), the MR of all litters was measured non-invasively as the rate of oxygen consumption, to determine whether or not mouse pups were able to express torpor. Three mice from the same litter were placed into 0.5–l respirometry chambers (one mouse/chamber), on two layers of paper towel and 1/3 of a cardboard toilet roll (3.5-cm long, 4.5-cm diameter) for shelter. Body mass (BM) and sex were determined before measurements. The MR was measured overnight from ~ 16:00 to 09:00 h without access to food and water using an open flow respirometry system (Sable Systems, TurboFOX Complete Field System, including a mass flow meter), while they were exposed to a constant T_a of 20 °C in a controlled temperature cabinet. Fresh outside air was pumped through the chamber at ~ 250 ml min^{-1}, dried with silica gel, and measured with a mass flow meter (Omega, FMA-5606, Stamford, CT, USA). After passing through the respirometry chamber, the gas was subsampled at a constant 100 ml min^{-1}, dried using silica gel, and % oxygen measured. Each chamber was measured in sequence for 3 min, followed by a reference reading (outside air); each chamber was measured every 12 min. For analyses, the average of the three lowest measured consecutive values was used (i.e. over 36 min). Based on the highest average BM, the first group measured was C2, followed by L1, C1 and L2. In the morning, if torpor was observed (MR well below the predicted basal MR, see below), the animal was removed from chamber using a glove, T_s was measured ventrally (infrared thermometer and FLIR thermal imaging camera) and the mouse was returned to its chamber to rewarm, while the measurement continued. In some instances, spontaneous rewarming occurred; so, T_s measurements during torpor were not possible. After rewarming at the end of the measurement, T_s and body mass were again

measured. Mice were individually marked by removing a small patch of fur and were returned to the litter. Markings were made by litter to prevent repeated measurements of the same individual. Three rounds of measurement were conducted: The first round lasted for eight nights (group 1: age 14–21 days, BM 5.1–8.2 g; $n = 24$), the second for eight nights (group 2: 27–35 days, BM 9.0–18.3 g; $n = 24$), no individual mouse was measured twice. The third round of measurements (4 nights) began 19 days later (group 3: 54–57 days, BM 25.1–30.6 g; $n = 12$) and some of these mice had been measured before.

Numeric values are presented as mean ± SD for 'n' the number of individuals measured. Individual basal metabolic rate ('BMR' because the young were still growing) was calculated using the equation for rodents: $BMR = 4.98 \times BM^{-0.33}$ (Hayssen and Lacy 1985). The body mass (BM) used for calculations was measured at the end of each respirometry trial. A torpor bout was defined as at least 2 MR readings (i.e., over 24 min) below the calculated 'BMR'. Minimum torpor metabolic rate (TMR) and normothermic resting MR (RMR) were calculated as mean out of the 3 lowest measurements in sequence (i.e., over 36 min). Total daily torpor (TDT) was calculated from the sum of all torpor bouts (usually 1–3, most often 1) of one animal during the entire measurement. Linear mixed-model fits and ANCOVAs were conducted using 'R' package version 3.1–140 (Pinheiro et al. 2019). The package "piecewiseSEM" (Lefcheck 2016) was used to calculate marginal r^2 values. Both total MR (ml O_2 h^{-1}) and mass-specific MR (ml O_2 g^{-1} h^{-1}) were analyzed (Fernandez-Verdejo et al. 2019); the MR as response variable and the BM as a covariate. Total and mass-specific regressions are reported for easier comparison with previous work and the values in the figures (Table 1). Initially, treatment and sex were included as fixed effects; however, treatment was non-significant for all regressions and sex was non-significant for all but the total TMR as a function of age. Therefore, treatment and sex were excluded from the final analyses, which included individuals as a random effect. The same procedures were used for regressions of total daily torpor (TDT) as a function of BM and age, torpor entry times for the first bout observed vs BM and age, and mass loss as a function of TDT.

Table 1 Regression equations for total MR (ml O_2 h^{-1}) and mass-specific MR (ml O_2 g^{-1} h^{-1}) as a function of body mass (BM in g) and age (days)

Total MR (ml O_2 h^{-1})
RMR = 25.8 + 1.33 BM; $p < 0.0001$; $r^2 = 0.71$
RMR = 21.7 + 0.75 age; $p < 0.0001$; $r^2 = 0.67$
TMR = − 7.41 + 1.89 BM; $p < 0.001$; $r^2 = 0.88$
TMR = − 11.65 + 0.97 age; $p < 0.0001$; $r^2 = 0.85$
Mass-specific MR (ml O_2 g^{-1} h^{-1})
RMR = 5.19 − 0.108 BM; $p < 0.0001$; $r^2 = 0.82$
RMR = 5.55 − 0.061 age; $p < 0.0001$; $r^2 = 0.81$
TMR = 0.641 + 0.042 BM; $p < 0.001$; $r^2 = 0.31$
TMR = 0.512 + 0.023 age; $p < 0.001$; $r^2 = 0.30$

Results

The BM of L1 mouse pups ($n = 10$) varied between 2.4 and 3.1 g (2.8 ± 0.2 g) at the age of 5 days on the first day of measurement. The surface temperature (T_s) at 0 min was 33.4 ± 0.3 °C and fell to 22.6 ± 0.3 °C ($n = 10$) after 30 min. The mean BM of L2 ($n = 10$) at 5 days was 4.1 ± 0.2 g and the T_s fell from 32.3 ± 0.5 °C g at 0 min to 23.7 ± 0.4 °C at 30 min. Shivering was observed from day 8 to day 13 after 10-min individual exposure to T_a 20 °C.

At 13–14 days, T_s at 0 min was 33.0 ± 0.4 °C and after 30 min stabilized at an average of 32.1 ± 0.8 °C ($n = 20$); the average body mass was 6.1 ± 0.4 g ($n = 20$), which resembles 21% of adult body mass (28.5 g).

All mouse pups from all four litters at 14 days and a BM of 6–7 g were able to enter into and arouse from torpor. As shown for one individual in (Fig. 1) after some periods of activity and rest at the beginning of the experiment (Fig. 1A), MR increased to high values of > 8 ml O_2 g^{-1} h^{-1} at lights off during the activity phase. At ~ 22 h, MR fell precipitously at torpor entry and a minimum TMR of ~ 0.6 ml O_2 g^{-1} h^{-1} (~ 7% of that during activity) was reached by midnight. The low TMR was maintained for ~ 9 h after which spontaneous arousal was initiated at ~ 09:30, characterized by a rapid rise of MR and T_b. The lowest T_s measured during torpor at that age was 24.6 °C. Torpor was also used at age 27–35 days at a BM of around 13 g (Fig. 1B), but torpor was not as pronounced as in younger mice and often was expressed as multiple short bouts. Torpor use further declined with growth (Fig. 1C).

During respirometry trials, 46 out of 60 measured mice (76.7%) used torpor during the night. Mean torpor use was 66.7% ($n = 20/30$) for L1/L2 and 86.7% ($n = 26/30$) for C1/C2. All mice with BM < 12 g used torpor. In group 3 (BM > 25.1 g, $n = 12$), four individuals (BM = 27.6 ± 2.4 g) entered torpor and eight individuals (BM = 28.8 ± 1.4 g) did not, but the mean BM did not differ (t test).

The minimum TMR and minimum RMR both total and mass specific were a function of BM and age (Table 1). The mass-specific RMR decreased significantly, whereas the TMR increased significantly with an increase of BM (Fig. 2). As animals grew, the TMR approached the 'BMR' (Fig. 2).

The torpor entry times, from the beginning of measurements to the first bout observed, were related to BM ($y = 4.9 + 0.28x$; $p < 0.0001$; $r^2 = 0.45$; Fig. 3A) and age ($y = 4.3 + 0.14x$; $p < 0.0001$; $r^2 = 0.36$). The clock times

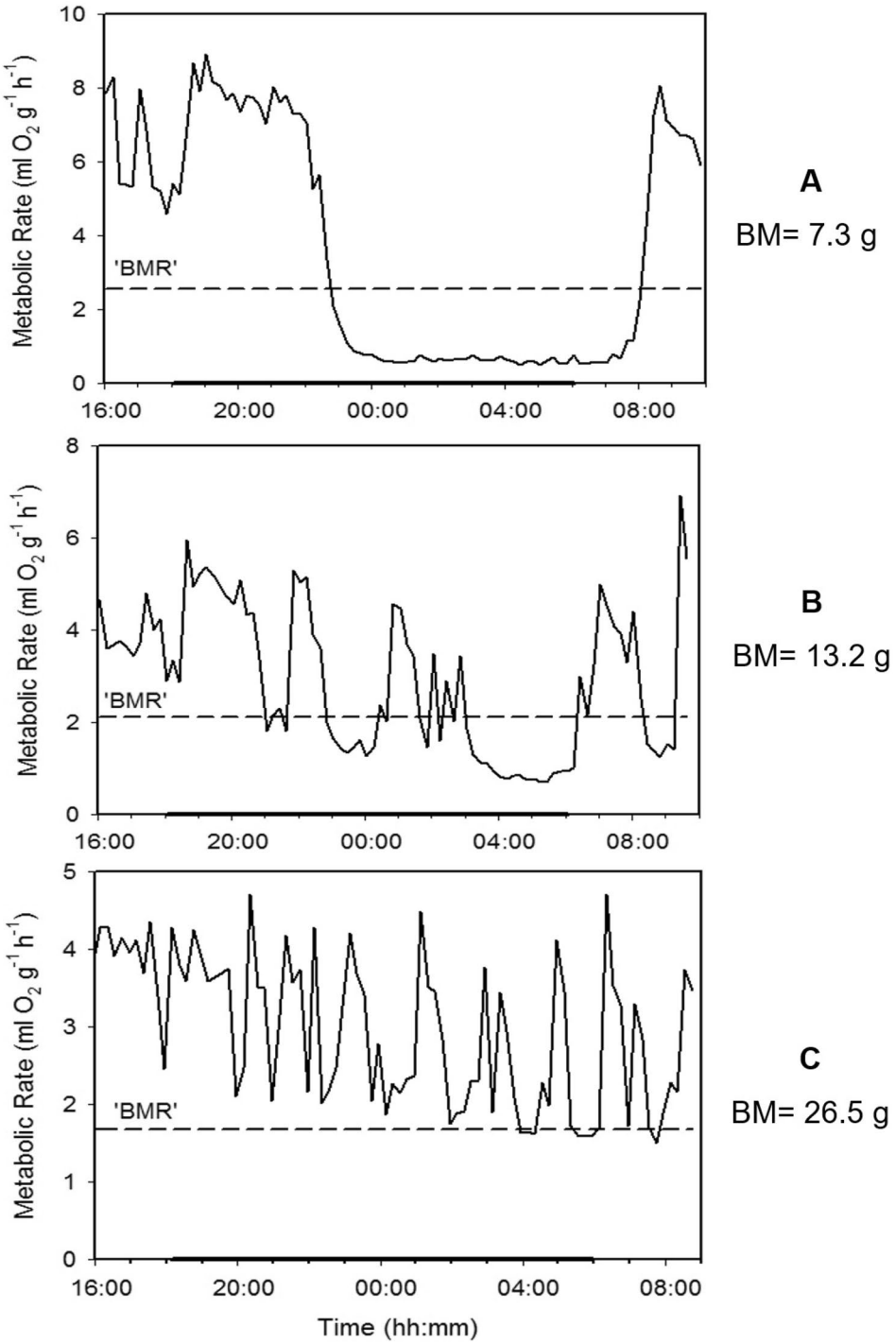

Fig. 1 Individual measurement of 3 mice (A, B, C) with different body mass and age (7.3 g, 21 days; 13.2 g, 28 days; 26.5 g, 56 days). Metabolic rate was measured from ~ 16:00 to ~ 09:00 h, indicating the reduction of torpor use with increase of body mass. 'BMR' = Basal Metabolic Rate was calculated from the body mass using the equation for rodents (Hayssen and Lacy 1985) for comparison. The black horizontal bar indicates darkness

for the entry into the first bout of torpor observed were also correlated with BM ($p < 0.0001$; $r^2 = 0.42$) and age ($p < 0.0001$; $r^2 = 0.32$). This was reflected in the total daily torpor duration (TDT), which also was inversely related to BM ($\log_{10} y = 2.3–0.083x$; $p < 0.\ 001$; $r^2 = 0.49$; Fig. 3B) and age ($\log_{10} y = 2.5–0.043x$; $p < 0.0001$; $r^2 = 0.42$). At the BM of 5.1 g, a maximum TDT of 720 min was observed; whereas, at a BM of 28.3 g, the longest TDT measured was 96 min. The longest individual uninterrupted torpor bout was 636 min (10.6 h) by a 5.1-g mouse.

The loss of BM of individuals decreased with TDT ($y = 3.98–0.324x$; $p < 0.0001$, $r^2 = 0.53$); the relationship improved slightly when the BM-loss axis was log-transformed ($\log_{10} y = 0.591–0.059x$; $p < 0.0001$; $r^2 = 0.56$) (Fig. 4).

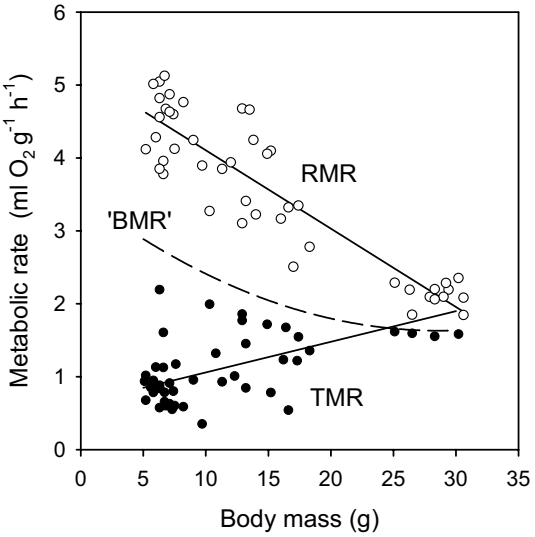

Fig. 2 Resting metabolic rate (RMR, $y = 5.19–0.108x$, $p < 0.0001$, $r^2 = 0.82$) and minimum torpor metabolic rate (TMR, $y = 0.641–0.042x$, $p < 0.001$, $r^2 = 0.31$) as a function of body mass. 'BMR' was calculated from the body mass using the equation for rodents (Hayssen and Lacy 1985) for comparison

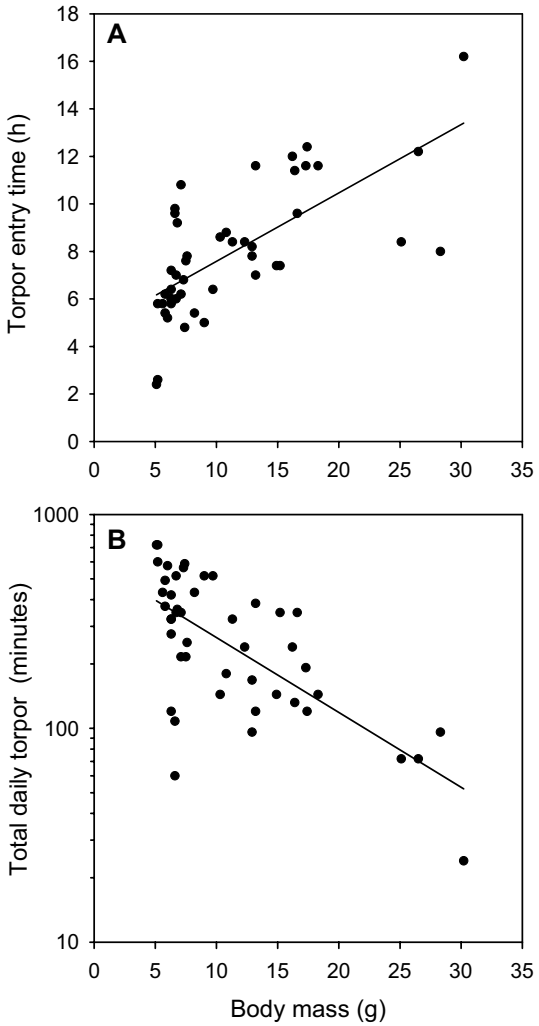

Fig. 3 **A** Time of torpor entry from the beginning of measurements as a function of body mass ($y = 4.9 + 0.28x$; $p < 0.0001$; $r^2 = 0.45$). **B** Total daily torpor duration (TDT, $\log_{10} y = 2.3–0.083x$, $p < 0.001$, $r^2 = 0.49$) as a function of body mass

Discussion

We provide the first evidence that white mouse pups can use torpor. Initially, when mice were less than 14 days of age, they were poikilothermic and unable to defend a high and constant T_b via an increase in endogenous heat production. However, after 14 days when endothermy was established and mouse pups could defend a constant T_b under mild cold exposure at ~ 20% of adult BM, they were able to express deep and prolonged daily torpor, with MR reduction by up to 90% and lasting for up to 12 h, and endothermic arousal. Although torpor was deep and long in small endothermic mouse pups, torpor duration decreased and the minimum mass-specific TMR during torpor increased with growth. This reduction in torpor use with size and age was accompanied by a decrease in RMR, suggesting that, under the mild thermal conditions used here, the reduced torpor expression is to a large extent explained by reduced thermoregulatory costs at higher BM. Exposure to low T_a and increased thermoregulatory costs likely would have increased torpor expression. However, as mice use torpor as adults, it seems that during the late growth phase, which usually occurs during the productive season in the wild, torpor in mouse pups is minimized as is the case in other small mammals (Wacker et al. 2017).

The physiological variables of torpor in the juvenile mice were similar to those measured under comparable thermal conditions for many small adult mammals expressing daily torpor (Ruf and Geiser 2015). Metabolic rate fell to ~ 10% of that observed during activity and to ~ 1/3 of 'BMR' on average at a BM < 10 g, T_s to about 25 °C, and most torpor bouts at that size lasted for about 1–10 h. This will result in a reduction of daily energy expenditure by about 10–50%, depending on the duration and depth of torpor.

Thus, our data on torpor in mouse pups are functionally important. However, as single mice were removed from the nest and measured as individuals, the ecological value of these new observations might be questioned. We contend that the findings are of significance also for free-ranging animals for several reasons. Cold or torpid pups have been found in nest boxes in the wild for sugar gliders, *Petaurus breviceps*, (Holloway and Geiser 2000), eastern pygmy possums, *Cercartetus nanus*, (Geiser unpublished) and common dormice, *Muscardinus avellanarius*, (Juskaitis 2005), suggesting that torpor is used during development in nature. With regard to our experimental protocol, if we would have

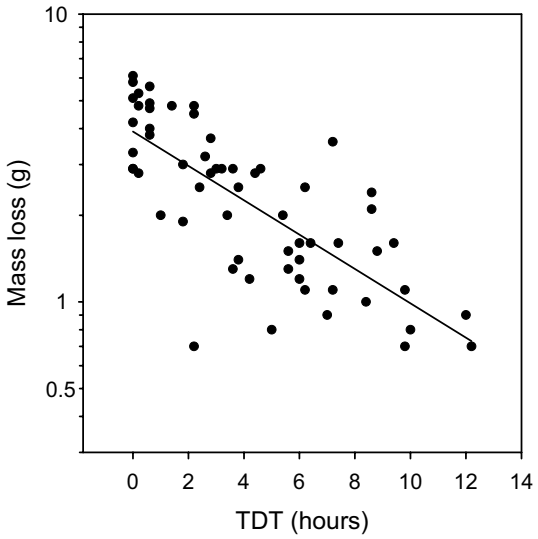

Fig. 4 Mass loss as a function of total torpor duration (TDT, $\log_{10}$ $y = 0.591–0.059x$, $p < 0.0001$, $r^2 = 0.56$)

kept the mouse pups in groups, it is possible that lower T_as or longer exposure periods may have been required for torpor induction. However, this remains to be tested because huddling enhances torpor in adult Japanese field mice (*Apodemus speciosus*), which increase torpor frequency with an increase in the number of huddling individuals (Eto et al. 2014).

Our new data are of significance for two major reasons (1) with regard to the functional ecology of developing small mammals and birds and (2) with regard to biomedical applications.

(i) Although it is well established that torpor use and depth increase with decreasing size in birds and mammals (Ruf and Geiser 2015), the understanding of torpor expression and its costs and benefits during development and later in life is scant. This is despite the fact that endothermy is attained at a fraction of adult body mass, at which stage heat loss to the environment will be substantial and the experience of young to gather food to fuel the metabolism required for maintenance of the high and constant T_b will be limited or entirely lacking. Food shortages during adverse conditions can result in death in a developing animal remaining homeothermic, as is the case for humans (Lummaa and Clutton-Brock 2002). Overall, this is an enormous waste of resources by the parents. While torpor use during development may slow development somewhat, it will increase the chances for survival to adulthood substantially and therefore enhance fitness. It is well established that food shortage during development results in a multitude of negative long-term effects in birds and mammals (Metcalfe and Monaghan 2001). However, the potential or even likely ability of torpor in overcoming or reducing these has not been examined. With regard to diversity of torpor expression during development, the oversight of torpor expression in juvenile house mice, considering that they have been used so extensively for physiological and other research in the laboratory and the wild, does suggest that torpor during development is used by many other species including some that are considered to be homeothermic as adults (Boersma 1986; Nuesslein-Hildesheim et al. 1995). Recent data show that even large species like king penguins (*Aptenodytes patagonicus*) show torpor during development (Eichhorn et al. 2011) supporting this prediction.

(ii) It has been long recognized by medical researchers that an understanding of how the tissues of animals capable of torpor remain functional at low T_b could benefit biomedical science (Carey et al. 2003). This is because unlike homeotherms such as humans, heterotherms can tolerate low T_bs and ischemia, potentially damaging conditions experienced during organ preservation, stroke and cardiac arrest. If such work is to be conducted on hibernators, this is not easy to do because many are hard to obtain, breed or maintain in captivity. In contrast, laboratory mice are easy to obtain, enter torpor both as juveniles and adults, and may be a suitable animal model especially with regard to cardiac function (Swoap and Gutilla 2009), because mouse hearts continue to beat to as low as about 10 °C, well below those of humans. Furthermore, the mechanisms that underlie the use of regulated low T_b in mice could be translated to improve survival of humans in trauma situations or even improve preservation of other organs for transplantations in humans (Carey et al. 2003). As mouse pups between 6 and 12 g have a high proclivity to enter torpor, they are likely to represent the 'torpor phenotype' more than adult mice and may be better suited as biomedical models especially when it comes to tissues. The small size of juveniles is of course limiting for whole animal physiology experiments. Another typical aspect of torpor is increased longevity, with heterotherms living longer on average than homeotherms (Turbill et al. 2011). Laboratory mice have been extensively used in longevity studies, but such data are often complicated by the use of caloric restriction. However, it is known that the tumor-preventative effect of torpor is abolished by housing mice at high T_a and hindering the use of torpor (Koizumi et al. 1996).

Our study shows that torpor can be used during development in white mice, a species used widely as laboratory animal. This is despite ad libitum feeding over many generations and maintenance at benign T_as usually not far below thermo-neutrality. This suggests that torpor in juveniles is an important evolutionary trait and that in the wild where animals are thermally and energetically challenged, torpor is widely employed by developing birds and mammals.

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