© 2016. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2016) 219, 2166-2172 doi:10.1242/jeb.137828

RESEARCH ARTICLE

Basking hamsters reduce resting metabolism, body temperature and energy costs during rewarming from torpor

Fritz Geiser*,‡, Kristina Gasch, Claudia Bieber, Gabrielle L. Stalder, Hanno Gerritsmann and Thomas Ruf

ABSTRACT

Basking can substantially reduce thermoregulatory energy expenditure of mammals. We tested the hypothesis that the largely white winter fur of hamsters (*Phodopus sungorus*), originating from Asian steppes, may be related to camouflage to permit sun basking on or near snow. Winter-acclimated hamsters in our study were largely white and had a high proclivity to bask when resting and torpid. Resting hamsters reduced metabolic rate (MR) significantly (>30%) when basking at ambient temperatures (T_a) of ∼15 and 0°C. Interestingly, body temperature (T_b) also was significantly reduced from 34.7±0.6°C (T_a 15°C, not basking) to 30.4±2.0°C (T_a 0°C, basking), which resulted in an extremely low (<50% of predicted) apparent thermal conductance. Induced torpor (food withheld) during respirometry at T_a 15°C occurred on 83.3±36.0% of days and the minimum torpor MR was 36% of basal MR at an average T_b of 22.0±2.6°C; movement to the basking lamp occurred at T_b<20.0°C. Energy expenditure for rewarming was significantly reduced (by >50%) during radiant heat-assisted rewarming; however, radiant heat per se without an endogenous contribution by animals did not strongly affect metabolism and T_b during torpor. Our data show that basking substantially modifies thermal energetics in hamsters, with a drop of resting T_b and MR not previously observed and a reduction of rewarming costs. The energy savings afforded by basking in hamsters suggest that this behaviour is of energetic significance not only for mammals living in deserts, where basking is common, but also for *P. sungorus* and probably other cold-climate mammals.

KEY WORDS: *Phodopus*, Passive warming, Energy conservation, Thermoregulation, Radiant heat

INTRODUCTION

Small mammals and birds have high energy requirements during cold exposure to a large extent because of the substantial heat loss over their large relative surface area (Tattersall et al., 2012). This can have serious consequences in the wild where access to food required for maintaining a high metabolic rate is often limited. To minimise energy loss and to survive such bottlenecks, small endotherms use several behavioural and physiological approaches.

A widely used and effective behavioural approach by mammals is basking in the sun to reduce normothermic thermoregulatory energy expenditure at low ambient temperature (T_a) (Bartholomew and Rainy, 1971; Geiser and Drury, 2003; Brown and Downs, 2007; Signer et al., 2011; Stannard et al., 2015). Basking has been shown to be effective in maintaining resting metabolic rate (RMR) of small mammals near basal metabolic rate (BMR) over a wide range of T_a well below thermoneutrality (Geiser and Drury, 2003; Scantlebury et al., 2010). Basking is also known to reduce metabolic rate (MR) in free-ranging ibex (*Capra ibex*) by up to 20% (Signer et al., 2011) and in rock hyrax (*Procavia capensis*) it increased body temperature (T_b) and probably reduced thermoregulatory energy expenditure at low T_a (Brown and Downs, 2007).

The most effective physiological approach from an energy conservation point of view is, however, torpor, which is characterised by substantial periodic reductions of T_b and MR to fractions of BMR (Boyer and Barnes, 1999; Ruf and Geiser, 2015). Torpor is of crucial importance for energy balance and survival in many small endotherms and is often expressed at low T_a. Nevertheless, although the torpid state is characterised by extremely low MRs, endothermic arousals at the end of a torpor bout to raise T_b from low to high normothermic levels require an enormous increase in MR, compromising overall energy savings gained from using torpor (Lyman et al., 1982). However, recent data show that the high energetic costs required for rewarming from torpor can be largely avoided by behavioural thermoregulation and specifically basking in the sun. Basking behaviour in the morning has been observed in several torpid desert or savanna mammals with T_b as low as 15°C (Geiser et al., 2002, 2004; Warnecke et al., 2008; Thompson et al., 2015). This is despite the fact that many of these species are widely considered to be entirely nocturnal and risk predation during the day, especially when movement is slowed (Rojas et al., 2012). Basking during rewarming is particularly important during daily torpor, which usually lasts <12 h within a 24 h cycle and therefore requires many potentially costly arousals (Ruf and Geiser, 2015). Although daily energy savings through the use of daily torpor are usually only 10–30% because of the energy expenditure during rewarming as well as activity, savings can be as high as 50% or more in animals with access to radiant heat (Geiser et al., 2004).

To date, essentially all information on basking and passive rewarming from torpor has been derived from work on desert and tropical mammals that are more or less brown and show little or no seasonal change in fur colour (Geiser et al., 2004; Dausmann, 2014). However, basking during rest and during passive rewarming is likely to also be of energetic importance in cold-temperate areas where endotherms must deal with large T_b–T_a differentials and thus high thermoregulatory costs in winter (Tattersall et al., 2012) that could be reduced by basking. Of special interest in this regard are those cold-climate species that show strong seasonal changes in fur colour from dark to light, which will affect the uptake of radiant heat as well as camouflage (Merritt, 2010).

A well-known example is the Djungarian hamster, *Phodopus sungorus* (body mass ∼30 g), which changes its fur from brown in

Research Institute of Wildlife Ecology, Department of Integrative Biology and Evolution, University of Veterinary Medicine Vienna, Savoyenstrasse 1, Vienna 1160, Austria.
*Present address: Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale, New South Wales 2351, Australia.

‡Author for correspondence (fgeiser@une.edu.au)

F.G., 0000-0001-7621-5049

Received 26 January 2016; Accepted 2 May 2016

List of abbreviations

BMR	basal metabolic rate
C	apparent thermal conductance
MR	metabolic rate
RMR	resting metabolic rate
T_a	ambient temperature
T_b	body temperature

summer (or when long photoperiod acclimated) to almost entirely white in winter (or when short photoperiod acclimated) (Steinlechner et al., 1986; Ruf et al., 1993; Hiebert et al., 2000; Geiser et al., 2013; Cubuk et al., 2015). White winter-acclimated individuals enter spontaneous daily torpor (food *ad libitum*), whereas brown summer-acclimated animals do not (Heldmaier and Steinlechner, 1981; Ruf et al., 1993; Geiser et al., 2013). Little is known about the ecology and biology of the species in the wild, but they live in steppes of central Asia that receive substantial amounts of sun in winter and they do not restrict activity to the night (Flint, 1966), as is also the case in captivity, especially when exposed to low T_a (Heldmaier et al., 1989; Ruf et al., 1991; Müller et al., 2015). It also seems highly unlikely that the selection of such a profound seasonal change in fur colour would occur in a strictly nocturnal animal, suggesting some diurnal activity. Nevertheless, it is generally assumed that the white fur colour in winter is mainly of importance for camouflage on snow at night. Although the thermal properties of *P. sungorus* fur have been measured (Walsberg, 1991), basking behaviour and the implications of basking on thermal energetics during rest and torpor have never been quantified to our knowledge.

Because the white fur colour of *P. sungorus* may have significant effects on the thermal energetics of the species during basking and probably contributes to its ability to bask during the day in the wild without being eaten, we aimed to investigate how offering a radiant heat source affects the basking behaviour and thermoregulatory energy expenditure of these hamsters. As energetic and thermal challenges will be critical, especially during cold winters, we investigated both normothermic and torpid winter-acclimated white individuals exposed to different thermal conditions with or without access to radiant heat. We hypothesised that, like other small mammals, *P. sungorus* would bask during both normothermia and torpor at low T_a if offered a radiant heat source, and that this behaviour would affect thermal energetics and reduce thermoregulatory energy expenditure.

MATERIALS AND METHODS

Animal maintenance

Adult *P. sungorus* (Pallas 1773) (n=10 individuals, 5 females, 5 males) born in August/September 2014 (4–5 months old at the beginning of the experiments) were used for our study. Hamsters were held in a ventilated room at the Research Institute of Wildlife Ecology under a natural photoperiod from summer (16 h:8 h light: dark) to winter (9.5 h:14.5 h light:dark; sunrise ∼07:00 h, sunset ∼17:15 h) in February when most measurements were performed and torpor is regularly expressed (Jefimow et al., 2011). Pelage colour of the animals was at stage 4, i.e. white except for a mid-dorsal dark stripe (Duncan and Goldman, 1984). As *P. sungorus* are strongly solitary and accept the presence of conspecifics of the other sex only during mating, animals were held individually. Each cage was provided with wood shavings and paper for nest construction. Water was accessible *ad libitum*. During holding periods, hamsters were fed *ad libitum* with standard hamster chow (ssniff®HA, ssniff GmbH, Soest, Germany). Animals were checked daily and T_a was recorded. Measurements were conducted between 27 January and 8 March 2015 when T_a in the holding room was 9±2°C.

The experiments were approved by the institutional ethics committee and the national authority according to §8ff of the Law of Animal Experiments, Tierversuchsgesetz-TVG (permit number BMWFW_68.205/0209-WF/V/3b/2014).

T_b measurements

To measure T_b throughout the experiments, all individuals were implanted intraperitoneally with small temperature-recording data loggers (custom made and calibrated at the Research Institute of Wildlife Ecology; storage capacity 100,000 temperature readings, accuracy ±0.1°C, programmed to record T_b at 2 min intervals). Logger mass after coating in paraffin/Elvax was 1.7 g, which is well below the recommended 10% of the body mass for implanted devices in small terrestrial mammals (Rojas et al., 2010). Coated loggers were sterilised before implantation. Surgical anaesthesia was induced by subcutaneous injection of 75 mg kg^{-1} ketamine (Ketamidor® 10%, Richter Pharma Wels, Austria) and 300 μg kg^{-1} Medetomidine (Domitor® 0.1%, Orion Corporation, Turku, Finland) and maintained by approximately 1.5% isoflurane in an oxygen stream via a facemask. Pre-emptive post-surgical analgesia (1 mg kg^{-1} Meloxicam) was provided subcutaneously. The animals were placed in dorsal recumbency on a heating pad and the operation field was prepared according to standard surgical procedures and covered by sterile surgical drapes. A midline incision was made and the abdominal cavity was opened through a ∼1 cm incision in the linea alba. Post-implantation, the peritoneum and abdominal muscles were sutured using synthetic absorbable surgical suture material (USP 4/0, Surgicryl PGA, SMI AG, Hünningen, Belgium) using the single button suture technique. The skin was sutured separately using the same synthetic absorbable surgical suture material, but applying an intracutaneous suture technique. During the entire procedure, vital parameters (respiration rate, peripheral haemoglobin oxygen saturation as measured by pulse oximetry, P_{O_2}, heart rate) were monitored. After implantation, animals were placed into their cages and the healing process was checked daily. Animals were allowed to recover from surgery at thermoneutral T_a (23–25°C) for 1 week. Implantations were carried out on 20 January 2015 and loggers were removed in early April 2015.

MR measurements

MR of hamsters was measured as the rate of oxygen consumption ($\dot{M}_{O_2}$) using open-flow respirometry with a Servomex paramagnetic oxygen analyser (Servopro 4100, Servomex, Crowborough, UK). The analyser was calibrated before measurements commenced and once during the measurement period. Animals were placed into four 750 ml Perspex respirometry tubes that allowed free movement and were placed within a temperature-controlled cabinet (TPK600, Feutron, Langenwetzendorf, Germany). Visually separated respirometry tubes were sealed at either end by a rubber stopper containing inlets for air on one side and outlets on the other, and also an inlet for shielded thermocouple probes to measure the T_a in the respirometry tubes. During respirometry measurements, a thin layer of wood shavings was provided on the respirometer floor for absorption of urine and faeces; food and water were not provided. The respirometry tubes were 25 cm long, 12 cm of which was covered by a cardboard tube to provide a refuge for the animals. The flow rate, measured with mass-flowmeters (FMA 3100, Omega Engineering, Stamford, CT, USA), through the respirometry chamber was about 800 ml min^{-1}. Four individual animal channels and one control channel (outside air) were measured in sequence for 1 min each; therefore, a reading for each animal was taken every 5 min. Channels were switched via solenoid valves and the washout from the tubing to the analyser was achieved within 10 s. Metabolism was measured either with or without access to radiant heat provided in the form of a heat lamp (Daylight Basking Spot, incandescence 75 W reflector globe, colour rendering index CRI 83, colour temperature 2560 K) placed at an angle of 90 deg and 15 cm above the transparent respirometer and at that distance provided approximately 35,000 lx illumination (~51 W m^{-2}) through the highly transmissive Perspex. The energy provided by this heat source was well below that of natural solar radiation during bright sunlight (~110,000 lx or ~161 W m^{-2}), but has been shown previously to effectively induce basking behaviour and reduce energy expenditure required for thermoregulation in small marsupials (Geiser and Drury, 2003; Warnecke and Geiser, 2010). The T_b was measured throughout these measurements as outlined above using the implanted temperature loggers. Animals were observed through a window throughout the daytime when measurements were conducted and their behaviour was recorded.

Experimental setup

Two experimental approaches were used: daytime measurements and overnight measurements.

For daytime measurements, animals were measured for several hours from the morning to the afternoon (from about 09:00 h to 16:00 h) to measure RMR at a T_a of ~15 and 0°C for about 2.5–3 h each, either with or without access to a radiant heat source for the entire duration of measurements (Fig. 1). Each animal was measured once with the heat lamp on and once with the heat lamp off. The T_a in the respirometry chamber was maintained at the same or similar temperature when the heat lamp was on or off by adjusting the T_a of the temperature-controlled cabinet. The T_a in the respirometry tubes during measurements was 14.9±0.3°C with the lamp off and 14.7±0.5°C with the lamp on; and −0.1±0.6°C with the lamp off and 0.6±0.7°C with the lamp on.

For overnight measurements, animals were measured from about 16:00 h to 14:00 h on the next day at a T_a of ~15°C. Food and water were withheld to induce torpor. Each animal was measured 1–3 times (mean 1.9±0.6 times) depending on their expression of torpor and animals were rested for >4 days between measurements with food and water *ad libitum*. Animals were observed in the morning soon after sunrise, and once their torpor MR (TMR) reached a steady-state minimum, the heat lamp was switched on (between 08:04 h and 09:40 h) for 1–1.5 h to assess their metabolic response. On N=11 occasions at T_a ~15°C, the heat lamp was switched on first at or near the TMR minimum, on N=1 occasion early during the rewarming phase, and on N=1 occasion during normothermia. The heat lamp was then switched off for brief periods, but switched on again for different time periods at T_a 15°C to assess the effect of radiant heat on MR and T_b. However, during some measurements (N=8), T_a was also permitted to increase when radiant heat was switched on to assess the potential change of MR and T_b during a change in T_a.

Calculations, definitions and statistics

MR during rest and torpor was averaged over at least 15 min when values were minimal and stable, and were calculated according to Withers (1977). The corresponding T_b and T_a were averaged over the same time period. The torpor threshold was defined as T_b <30.0°C (i.e. a fall of T_b by >5°C below normothermic resting T_b; Ruf and Geiser, 2015). Apparent thermal conductance C was calculated using: C=MR/(T_b−T_a) (Bradley and Deavers, 1980). The average energy expenditure of rewarming for fully endothermic and radiant heat-assisted rewarming was calculated during arousals in which T_b increased by >5.0°C; the average energy expenditure for raising T_b by 1.0°C was also calculated. Maximum MR during activity at night, during fully endothermic rewarming and during radiant heat-assisted rewarming was calculated from the single highest MR value measured. Maximum cooling and rewarming rates (°C min^{-1}) for fully endothermic and radiant heat-assisted rewarming were determined over 10 min.

To adjust for repeated measures, we computed linear mixed effect models entering animal ID as a random factor (R package nlme v3.1-118; https://cran.r-project.org/web/packages/nlme/nlme.pdf). F- and P-values given in the text correspond to models that minimised Akaike's information criterion (AIC). For the response variable RMR, the independent variables log body mass, T_a and lamp on/off were entered as fixed predictors. T_a and lamp on/off were also used as independent variables in models testing for differences in T_b. For energy expenditure during rewarming, we used lamp on/off and mean T_b–T_a gradient as predictors, as well as log body mass of individuals as a covariate. The log body mass was used because the AICs of these models were lower than when using body mass. We used total MR with log body mass entered as a covariate for statistical analyses to avoid errors inherent in using indices such as mass-specific MR (e.g. Packard and Boardman, 1988; Hayes, 2001). However, to ease visual comparisons, we still show some mass-specific MR in the figures. Linear regressions were fitted by the least squares method. Values are expressed as means with s.d. for n individuals measured; N is the number of measurements. All statistical tests were carried out using R 3.2.2 (R Core Team 2014; http://www.r-project.org).

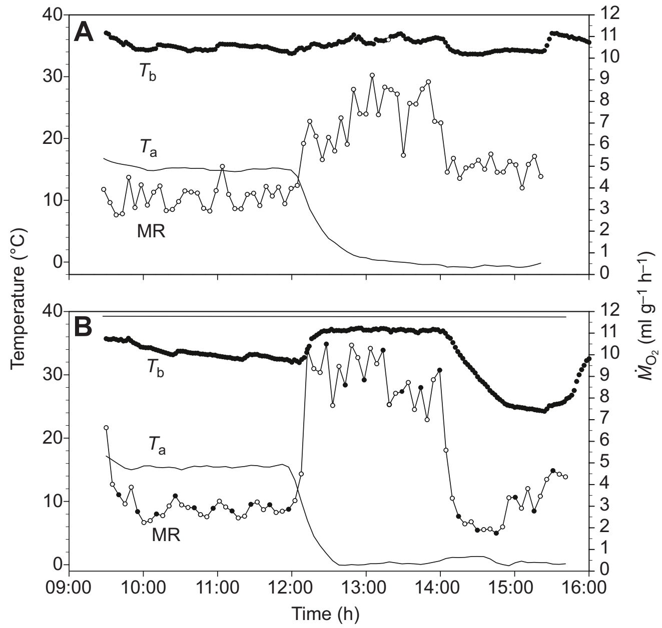

Fig. 1. Body temperature, metabolic rate and ambient temperature in *Phodopus sungorus* as a function of time during daytime measurements. (A) Heat lamp off; (B) heat lamp on for the entire time, as indicated by the bar at the top of the graph. T_b, body temperature; T_a, ambient temperature; MR, metabolic rate, measured as the rate of oxygen consumption ($\dot{M}_{O_2}$).

RESULTS

Daytime measurements

When the heat lamp was on, all individuals basked during rest phase respirometry measurements. If not positioned beneath the heat lamp, hamsters moved from their tube refuge to under the heat lamp and adopted a curled position sitting on their hind legs and parted their dorsal hair to allow radiant heat to penetrate to the skin.

The MR and resting T_b of hamsters during short-term daytime measurements were strongly affected by radiant heat exposure (Fig. 1). When the heat lamp was off and the hamster was not basking at T_a 15°C (Fig. 1A), the MR and T_b remained high and fluctuated somewhat. Both MR and T_b increased initially when T_a was lowered to 0°C and the hamster became active, but MR then fell to resting values above those at T_a 15°C. When the heat lamp was on and the hamster was basking (Fig. 1B), the RMR was lower at T_a 15°C and then the T_b declined to ∼32°C with time. A more extreme response was observed when T_a was lowered to 0°C (Fig. 1B). Initially, MR and T_b increased again during a bout of activity, but when the basking hamster returned to rest it substantially reduced both MR and T_b well below the values when it was not basking and interestingly below the basking MR and T_b at T_a 15°C. After removal of hamsters from the respirometer at ∼15:30 h, their T_b rose again.

The mean RMR was significantly ($F_{1,25}$=125.36, P<0.001) reduced by >30% on average at both T_a 15 and 0°C when animals had access to radiant heat (Fig. 2A; mean body mass 26.8±2.3 g). In non-basking hamsters, RMR increased with decreasing T_a as expected, and was 1.9- to 2.2-fold of BMR on average. In contrast, when hamsters were basking, average RMR was only 1.3- to 1.4-fold of the BMR and the slope for the RMR–T_a relationship was not significantly different from zero (t=1.43, P=0.16). Somewhat unexpectedly, animals also reduced T_b substantially, on average by ∼2°C, when they had access to radiant heat (Fig. 2B; $F_{1,25}$=22.90, P<0.001) and the maximum cooling rate over 10 min for T_b during basking at T_a 0°C was 0.257±0.080°C min^{-1} (n=9). T_b fell from a mean of 34.7±0.6°C to 32.8±1.2°C at T_a 15°C and from 32.4±1.1°C to 30.4±2.0°C at T_a 0°C; a few individuals had a T_b of <30°C at the time of minimum MR. Although this by our definition is torpor, we included these values here under ‘daytime measurements’ for comparison of values measured under similar experimental conditions and because they were well above the minima observed during torpor in our long-term measurements.

As a consequence of the low RMR and T_b, apparent thermal conductance (C) of basking hamsters was extremely low (Fig. 2C). At T_a 15°C and without radiant heat, C was close to that predicted from body mass. During all other measurements, C was well below that predicted and the lowest values (47% of predicted) were observed in basking hamsters at T_a 0°C with radiant heat provided, with a mean of 0.088±0.015 ml O_2 g^{-1} h^{-1} °C^{-1}. Both T_a ($F_{1,25}$=94.87, P<0.001) and the heat lamp ($F_{1,25}$=85.72, P<0.001) significantly affected C, but the slopes did not differ.

Overnight measurements

When food was withheld overnight, 9 of the 10 hamsters used torpor (i.e. induced torpor) on 83.3±36.0% of days during respirometry measurements (n=8 always used torpor, n=1 once in three trials, n=1 never in two trials). All individuals that entered torpor basked. When in the tube refuge, torpid hamsters moved under the heat lamp, although sometimes after some delay. Torpid hamsters also usually adopted a curled position, sitting on their hind legs, and parted their dorsal hair allowing radiant heat to penetrate to the skin, but occasionally they stretched out flat under the lamp. The lowest

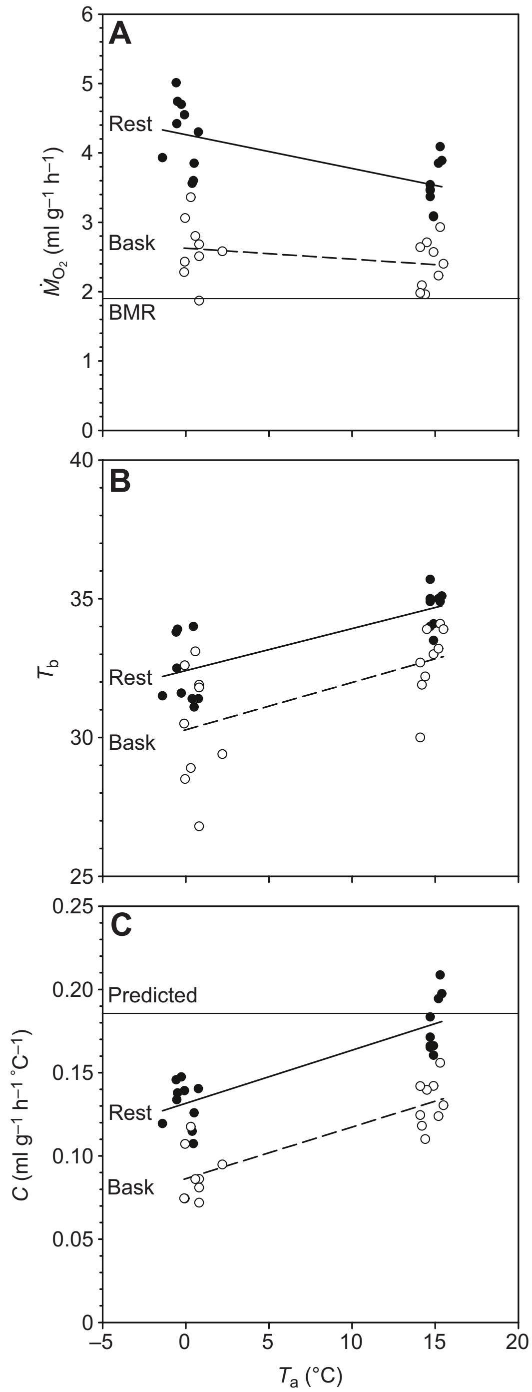

Fig. 2. $\dot{M}_{O_2}$, T_b and apparent thermal conductance as a function of T_a in resting *P. sungorus* with the heat lamp off (rest) and with the heat lamp on (bask). Basal metabolic rate (BMR) was obtained from Ruf and Geiser (2015) and the predicted conductance from Bradley and Deavers (1980). Linear regressions were calculated to identify the slope and intersect for comparison. (A) $\dot{M}_{O_2}$: rest y=4.26–0.049x, r^2=0.44; bask y=2.626–0.0158x, r^2=0.084; (B) T_b: rest 32.41+0.15x, r^2=0.61; bask y=30.28+0.17x, r^2=0.35; (C) apparent thermal conductance (C): rest: y=0.136+0.0032x, r^2=0.73; bask: y=0.086 +0.0031x, r^2=0.71.

T_b at which movement to the heat lamp was observed was 19.8°C and at these low T_b movement was a slow uncoordinated wobble. Loss of body mass in individuals expressing torpor was 2.71±0.35 g (n=9), to ∼65% of the body mass reduction of those remaining normothermic (4.15±1.06 g, n=2) throughout measurements.

Most hamsters that used torpor during respirometry measurements used one or two bouts of torpor. Single bouts were usually expressed in the morning. When two bouts were expressed, the first bout occurred around or after midnight and the second occurred in the morning (Fig. 3A). Only on two occasions were three bouts of torpor expressed, with the first occurring before midnight and the others at similar times to the other measurements (Fig. 3B). The mean steady-state torpor values expressed during the most pronounced torpor bout of each individual (n=9) and the corresponding T_a and body mass were: TMR=0.686±0.215 ml O_2 g^{-1} h^{-1}, T_b=22.0±2.6°C, T_a=15.1±0.8°C, C=0.113±0.058 ml O_2 g^{-1} h^{-1} °C^{-1} and body mass=25.1±2.8 g).

Torpor entry was characterised by the well-known rapid reduction of MR followed by a fall in T_b that resulted in a further gradual reduction in MR in turn (Fig. 3); the maximum cooling rate for T_b during torpor entry over 10 min at T_a 15°C was 0.173±0.016°C min^{-1} (n=9). Because hamsters have a relative high minimum T_b during torpor, the TMR often increased slightly after torpor entry for maintenance of T_b (e.g. at ∼03:00 h in Fig. 3B). Endothermic arousal from the first torpor bout when no radiant heat was provided (Fig. 3A at ∼06:00 h, Fig. 3B at ∼05:00 h) required a substantial increase in MR to maxima near those observed during activity at night. In contrast, when the heat lamp was switched on near the T_b and TMR minimum (Fig. 3A at 09:23 h), the animal again increased its MR, but this increase was less steep and less pronounced than during fully endothermic rewarming. This occurred despite a greater increase of T_b (T_b increase by 10.5°C during radiant heat-assisted rewarming) than during the previous fully endothermic arousal (T_b increase by 8.5°C at ∼06:00 h). The torpid hamster in Fig. 3B maintained a low MR and even reduced T_b somewhat when the heat lamp was switched on the first time at 08:51 h. Because this hamster remained torpid at T_a 15°C even when the heat lamp was switched off at 10:14 h, the lamp was switched on again at 10:58 h, but this time the T_a was allowed to increase. On this occasion, T_b increased with T_a, TMR increased somewhat but remained below or near BMR, and only after the heat lamp was switched off again and T_a fell was endothermic rewarming initiated, with an increase in both MR and T_b.

The mean maximum MR during radiant heat-assisted rewarming (4.64±1.63 ml O_2 g^{-1} h^{-1}) was significantly ($F_{2,26}$=38.38, P<0.001) below that during activity at night (mean 8.33±1.14 ml O_2 g^{-1} h^{-1}) and endothermic rewarming (mean 7.81±1.54 ml O_2 g^{-1} h^{-1}). Interestingly, one hamster that was flat out on its belly under the heat lamp and did not part its fur had the highest maximum MR (7.20 ml O_2 g^{-1} h^{-1}) observed during radiant heat-assisted rewarming. The maximum rate of rewarming over 10 min did not differ between endogenous (0.27±0.09°C min^{-1}) and radiant heat-assisted rewarming (0.27±0.12°C min^{-1}).

The average energy expenditure for rewarming differed substantially between fully endothermic and radiant heat-assisted arousals even when radiant heat was not provided for the entire rewarming process (Fig. 4). Fully endothermic rewarming at T_a 15°C required an average MR of 100.85±25.98 ml O_2 h^{-1} (T_b increase of 9.6±2.6°C). Radiant heat-assisted rewarming required an average MR of only 44.92±16.20 ml O_2 h^{-1} (T_b increase of 11.6±2.2°C) for all rewarming measurements at T_a 15°C and those in which T_a was allowed to increase to an average of 19.3±2.2°C. MR during radiant heat-assisted rewarming at T_a 15°C was not significantly raised in comparison to the times when T_a was permitted to rise. The mean total MR (ml O_2 h^{-1}) required for rewarming (Fig. 4A) was significantly affected by basking ($F_{1,10}$=95.27, P<0.0001) after adjusting for body mass and the T_b–T_a gradient. Similar relationships were observed when the average mass-specific MR required for raising T_b by 1°C during rewarming was considered, with a 64% reduction when animals were basking (Fig. 4B).

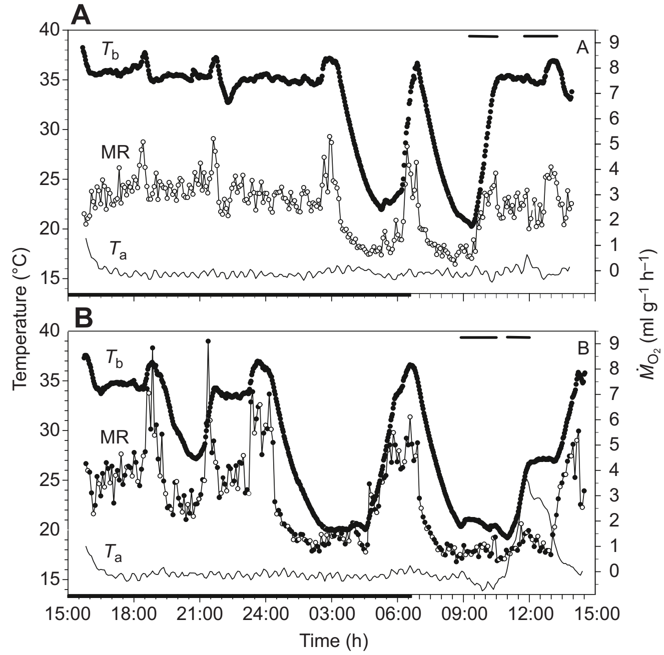

Fig. 3. T_b, MR and T_a in *P. sungorus* measured overnight. (A) Female hamster; (B) male hamster. The times at which heat lamps were switched on are shown as bars at the top of each panel; night is indicated as black horizontal bars at the bottom of each panel. MR was measured as $\dot{M}_{O_2}$.

DISCUSSION

Our study shows that winter-acclimated hamsters provided with access to a radiant heat source use basking extensively both when resting and during torpor. In resting individuals, basking significantly reduced the MR, but also the T_b and apparent C. During steady-state torpor, the TMR and T_b were not strongly affected by the radiant heat provided; however, the energetic cost of radiant heat-assisted endothermic rewarming was less than half of that during fully endothermic rewarming.

In general terms, our observations on thermal energetics on non-basking hamsters were similar to those reported previously. The resting T_b of 34.7°C at T_a 15°C was similar to that previously reported under similar thermal conditions (Ruf et al., 1993) and so

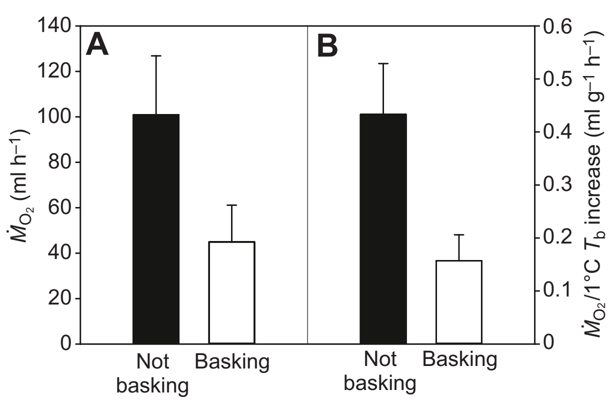

Fig. 4. Average energy expenditure required for rewarming in *P. sungorus*. Energy expenditure was measured as $\dot{M}_{O_2}$, and is given for (A) total rewarming from torpor and (B) an increase of T_b by 1°C.

was the decrease of RMR with T_a (Heldmaier and Steinlechner, 1981), although our values were slightly lower. The torpor patterns of hamsters observed here were somewhat unusual because hamsters often expressed more than one torpor bout per day, but it is known that multiple bouts per day may be used by the species, especially when food is withheld (Steinlechner et al., 1986; Diedrich et al., 2015), as in our measurements. The advantage of multiple torpor bouts in our study was that we could compare fully endothermic with radiant heat-assisted rewarming in the same individual on the same day (Fig. 3). With regard to physiological variables during steady-state torpor, the minimum T_b of about 22°C was similar to that measured under similar thermal conditions (Heldmaier and Steinlechner, 1981; Diedrich et al., 2015). However, the mean minimum TMR measured here was only 34% of that measured by Heldmaier and Steinlechner (1981), but similar to those reported more recently at ∼1/3 of BMR (Diedrich et al., 2015; Ruf and Geiser, 2015).

During basking, the mean minimum apparent C during rest was only 47% of that predicted from body mass for a resting mammal (Bradley and Deavers, 1980) and only 78% of that in *P. sungorus* in steady-state torpor. The former is similar to the predicted C for a mammal 5.6-fold the size of *P. sungorus*. The energy saving afforded by this reduced heat loss is significant at 33–39% and would affect daily energy balance. The C calculated from the RMR–T_a slope (Fig. 2A) was even lower; however, this calculation assumes a constant T_b, which was of course not the case in our measurements.

Our hypothesis that hamsters would bask during both rest and torpor was supported by our study, because animals always actively moved towards the heat lamp when it was provided, similar to other small mammals (Warnecke and Geiser, 2010). Further, as predicted, basking significantly reduced thermoregulatory energy expenditure. This is not surprising because the solar heat gain of *P. sungorus* winter coats is about 20% of the incoming radiation (Walsberg, 1991) and to maximise heat gain most hamsters parted their dorsal fur to allow heat to penetrate to the skin. What is surprising is that hamsters also significantly reduced T_b and thus C during basking. This unexpected observation is probably explained by the fact that hamsters with an external radiant heat source relaxed endothermic thermoregulation and maintenance of a high normothermic T_b set point. This new finding not only is of importance to the resulting energy savings but also has implications for the mechanisms controlling thermoregulatory heat production. It appears that the sensation of incoming external heat is integrated with the hypothalamic T_b set point and results in a lower threshold for increasing thermoregulatory heat production (Hammel et al., 1963; Glotzbach and Heller, 1975), causing a drop of T_b. However, as *P. sungorus* do not lower T_b when exposed to increasing T_a, the sensation of the incoming radiation must be interpreted differently, perhaps via thermoreceptors oriented towards the lamp or the differential between peripheral thermoreceptors oriented towards or away from the lamp. Another explanation might be that the reduced T_b during basking maximises the dorsal heat uptake because of the increased temperature differential, and also minimises ventral heat loss. Differential vasoconstrictions could further aid in this (Tattersall et al., 2016). The T_b and MR reduction makes sense from an energetic and ecological point of view because in the presence of radiant heat the animals can return T_b to normothermic values at little energetic cost. Interestingly, cooling rate in resting basking hamsters (T_a 0°C) was ∼1.5-fold faster than during torpor entry (T_a 15°C), but this is probably explained by exposure to the lower T_a, and therefore suggests a similar physiological process. Important for our study is the frequent basking behaviour, which suggests that it may be of ecological significance for this species in the wild.

Considering the energetic advantages, basking behaviour might be expected for hamsters with a high T_b, but for torpid hamsters with a T_b near or below 20°C this may incur a potential cost because movement is slowed and the risk of predation is increased (Rojas et al., 2012). However, basking has been observed in wild dasyurid marsupials not only during rest in the afternoon but also in the morning when animals are rewarming from torpor and therefore must remain concealed from diurnal predators (Geiser et al., 2002; Warnecke et al., 2008; Rojas et al., 2012), as would be the case for white *P. sungorus* on or near snow. Important in this regard is that in the past, differences in fur colour among dasyurid populations were considered to be of little importance from energetic, thermal and camouflage points of view because animals were considered to be nocturnal. Although movement at low torpor T_b obviously is slowed, the hamsters in our study were never far from their tube refuge and must have been aware of their surroundings, otherwise they would not have moved under the heat lamp. In the wild, small marsupial mammals often bask at low T_b between 15 and 20°C during rewarming from torpor, but they always do so near a soil crack or rock crevice refuge and even at low T_b can move fast enough to cover small distances and avoid predation (Rojas et al., 2012). Deeply torpid animals are often stiff and immobile (Lyman et al., 1982) and therefore there must be a reason for this ability of hamsters to move at low T_b. Basking behaviour at low T_b in *P. sungorus* further supports the view that it may be of ecological and energetic significance in this species in the wild.

Our interpretation might be criticised because we have only limited information on the diurnal activity of *P. sungorus* in nature based on trapping and diurnal raptor pellets (Flint, 1966), and it is often assumed that the species is nocturnal. However, it has been shown that when *P. sungorus* are held at a low T_a of 5°C they are almost equally active during the day and night (Heldmaier et al., 1989). It appears that during thermal and energetic challenges, a metabolic feedback affects the organisation of the circadian rhythm and induces diurnality in small nocturnal rodents (van der Vinne et al., 2014). For Australian carnivorous dasyurid marsupials, considered nocturnal in the past, radio-telemetry has shown that some are in fact entirely or to a large extent diurnal in winter (Warnecke et al., 2008; Körtner et al., 2010). We predict that such studies on *P. sungorus* in the wild will reveal not only that the species is partially diurnal but also that it uses basking near or on snow for energy conservation. This also may be the case for other species with a white coat in winter.

Interestingly, and in contrast to dasyurids (Geiser and Drury, 2003; Warnecke and Geiser, 2010), the T_b of torpid *P. sungorus* did not always increase when radiant heat was provided – this occurred only if the hamsters contributed endogenous heat to the rewarming process. This is probably due to two major factors. *Phodopus sungorus*, unlike dasyurids, have extremely dense and thick fur, which will increase insulation, but interferes with the uptake of radiant heat (Walsberg, 1991). However, our data show that enough heat, probably aided by parted fur, was absorbed for reducing thermoregulatory and rewarming costs. The other important consideration in this regard is of course the amount of radiant heat provided by the heat lamp, which was only ∼1/3 of that provided by the sun. In the wild, the ample radiant heat from the sun is likely to be even more significant for food-independent energy absorption.

Intuitively, one might expect basking to allow resting animals to maintain a stable T_b with reduced thermoregulatory energy expenditure, or even to result in an increase of T_b as in dunnarts and rock hyrax (Geiser and Drury, 2003; Brown and Downs, 2007). Our results show that the opposite can be the case, as basking in *P. sungorus* was associated with profound decreases in T_b. This indicates that intermittent reductions of T_b in free-living mammals may not always reflect responses to low T_a, but could, almost conversely, indicate physiological adjustments to high solar radiation in cold environments.

Acknowledgements

We thank Walter Arnold for providing accommodation and access to facilities at the Research Institute of Wildlife Ecology, Gerhard Fluch for preparing and calibrating the data loggers, and Jessica Cornils, Bronwyn McAllan, Martina Sturm, Sylvain Giroud, Franz Hoelzl and Nikolaus Huber for help and discussions.

Competing interests

The authors declare no competing or financial interests.

Author contributions

F.G., T.R. and C.B. designed the experiments. F.G., K.G. and T.R. conducted the experiments. G.L.S. and H.G. performed the surgeries. F.G. and T.R. analysed the data. All authors contributed to the writing of the manuscript.

Funding

The work was supported by the Australian Research Council and the Research Institute of Wildlife Ecology.

References

Bartholomew, G. A. and Rainy, M. (1971). Regulation of body temperature in the rock hyrax, *Heterohyrax brucei*. *J. Mammal.* **52**, 81-95.

Boyer, B. B. and Barnes, B. M. (1999). Molecular and metabolic aspects of mammalian hibernation. *Bioscience* **49**, 713-724.

Bradley, S. R. and Deavers, D. R. (1980). A re-examination of the relationship between thermal conductance and body weight in mammals. *Comp. Biochem. Physiol*. **65**, 465-476.

Brown, K. J. and Downs, C. T. (2007). Basking behaviour in the rock hyrax (*Procavia capensis*) during winter. *Afr. Zool.* **42**, 70-79.

Cubuk, C., Bank, J. H. H. and Herwig, A. (2015). The chemistry of cold: mechanisms of torpor regulation in the Siberian hamster. *Physiology* **31**, 51-59.

Dausmann, K. H. (2014). Flexible patterns in energy savings: heterothermy in primates. *J. Zool.* **292**, 101-111.

Diedrich, V., Kumstel, S. and Steinlechner, S. (2015). Spontaneous daily torpor and fasting-induced torpor in Djungarian hamsters are characterized by distinct patterns of metabolic rate. *J. Comp. Physiol. B* **185**, 355-366.

Duncan, M. J. and Goldman, B. D. (1984). Hormonal regulation of the annual pelage color cycle in the Djungarian hamster, *Phodopus sungorus*. II Role of prolactin. *J. Exp. Zool.* **230**, 97-103.

Flint, W. E. (1966). *Die Zwerghamster der paläarktischen Fauna*. Wittenberg Lutherstadt: A Ziemsen Verlag.

Geiser, F. and Drury, R. L. (2003). Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor. *J. Comp. Physiol. B* **173**, 55-60.

Geiser, F., Goodship, N. and Pavey, C. R. (2002). Was basking important in the evolution of mammalian endothermy? *Naturwissenschaften* **89**, 412-414.

Geiser, F., Drury, R. L., Körtner, G., Turbill, C., Pavey, C. R. and Brigham, R. M. (2004). Passive rewarming from torpor in mammals and birds: energetic, ecological and evolutionary implications. In *Life in the Cold: Evolution, Mechanisms, Adaptation, and Application* (ed. B. M. Barnes and H. V. Carey), pp 51-62. 12th International Hibernation Symposium. Biological Papers, University of Alaska #27. Fairbanks: Institute of Arctic Biology.

Geiser, F., Klingenspor, M. and McAllan, B. M. (2013). A functional nexus between photoperiod acclimation, torpor expression and somatic fatty acid composition in a heterothermic mammal. *PLoS ONE* **8**, e63803.

Glotzbach, S. F. and Heller, H. C. (1975). CNS regulation of metabolic rate in the kangaroo rat (*Dipodomys ingens*). *Am. J. Physiol.* **228**, 1880-1866.

Hammel, H. T., Jackson, D. C., Stolwijk, J. A. J., Hardy, J. D. and Strømme, S. B. (1963). Temperature regulation by hypothalamic proportional control with an adjustable set point. *J. Appl. Physiol.* **18**, 1146-1154.

Hayes, J. P. (2001). Mass-specific and whole-animal metabolism are not the same concept. *Physiol. Biochem. Zool.* **74**, 147-150.

Heldmaier, G. and Steinlechner, S. (1981). Seasonal pattern and energetics of short daily torpor in the Djungarian hamster, *Phodopus sungorus*. *Oecologia* **48**, 265-270.

Heldmaier, G., Steinlechner, S., Ruf, T., Wiesinger, H. and Klingenspor, M. (1989). Photoperiod and thermoregulation in vertebrates: body temperature rhythms and thermogenic acclimation. *J. Biol. Rhythms* **4**, 139-153.

Hiebert, S. M., Fulkerson, E., Lindermayer, K. T. and McClure, S. D. (2000). The effect of temperature on preference for dietary unsaturated fatty acids in the Djungarian hamster (*Phodopus sungorus*). *Can. J. Zool.* **78**, 1361-1368.

Jefimow, M., Glabska, M. and Wojciechowski, M. S. (2011). Social thermoregulation and torpor in the Siberian hamster. *J. Exp. Biol.* **214**, 1100-1108.

Körtner, G., Rojas, A. D. and Geiser, F. (2010). Thermal biology, torpor use and activity patterns of a small diurnal marsupial from a tropical desert: sexual differences. *J. Comp. Physiol. B* **180**, 869-876.

Lyman, C. P., Willis, J. S., Malan, A. and Wang, L. C. H. (1982). *Hibernation and Torpor in Mammals and Birds*. New York: Academic Press.

Merritt, J. F. (2010). *The Biology of Small Mammals*. Maryland: Johns Hopkins University Press.

Müller, D., Hauer, J., Schöttner, K., Fritzsche, P. and Weinert, D. (2015). Seasonal adaptation of dwarf hamsters (Genus *Phodopus*): differences between species and their geographic origin. *J. Comp. Physiol. B* **185**, 917-930.

Packard, G. C. and Boardman, T. J. (1988). The misuse of ratios, indices, and percentages in ecophysiological research. *Physiol. Zool.* **61**, 1-9.

Rojas, A. D., Körtner, G. and Geiser, F. (2010). Do implanted transmitters affect maximum running speed of two small marsupials? *J. Mammal.* **91**, 1360-1364.

Rojas, A. D., Körtner, G. and Geiser, F. (2012). Cool running: locomotor performance at low body temperature in mammals. *Biol. Letters* **8**, 868-870.

Ruf, T. and Geiser, F. (2015). Daily torpor and hibernation and birds and mammals. *Biol. Rev.* **90**, 891-926.

Ruf, T., Klingenspor, M., Preis, H. and Heldmaier, G. (1991). Daily torpor in the Djungarian hamster (*Phodopus sungorus*): interactions with food intake, activity, and social behaviour. *J. Comp. Physiol. B* **160**, 609-615.

Ruf, T., Stieglitz, A., Steinlechner, S., Blank, J. L. and Heldmaier, G. (1993). Cold exposure and food restriction facilitate physiological responses to short photoperiod in Djungarian hamsters (*Phodopus sungorus*). *J. Exp. Zool.* **267**, 104-112.

Scantlebury, M., Krackow, S., Pillay, N., Bennett, N. and Schradin, C. (2010). Basking is affected by season and influences oxygen consumption in desert-living striped mice. *J. Zool.* **281**, 132-139.

Signer, C., Ruf, T. and Arnold, W. (2011). Hypometabolism and basking: the strategies of Alpine ibex to endure harsh over-wintering conditions. *Funct. Ecol.* **25**, 537-547.

Stannard, H. J., Fabian, M. and Old, J. M. (2015). To bask or not to bask: behavioural thermoregulation in two species of dasyurid, *Phascogale calura* and *Antechinomys laniger*. *J. Thermal Biol.* **53**, 66-71.

Steinlechner, S., Heldmaier, G., Weber, C. and Ruf, T. (1986). Role of photoperiod: pineal gland interaction in torpor control. In *Living in the Cold* (ed. H. C. Heller, X. J. Musacchia and L. C. H. Wang), pp. 301-307. New York: Elsevier.

Tattersall, G. J., Sinclair, B. J., Withers, P. C., Field, P. A., Seebacher, F., Cooper, C. E. and Maloney, S. K. (2012). Coping with thermal challenges: physiological adaptations to environmental temperature. *Compr. Physiol.* **2**, 2151-2202.

Tattersall, G. J., Leite, C. A. C., Sanders, C. E., Cadena, V., Andrade, D. V., Abe, A. S. and Milsom, W. K. (2016). Seasonal reproductive endothermy in tegu lizards. *Sci. Adv.* **2**, e1500951.

Thompson, M. L., Mzilikazi, N., Bennett, N. C. and McKechnie, A. E. (2015). Solar radiation during rewarming from torpor in elephant shrews: supplementation or substitution of endogenous heat production? *PLoS ONE* **10**, e0120442.

Van der Vinne, V., Riede, S. J., Gorter, J. A., Eijer, W. G., Sellix, M. T., Menaker, M., Daan, S. Pilorz, V. and Hut, R. A. (2014). Cold and hunger induce diurnality in a nocturnal mammal. *Proc. Natl. Acad. Sci. USA* **111**, 15256-15260.

Walsberg, G. E. (1991). Thermal effects of seasonal coat change in three subarctic mammals. *J. Thermal Biol.* **16**, 291-296.

Warnecke, L. and Geiser, F. (2010). The energetics of basking behaviour and torpor in a small marsupial exposed to simulated natural conditions. *J. Comp. Physiol. B* **180**, 437-445.

Warnecke, L., Turner, J. M. and Geiser, F. (2008). Torpor and basking in a small arid zone marsupial. *Naturwissenschaften* **95**, 73-78.

Withers, P. C. (1977). Measurements of VO_2, VCO_2, and evaporative water loss with a flow-through mask. *J. Appl. Physiol.* **42**, 120-123.