



Thermoregulation by an Australian murine rodent, the ash-grey mouse (*Pseudomys albocinereus*)

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ABSTRACT

We examine here the thermal physiology of the ash-grey mouse, as there is a paucity of data to explain how Australian rodents meet thermoregulatory demands. Most ash-grey mice remained normothermic over a range of ambient temperatures (10 °C to 30 °C), although they became hyperthermic at high ambient temperatures. One individual entered torpor at ambient temperatures of 20 °C and 25 °C, with minimal body temperatures of 24.5 °C and 28.4 °C respectively, before spontaneously arousing. This is the first evidence of torpor use by an Australian murine rodent. Our data suggest that although ash-grey mice have the physiological ability to use torpor, it is used rarely, presumably due to other behavioural and physiological adaptations. Their higher-than-expected basal metabolic rate ($1.56 \pm 0.25 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$) indicates that ash-grey mice do not have a frugal approach to energy expenditure. Other standard physiological variables were typical of a generalised rodent. A readily-available omnivorous diet, nocturnal activity, semi-fossorial habit and social behaviour presumably allow a high energy lifestyle. A reluctance to use torpor, despite an apparent physiological ability to do so, supports the idea that the use of torpor reflects a net balance between the costs and benefits of a heterothermic thermoregulatory strategy.

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1. Introduction

Torpor is the controlled reduction of body temperature (T_b) to <30 °C, metabolic rate (MR) to less than basal metabolic rate (BMR), and physical activity to a hunched posture and lack of responsiveness (Geiser, 1998; Barclay et al., 2001; Geiser, 2004a; Melvin and Andrews, 2009). It is used by endotherms to reduce energy and water requirements at ambient temperatures below thermoneutrality. Torpor is not an inability to thermoregulate, but is a controlled process (Mrosovsky, 1990; Geiser, 2004b; Withers and Cooper, 2010) that differs from pathological hypothermia by the ability to spontaneously arouse using endogenous metabolic heat production (Lyman et al., 1982; Wang, 1989). Torpor may be a response to food or water deprivation (e.g. pocket mice *Perognathus* spp, Tucker, 1966; gerbils, *Gerbillus pusillus*, Buffenstein, 1985; spiny mice *Acomys russatus*, Ehrhardt et al., 2005), or occur spontaneously

even when food and water are feely available (e.g. white-footed mice *Peromyscus leucopus*, Gaetner et al., 1973; hamsters *Phodopus* spp, Figala et al., 1973; pouched mice *Saccostomus campestris*, Ellison and Skinner, 1992). The energetic and hygric savings associated with torpor are important for the survival of animals inhabiting not only cold habitats but also temperate, arid and even tropical environments (Lovegrove, 2000; Geiser, 2004a).

Rodents have an obvious ability to survive in a wide range of environments, which has led to many studies of physiological adaptations for various rodent families. Torpor is prevalent amongst rodents worldwide, and indeed rodents are the best-studied group of heterotherms (Kayser, 1961; Geiser, 1994; Geiser and Ruf, 1995; Cooper and Geiser, 2008; Withers and Cooper, 2010). There is, however, a surprising lack of physiological data for Australian rodents, despite them being a successful element of the Australian fauna (Geiser, 2004a). Approximately a third of all small (<600 g) Australian mammals are rodents (Withers et al., 2004), but there is currently no quantitative evidence of torpor for any Australian rodent despite the prevalence of torpor use amongst sympatric Australian marsupials and bats (Lovegrove, 2000; Geiser, 2004a; Withers et al., 2004).

Predavec (1997) concluded that the Australian sandy inland mouse (*Pseudomys hermannsburgensis*) uses torpor, with some individuals surviving T_b as low as 21 °C. Other studies however (MacMillen et al., 1972; Geiser, 2004a; Tomlinson et al., 2007) found that sandy inland mice were unlikely to use torpor, with low T_b resulting only from

Abbreviations: ANOVA, Analysis of variance; BMR, Basal metabolic rate; EHL, Evaporative heat loss; EWL, Evaporative water loss; MHP, Metabolic heat production; MR, Metabolic rate; N, Number of individuals; N, number of measurements; PIT, Passive implantable transponder; PRWE, Point of relative water economy; RER, Respiratory exchange ratio; RH, Relative humidity; RWE, Relative water economy; SE, Standard error; T_a , Ambient temperature; T_b , Body temperature; VB, Visual Basic version 6; VCO_2 , Rate of carbon dioxide production; VO_2 , Rate of oxygen consumption.

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pathological hypothermia, which they can survive, but from which the mice are unable to spontaneously arouse. Other Australian rodents, including the swamp rat (*Rattus lutreolus*; Collins, 1973a,b) and hopping mice (*Notomys alexis* and *N. cervinus*; MacMillen and Lee, 1970; Withers et al., 1979; Dawson and Dawson, 1982), appear strictly homeothermic. The only rodent in Australia to show unequivocal evidence of torpor is the introduced house mouse (*Mus musculus*; Fertig and Edmonds, 1969; Hudson and Scott, 1979; Morton, 1978; Tomlinson et al., 2007). Although torpor offers obvious energetic and hygric advantages, is common amongst rodents in general, and is an important survival strategy for Australian marsupials and bats, Australian rodents seem to use other strategies to survive in environmental extremes. Why don't Australian rodents use torpor? Heterothermy is not particularly common amongst murine rodents, but their predominately Asian distribution means that they have not received the same research attention as many of the northern hemisphere rodent lineages (Lovegrove, 2012). Is homeothermy without torpor a phylogenetic characteristic of Australia's rodent fauna, or does it reflect a lack of research in this area? Geiser (2004a) suggests that "there is no reason to predict that Australian rodents avoid torpor use" and further investigation into the thermoregulatory strategy of Australian rodents is required.

Here we investigate the thermal physiology of the ash-grey mouse (*Pseudomys albocinereus*), to determine if this native Australian murine rodent uses torpor, or if it has other physiological adaptations that allow it to achieve energy and water balance. Ash-grey mice are small (15–40 g) rodents that inhabit shrub and tree heathlands in the semi-arid areas of south-western Australia (Morris and Bradshaw, 1981; Nowak, 1991; Menkhorst, 2001). They are nocturnal, sheltering in shallow burrows during the day and feeding on an omnivorous diet of arthropods, seeds, lichen and vegetation (Nowak, 1991; Murray et al., 1999). A high water flux rate during winter reflects a predominantly herbivorous diet during the wetter months, while the diet is dominated by arthropods in the drier months (Morris and Bradshaw, 1981). Ash-grey mice, along with many other species of *Pseudomys*, are social, with several individuals inhabiting the same burrow (generally one adult male, one to two adult females and the young of different generations; Nowak, 1991). Ash-grey mice reproduce year round, with peak reproduction occurring after winter rainfall (Nowak, 1991).

2. Material and methods

Eleven (3 female, 8 male) adult ash-grey mice (*P. albocinereus*) were trapped in pit traps at Cataby (30°44'S 115°32'E), approximately 160 km North of Perth, Western Australia, where mean monthly temperatures range from 7–18 °C minimum to 18–35 °C maximum, and annual rainfall is 541 mm (data for Badgingarra weather station; http://www.bom.gov.au/climate/averages/tables/cw_009037.shtml). Ash-grey mice were housed indoors in individual cages at an ambient temperature (T_a) of approximately 22 °C, with 12L:12D photoperiod. Mice were provided with food (mouse pellets, sunflower and millet seed, fresh fruit and vegetables) and water *ad libitum*, except the night preceding eight-hour experiments when food was withheld to ensure the animals were in a post-absorptive state. Temperature-sensitive passive implantable transponders (PITs; Respironics G2 E-mitters) were implanted into the intra-peritoneal cavity of five mice under general anaesthesia (2–3% isoflurane in O_2). Experiments commenced at least two weeks after surgery to allow the mice to recover. Mice were collected and held under a scientific license from the West Australian Department of Environment and Conservation and the study was approved by Curtin University and the University of Western Australia animal ethics committees.

Metabolic rate, measured as oxygen consumption (VO_2) and carbon dioxide production (VCO_2), was measured simultaneously with evaporative water loss (EWL) using flow through respirometry. Air flowed through a tubular glass metabolic chamber (770 cm^3) at a constant rate of 542 $mL\ min^{-1}$ controlled by a MKS 1159B-02000RV mass-flow meter in conjunction with a Sierra electronic flow controller. Excurrent

air passed over a Vaisala MNP45A thin film capacitance relative humidity (RH)/ T_a probe, with a subsample flowing through a column of drierite, a Servomex 574 O_2 analyser and a Qubit Systems S153 CO_2 analyser. The gas analysers and RH/ T_a probes were interfaced to a computer using Brymen voltmeters (TBM859CF and BM202) and data were recorded every 20 s using a custom-written Visual Basic (version 6) programme (P. Withers). Mice were measured at T_a of 10 °C (N = 10), 15 °C (N = 10), 20 °C (N = 11), 24 °C (N = 10), 29 °C (N = 11) and 34 °C (N = 8), in random order. Experimental duration was approximately 20 h at each temperature, commencing at 1900 h, except for at $T_a = 10$ °C, 29 °C and 34 °C where experiments were shorter to ensure animal welfare by minimising the period of exposure to more extreme T_a . At $T_a = 10$ °C, experiments commenced at around 01:00 and lasted for about 14 h; at $T_a = 29$ °C, they commenced about 07:00 h and lasted for approx. 8 h; and at 34 °C they commenced at about 10:00 h and lasted 4–5 h. For the five mice implanted with a PIT, Vital View software was used to record core T_b every 20 s for the duration of the experiment via a receiver pad (Respironics e-mitter ER4000) placed under the metabolic chamber and linked to a PC. For the mice that did not have an intra-peritoneal PIT, T_b was measured using an Omega-HH25TC meter with a plastic-tipped thermocouple inserted approximately 1.5 cm into the rectum immediately after removal from the metabolic chamber.

Calibration of the mass flow-meter was undertaken using a Gilian Gilibrator 2, traceable to a national standard. The oxygen analysers were two-point calibrated using compressed nitrogen (0% O_2) and dry ambient air (20.95% O_2). Calibration of the CO_2 analysers was achieved using compressed nitrogen (0% CO_2) and a certified gas mix (0.53% CO_2 ; BOC, Perth, Western Australia). The calibration of the relative humidity probes was confirmed using 1% RH air (dried with drierite to approximately 0.005 $mg\ L^{-1}$) and 100% RH air (saturated by breathing on the probe). The PITs were calibrated against a thermometer traceable to a national standard at $T_a = 18$ °C, 20 °C, 25 °C, 30 °C, 35 °C and 40 °C, both before implantation and after completion of all experiments.

All values are presented as mean \pm S.E., with the number of individuals (N) and the number of measurements (n). Mean minimum VO_2 , VCO_2 , EWL and T_b were calculated for 20-minute periods (after Withers, 2001 and Cooper and Withers, 2010). The respiratory exchange ratio (RER) was calculated as VCO_2/VO_2 , wet thermal conductance (C_{wet}) as $MHP/(T_b - T_a)$, and dry thermal conductance (C_{dry}) as $(MHP - EHL)/(T_b - T_a)$. MR was converted to metabolic heat production (MHP) using the oxy-caloric coefficient for the measured RER for that experiment, and EWL was converted to evaporative heat loss (EHL) using 2.4 $J\ mg\ H_2O^{-1}$ after Withers (1992). Relative water economy was calculated as MWP/EWL , where metabolic water production (MWP) was also calculated from VO_2 using the measured RER for that experiment after Withers (1992). The point of relative water economy (PRWE) was determined by linear regression as the T_a at which $RWE = 1$.

The effect of T_a on physiological variables was analysed by analysis of variance (ANOVA), with *a priori* contrasts and Student–Newman–Keuls (SNK) post-hoc tests. BMR, EWL, T_b and C_{wet} were compared to those of other rodents (Schmidt-Nielsen and Schmidt-Nielsen, 1950; Dawson, 1955; Lindeborg, 1955; Bartholomew and MacMillen, 1961; MacMillen, 1965, 1983; Hudson and Rummel, 1966; Chew et al., 1967; Church, 1969; MacMillen and Lee, 1970; Hart, 1971; Baudinette, 1973; Collins, 1973a,b; Collins and Bradshaw, 1973; Kenagy, 1973; Haines et al., 1974; Gettinger, 1975; Withers, 1977; Withers et al., 1979; Wickler, 1980; Scheck, 1982; Chappell, 1985; Hinds and MacMillen, 1985; Ouafara et al., 1987; MacArthur, 1989; Downes and Perrin, 1994; Richter et al., 1997; Cortés et al., 2000, 2003; Tracy and Walsberg, 2000; Arends and McNab, 2001; Liu et al., 2004; Lovegrove, 2003; Ehrhardt et al., 2005; Tirado et al., 2007; Tomlinson et al., 2007; McNab, 2008; Zhu et al., 2008; and references therein) using linear regression of \log_{10} transformed variables (except T_b , which was not logged). Anti-logged prediction values were calculated after Hayes

and Shonkwiler (2006, 2007). All variables were then examined for a phylogenetic signal (K^* and its probability; Blomberg et al., 2003) and rendered independent of phylogeny using autoregression (Cheverud and Dow, 1985; Rohlf, 2001) with a phylogeny derived from the mammal super-tree of Bininda-Emonds et al., (2007). Phylogenetic analysis was achieved with a custom written VB programme (P. Withers). Conformation to the conventional and phylogenetically independent allometric relationships was determined by the 95% prediction limits for the regression after Cooper and Withers (2006). Statistical analyses were conducted using Statistix (version 1.8; Statistix) and SPSS (v17 for windows; SPSS Inc.).

3. Results

The mean body mass of ash-grey mice ($N=11$) was 27.9 ± 0.81 g over all experiments ($n=60$). Ash-grey mice rested quietly in the metabolic chamber during measurements, curled up with piloerection at low T_a and sprawled out with depressed fur at high T_a . T_b was significantly influenced by T_a ($F_{5,52}=5.82$, $P<0.001$; Fig. 1), with an increase in T_b at $T_a=34$ °C ($T_b=37.9 \pm 0.58$ °C; SNK $P \leq 0.001$); there was no significant T_a effect at any other T_a (SNK $P \geq 0.263$; mean $T_b=35.2 \pm 0.16$ °C, $N=11$, $n=58$). One individual female ash-grey mouse went torpid (defined as $T_b < 30$ °C and $MR < BMR$, with spontaneous rewarming) at $T_a=20$ °C with a minimum T_b of 24.5 °C, and at $T_a=25$ °C with a minimum T_b of 28.4 °C. At $T_a=20$ °C, torpor commenced at 07:52 h and there was a brief arousal at 12:03 h, before torpor re-commenced at 13:00 h, lasting till 16:05 h. Torpor at $T_a=24$ °C followed a similar pattern but the duration was shorter, commencing at 08:31 h, arousal occurring at 10:39 h, and then a second bout occurring from 11:34 h until 14:59 h (Fig. 2). Cooling rates during torpor ranged from 0.76 °C h^{-1} to 2.69 °C h^{-1} ($T_a=24$ °C and 20 °C respectively) and rewarming rates were 1.5 °C h^{-1} at both T_a . The mouse achieved maximum post-torpor T_b s of 34.8 °C and 35.0 °C at $T_a=20$ °C and 24 °C respectively.

VO_2 was significantly affected by T_a ($F_{5,54}=24.4$, $P<0.001$; Fig. 1). Polynomial contrasts suggested significant linear and quadratic ($P \leq 0.001$) relationships between T_a and VO_2 . When $T_a=34$ °C was removed from the analysis, only the negative linear relationship remained ($P<0.001$), indicating that VO_2 began to increase at $T_a=34$ °C. Minimal MR occurred at $T_a=29$ °C and was 1.56 ± 0.252 mL $O_2 g^{-1} h^{-1}$; we define this as BMR. T_a did not influence RER ($F_{5,54}=1.96$, $P=0.099$) with a mean RER for the mice at all T_a ($N=8$, $n=42$) of 0.82 ± 0.018 . Consequently, VCO_2 mirrored VO_2 , so VCO_2 is not presented separately here. For the single torpid mouse, MR at $T_a=20$ °C decreased to 1.02 mL $O_2 g^{-1} h^{-1}$ or 44% of normothermic MR, and to 1.22 mL $O_2 g^{-1} h^{-1}$ or 73% of normothermic MR at $T_a=24$ °C.

T_a had a significant effect on C_{wet} ($F_{5,52}=23.9$, $P<0.001$) and C_{dry} ($F_{5,52}=11.2$, $P<0.001$; Fig. 1), with both differing at $T_a=34$ °C from all other T_a (SNK $P \leq 0.001$). Polynomial contrasts indicated significant linear and quadratic ($P<0.001$) relationships between both C_{wet} and C_{dry} , and these remained after $T_a=34$ °C was removed from the model ($P \leq 0.021$). Standard C_{wet} at thermoneutrality ($T_a=29$ °C) was 4.99 ± 0.54 J $g^{-1} h^{-1} °C^{-1}$, and standard C_{dry} was 4.23 ± 0.48 J $g^{-1} h^{-1} °C^{-1}$ ($N=11$, $n=11$).

There was a significant effect of T_a on EWL of the mice ($F_{5,54}=15.0$, $P<0.001$; Fig. 1), with EWL increasing dramatically at $T_a=34$ °C (4.69 ± 0.81 mg $H_2O g^{-1} h^{-1}$) compared with that at lower T_a (SNK $P \leq 0.001$; mean EWL = 1.68 ± 0.062 mg $H_2O g^{-1} h^{-1}$, $n=52$, $N=11$). Polynomial contrasts indicated linear and quadratic ($P<0.001$) relationships between EWL and T_a ; however, when EWL at $T_a=34$ °C was removed from the model there was no significant T_a effect ($F_{4,47}=1.146$, $P=0.347$) and no significant linear or quadratic contrasts ($P \geq 0.213$). Standard EWL of ash-grey mice (at $T_a=29$ °C) was 1.92 ± 0.21 mg $H_2O g^{-1} h^{-1}$. RWE was significantly influenced by T_a ($F_{5,54}=37.9$, $P<0.001$) with polynomial contrasts indicating a significant linear relationship; $RWE = -0.0517(T_a) + 2.01$ ($P<0.001$;

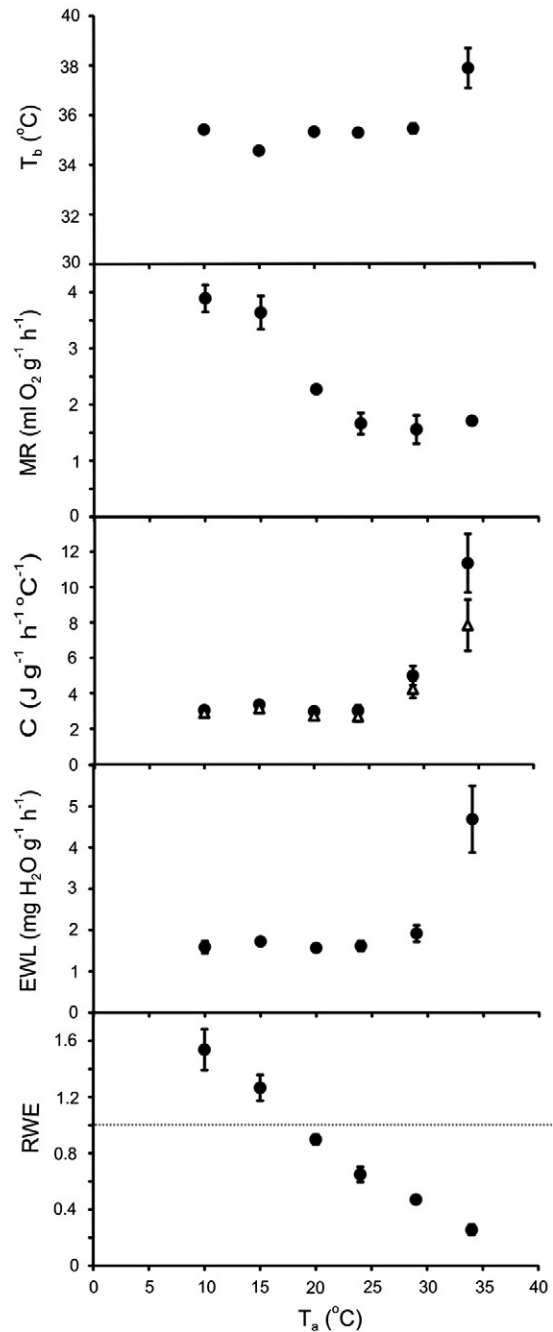


Fig. 1. Effect of ambient temperature (T_a) on body temperature (T_b), metabolic rate (MR), wet (dark circles) and dry (white triangles) thermal conductance (C), evaporative water loss (EWL) and relative water economy (RWE) of ash-grey mice. Values are mean \pm SE, $N=8$ at $T_a=34$ °C, 10 at $T_a=10$ °C, 15 °C and 24 °C and 11 at $T_a=20$ °C and 29 °C. Dashed line indicates $RWE=1$ (i.e. metabolic water production = evaporative water loss).

Fig. 1). The PRWE was at $T_a=19.5$ °C. EWL of the torpid mouse was reduced to 68–78% of that during normothermia, to 1.08 and 1.27 mg $H_2O g^{-1} h^{-1}$ at $T_a=20$ and 24 °C respectively.

There were significant conventional allometric relationships for all physiological variables of rodents except T_b (Table 1). Ash-grey mice conformed to all conventional allometric relationships except for BMR, which was 181% of predicted and fell above the 95% prediction limits for the regression. There was a weak but significant phylogenetic pattern for all physiological variables except C_{wet} . After accounting for this phylogenetic pattern, the T_b , EWL and C_{wet} of ash-grey mice still conformed to those of other rodents, but BMR was still

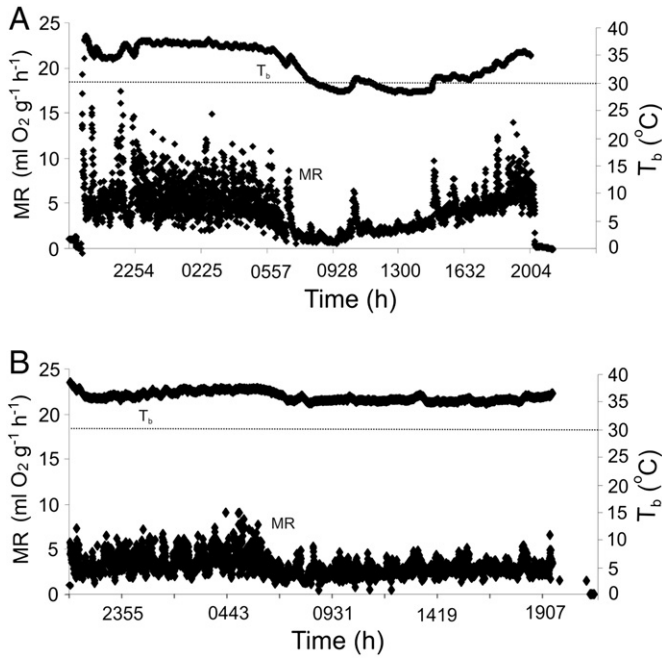


Fig. 2. Metabolic rate (MR) and body temperature (T_b) of two ash-grey mice, showing A) a torpor bout and B) normothermia at $T_a = 25$ °C. The dashed line at $T_b = 30$ °C indicates the threshold for torpor.

significantly higher than expected for an equivalently-sized rodent (Table 1).

4. Discussion

For the majority of the ash-grey mice studied here, patterns of T_b , MR, C and EWL with changing T_a were consistent with those expected for a typical endotherm and for other rodents in general (e.g. Dawson, 1955; Chew et al., 1967; MacMillen and Lee, 1970; Collins, 1973a,b; Chappell, 1985; Tomlinson et al., 2007). One individual ash-grey mouse entered torpor twice at T_a s below thermoneutrality. This physiological state was indisputably torpor rather than pathological hypothermia as the mouse spontaneously aroused (undisturbed) to a normothermic T_b within the metabolic chamber, at a constant T_a (Fig. 2). This is the first unequivocal record of torpor for a native Australian rodent. As is widely appreciated for other endotherms, including rodents, the physiological consequence of torpor is reduced energy and water expenditure during the period of heterothermia. The torpid ash-grey mouse lowered T_b by up to 9.2 °C, reducing MR to 44% and EWL to 68% of normothermic values. Metabolic and hygric savings from torpor were less than those for other rodents such as the golden spiny mouse, which reduces MR to approximately 17% (Ehrhardt et al., 2005) and torpid gerbils, which reduce daily EWL to 27%, of normothermic rates (Buffenstein, 1985). This presumably reflects the high torpor T_b and slow rewarming rate of the ash-grey mouse, both of which differed significantly from that

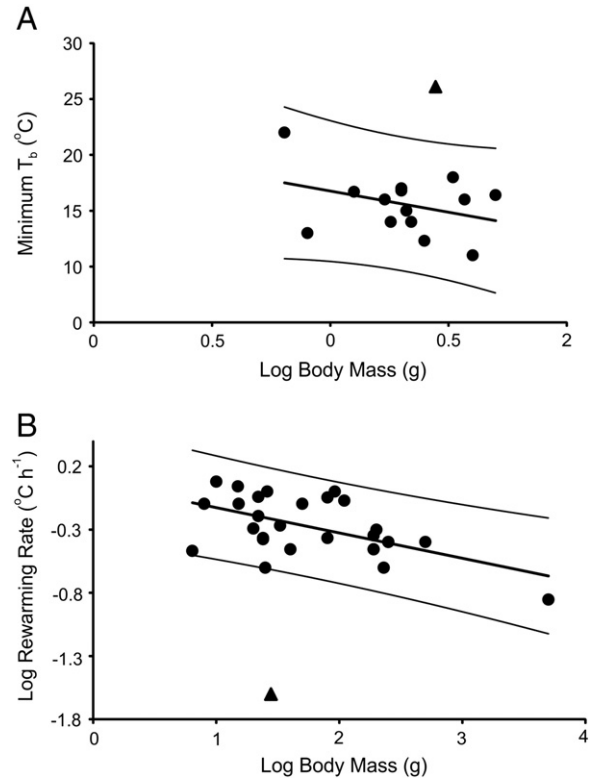


Fig. 3. Allometric relationship for A) minimum torpor body temperature ($N = 14$) and B) rewarming rate ($N = 28$) for rodents (circles, data from Geiser and Baudinette, 1990) with 95% prediction limits for a further datum. The ash-grey mouse is included as a triangle.

predicted for an equivalently-sized rodent (Fig. 3; data from Geiser and Baudinette, 1990).

None of the other ten ash-grey mice became torpid during experiments. Some animals are reluctant to enter torpor in a metabolic system (e.g. numbats, *Myrmecobius fasciatus*; Cooper and Withers, 2002, 2004) or in captivity in general (Geiser et al., 2000), so absence of torpor in the laboratory despite an ability to become heterothermic may not be surprising. Although ash-grey mice clearly have the physiological capacity for torpor, they appear reluctant to use this as a survival strategy, and certainly do not undergo torpor as readily as many small Australian marsupials or bats (Geiser, 2004b). On cold mornings during trapping, no ash-grey mice were found torpid in the pit traps, while almost all of the marsupials caught (dunnarts, *Sminthopsis* spp.; honey possums, *Tarsipes rostratus*) were torpid (authors, pers. obs.). Furthermore, the high torpor T_b , slow rewarming rate (cf. Geiser, 1990) and relatively minor metabolic reduction of the single torpid individual, together with a more common response of homoeothermy, suggest that torpor is not the primary thermoregulatory strategy for this species. The individual that entered torpor was the smallest mouse (17.3 g); it is likely the larger individuals had sufficient energy reserves to maintain

Table 1

Comparison of the ash-grey mouse to rodent allometric relationships for basal metabolic rate (BMR), body temperature (T_b), wet thermal conductance (C_{wet}) and evaporative water loss (EWL), both before (conventional) and after correction for phylogenetic history by autoregression (phylogenetically independent). Data are \log_{10} transformed (except T_b); N = sample size for the regression; % pred indicates the value for the ash-grey mouse as a % of the predicted value for a body mass of 27.9 g (or difference from predicted for T_b); inside 95% PL indicates if the datum for the ash-grey mouse falls within the 95% prediction limits for a further datum; K^* is Blomberg's index for phylogenetic signal, with its probability (P) value. Data sources as in text.

Variable	N	Conventional					K^*	P for K^*	Phylogenetically Independent			
		Slope	P	R^2	% pred	Inside 95% PL			Slope	P	R^2	Inside 95% PL
BMR	238	0.68 ± 0.013	<0.001	0.923	181	Above	0.428	<0.001	0.71 ± 0.016	<0.001	0.859	Above
T_b	176	0.27 ± 0.159	0.089	0.017	-1.3 °C	Yes	0.915	<0.001	0.36 ± 0.179	0.047	0.023	Yes
C_{wet}	21	0.53 ± 0.126	<0.001	0.482	136.8	Yes	0.282	0.128	0.15 ± 0.081	0.072	0.160	Yes
EWL	70	0.66 ± 0.0051	<0.001	0.712	77.9	Yes	0.598	<0.001	0.57 ± 0.065	<0.001	0.530	Yes

homeothermy throughout the 20 hour experimental duration, where this smaller individual could not.

There are substantial ecological and physiological consequences of heterothermy due to the temperature-dependence of biological processes (McNab, 2002; Humphries et al., 2003; Stawski and Geiser, 2010; Withers and Cooper, 2010). Sensory and motor functions are reduced during torpor, leading to increased risk of predation and reduced competitive ability. Physiological processes such as active transport across cell membranes, protein synthesis, mitosis and sleep slow or cease during torpor, with negative effects on immune-competence, reproductive output, the neurological system, circulation, ion balance and lipid peroxidation (Humphries et al., 2003; Stawski and Geiser, 2010). Therefore, there are fundamental advantages to maintaining a high and stable body temperature, so long as the high energetic costs of maintaining endothermic homeothermy can be met (McNab, 2002; Withers and Cooper, 2010). Using torpor is advantageous in spite of its costs when not enough energy is available, or when it is too costly to maintain homeothermy. This explains why ash-grey mice as well as species such as sugar gliders (*Petaurus breviceps*; Christian and Geiser, 2007) and chipmunks (*Tamias striatus*; Landry-Cuerrier et al., 2008) use torpor only as a last resort to survive critical energy bottlenecks, rather than as a routine energy conservation strategy.

Various aspects of the ash-grey mouse's normothermic physiology also suggest that homeothermy may be the ash-grey mouse's predominant thermoregulatory strategy, despite the importance of heterothermy for many sympatric marsupials and bats (Geiser, 2004b). The ash-grey mouse has a high BMR compared to rodents in general, indicating physiological adaptation to a high-energy lifestyle rather than a physiology consistent with energy conservation. Heterothermy in rodents is generally correlated with a low BMR, presumably as a result of similar pressures for a frugal energy lifestyle; species with a habitat, diet or life history that necessitates an adaptively low BMR are also likely to obtain an adaptive advantage from the energetic and hygric consequences of torpor (Cooper and Geiser, 2008). The BMR of the ash-grey mouse also falls above McNab's (1983) boundary curve for endothermy, predicting homeothermy. T_b , C_{wet} and EWL of the ash-grey mouse did not differ from other rodents, despite its semi-arid distribution, suggesting that other non-physiological strategies may relieve environmental pressures. The PRWE (considered an index of adaptation to aridity) of ash-grey mice was similar to that of other rodents, which does not suggest any particular adaptation to water conservation (MacMillen and Hinds, 1983).

A combination of an omnivorous diet, nocturnal activity, semi-fossorial habit and sociality may negate the need for torpor under most circumstances, and enable ash-grey mice to exploit a high energy strategy despite their semi-arid distribution. Their omnivorous diet means that a wide range of items are potential food, a factor identified as contributing to their wide distribution (Morris and Bradshaw, 1981). Availability of dietary components such as seed and vegetation are likely to be less variable over the short term than foods such as insects and nectar, on which highly heterothermic species such as dasyurids, small possums and bats feed (McNab, 2002). Lovegrove (2000) recognised resource predictability as an important factor determining heterothermy of small mammals. Resources are likely to be comparatively predictable for omnivorous ash-grey mice compared to nectarivorous or insectivorous sympatric marsupials and bats.

Nocturnal activity allows ash-grey mice to avoid high daytime temperatures, and sheltering in humid burrows during the day not only provides a relatively stable microclimate but also reduces EWL, so the absolute reduction in EWL achieved by torpid individuals in burrows is likely to be of little ecological benefit (MacMillen, 1983). Sociality means that ash-grey mice have the potential to huddle to create a warmer microclimate and reduce heat loss. Huddling has been noted for species such as the white-footed mouse (*Peromyscus leucopus*) as an adaptation to survive low T_a in winter. Huddling in groups of three reduced the daily energy expenditure of white-footed mice by 16–33%

compared to mice housed individually (Vogt and Lynch, 1982). Sociality may also explain the lack of torpor by the Australian sandy inland mouse (Tomlinson et al., 2007).

Despite an apparent reluctance to use torpor at low T_a , hyperthermia at high T_a was a consistent feature of thermoregulation by ash-grey mice. At $T_a = 34$ °C, T_b increased by 2.5 °C compared to normothermic T_b , accompanied by an increase in all other measured physiological variables. Hyperthermia has been observed in many other rodents, e.g. Australian hopping mice, kangaroo mice, swamp rats, cactus mice and various heteromyid rodents (Bartholomew and MacMillen, 1961; MacMillen, 1965; Hudson and Rummel, 1966; MacMillen and Lee, 1970). The observed hyperthermia is likely a strategy to reduce water loss otherwise required for evaporative cooling (e.g. *Microdipodops pallidus* Bartholomew and MacMillen, 1961). Increasing T_b from 35.4 °C to 37.8 °C resulted in water savings of 7.84 mg H₂O g⁻¹ h⁻¹ for ash-grey mice.

We conclude that an omnivorous diet, nocturnality, semi-fossoriality and sociality explain the high-energy turnover rather than energy-conserving strategy of the ash-grey mouse. This high-energy strategy explains its reluctance to enter torpor during short-term energy deprivation. Nevertheless, it has the capacity to enter and spontaneously arouse from at least shallow torpor. This is the first unequivocal evidence of torpor use by an endemic Australian murine rodent.

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