

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

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Summary statement: We provide the first evidence that basking reduces resting energy expenditure, body temperature and rewarming costs from torpor in hamsters, and identify unexpected thermoregulatory responses.

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 $34.7 \pm 0.6^\circ\text{C}$ (T_a 15°C not basking) to $30.4 \pm 2.0^\circ\text{C}$ (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 $83.3 \pm 36.0\%$ of days and the minimum torpor MR was 36% of basal MR at an average T_b of $22.0 \pm 2.6^\circ\text{C}$; movement to the basking lamp occurred at $T_b < 20.0^\circ\text{C}$. 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 likely other cold-climate mammals.

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 often is 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 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 MR (RMR) of small mammals near basal MR (BMR) over a wide range of ambient temperatures (T_a) well below thermo-neutrality (Geiser and Drury 2003; Scantlebury et al. 2010). Basking also is known to reduce metabolic rate in free-ranging ibex (*Capra ibex*) by up to 20% (Signer et al. 2011) and in rock hyrax (*Procavia capensis*) it increased T_b and likely 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 body temperature (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 often is expressed at low T_a . Nevertheless, although the torpid state is characterized 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 behavioral thermoregulation and specifically basking in the sun. Basking behavior 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; Warnecke et al. 2008; Geiser et al. 2004; 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 especially important during daily torpor, which usually lasts <12

hours within a 24-hour 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 to 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 more or less brown desert and tropical mammals that 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 be also 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 ~30g), which changes its fur from brown in 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 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 likely 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 its basking behaviour and thermoregulatory energy expenditure. 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 hypothesized that, like other small mammals, *P. sungorus* would bask both during 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.

Methods

Animal maintenance

Adult *P. sungorus* ($n=10$, 5 females, 5 males) born in August/September 2014 (i.e. 4-5 months old at the beginning of 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 (LD 16:8) to winter (LD 9.5:14.5 to 11:13; sunrise ~07:00 hours, sunset ~17:15 hours) in February when most measurements were performed and torpor is regularly expressed (Jefimow et al. 2011). Pelage colour of animals was at stage 4; i.e. white except for mid-dorsal dark stripe (Duncan and Goldman 1984). Since *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 $9\pm2^\circ\text{C}$.

Body temperature 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 weight after coating in Paraffin/Elvax was 1.7g, 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 sterilized before implantation. Surgical anaesthesia was induced by subcutaneous injection of 75 mg/kg Ketamine (Ketamidor® 10%, Richter Pharma Wels, Austria) and 300 µg/kg Medetomidine (Domitor® 0.1%, Orion Corporation, Turku, Finland) and maintained by approximately 1.5% isoflurane in an oxygen stream via a facemask. Preemptive post-surgical analgesia (1 mg/kg 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, 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, pO_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_{as} (23 to 25 °C) for one week. Implantations were carried out on 20 January 2015 and loggers were removed in early April 2015.

Metabolic rate measurements

Metabolic rates of hamsters were measured as the rate of oxygen consumption 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 on either end by a rubber stopper containing inlets for air on one side and outlets on the other, and also the 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 feces; 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 800ml/minute. Four individual animal channels and one control channel (outside air) were measured in sequence for one minute each, therefore a reading of each animal was taken every 5 minutes. Channels were switched via solenoid valves and the washout from the tubing to the analyser was achieved within 10 seconds. Metabolism was measured either with or without access to radiant heat provided in the form of a heat lamp (Daylight Basking Spot, incandescence 75W reflector globe, colour rendering index CRI 83, colour temperature 2560K) placed at an angle of 90° and 15 cm above the transparent respirometer and at that distance provided approximately 35,000 lux illumination ($\sim 51 \text{ W/m}^2$) through the highly transmissive perspex. The energy provided by this heat source was well below that of natural solar radiation during bright sunlight ($\sim 110,000 \text{ lux}$ or $\sim 161 \text{ W/m}^2$), 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:

1. Daytime measurements: Animals were measured during the daytime for several hours from the morning to the afternoon (from about 09:00 to 16:00 hours) to measure resting MR (RMR) at T_a s of ~ 15 and 0°C for about 2.5-3 hours each either with or without access to a radiant heat source for the entire time 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 $14.9 \pm 0.3^\circ\text{C}$ (lamp off) and $14.7 \pm 0.5^\circ\text{C}$ (lamp on) and $-0.1 \pm 0.6^\circ\text{C}$ (lamp off) and $0.6 \pm 0.7^\circ\text{C}$ (lamp on).

2. Overnight measurements: Animals were measured overnight (from about 16:00 to 14:00 hours) at $T_a \sim 15^\circ\text{C}$. Food and water were withheld to induce torpor. Each animal was measured 1 to 3 times (mean 1.9 ± 0.6 times) depending on their expression of torpor and 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 hours and 09:40 hours) for 1 to 1.5 h to assess their metabolic response. On N=11 occasions at $T_a \sim 15^\circ\text{C}$ 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 $T_a \sim 15^\circ\text{C}$ 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

Metabolic rates during rest and torpor were averaged over at least 15 minutes when values were minimal and stable and 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 $T_b < 30.0^\circ\text{C}$ (i.e. a fall of T_b by $>5^\circ\text{C}$ below normothermic, resting T_b , Ruf and Geiser 2015).

Apparent thermal conductance 'C' was calculated using: $C = \text{MR} / (T_b - T_a)$ (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 $>5.0^\circ\text{C}$; the average energy expenditure for raising T_b by 1.0°C was also calculated. Maximum MRs during activity at night, during fully endothermic rewarming and during radiant heat-assisted rewarming were calculated from the single highest MR value measured. Maximum cooling and rewarming rates ($^\circ\text{C}/\text{min}$) for fully endothermic and radiant heat-assisted rewarming were determined over 10 minutes.

To adjust for repeated measures, we computed linear mixed effect models entering animal ID as a random factor (R package nlme, [Pinheiro et al. 2014](#)). 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 & 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. Numeric values are expressed as means with SD for 'n' the number of individuals measured; 'N' is the number of measurements. All statistical tests were carried out using R 3.2.2 (R Core Team 2014).

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. 1A, B). 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 returned to resting values above those at T_a 15°C. When the heat lamp was on and the hamster was basking (Fig. 1B) the resting MR was lower at T_a 15°C and the T_b declined to ~32°C with time (Fig. 1A). 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 hours 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,B; 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 1.3-1.4-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 $\sim 2^\circ\text{C}$, when they had access to radiant heat ($F_{1,25}=22.90$, $p<0.001$) and the maximum cooling rate over 10 minutes for T_b during basking at T_a 0°C was $0.257\pm 0.080^\circ\text{C}/\text{min}$ ($n=9$). T_b fell from a mean of $34.7\pm 0.6^\circ\text{C}$ to $32.8\pm 1.2^\circ\text{C}$ at T_a 15°C and from $32.4\pm 1.1^\circ\text{C}$ to $30.4\pm 2.0^\circ\text{C}$ at T_a 0°C ; a few individuals had a T_b of $<30^\circ\text{C}$ 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 RMRs and T_b s, 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 $0.088\pm 0.015 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$. Both T_a ($F_{1,25}=94.87$, $p<0.001$) and heat lamp ($F_{1,25}=85.72$, $p<0.001$) significantly affected conductance, but the slopes did not differ.

Overnight measurements

When food was withheld overnight, nine of the ten hamsters used torpor (i.e. induced torpor) on $83.3\pm 36.0\%$ of days during respirometry measurements ($n=8$ always used torpor, $n=1$ once of 3 trials, $n=1$ never in 2 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 T_b at which movement to the heat lamp was observed was 19.8°C and at these low T_b s movement was a slow uncoordinated wobble. Loss of body mass in individuals expressing torpor was $2.71\pm 0.35\text{g}$ ($n=9$), $\sim 65\%$ of those remaining normothermic $4.15\pm 1.06\text{g}$ ($n=2$) 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 in the morning (Fig. 3A). Only on two occasions three bouts of torpor were expressed, with the first occurring before midnight and the others at similar times as for 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 are shown in brackets (TMR = 0.686 ± 0.215 ml O_2 g^{-1} h^{-1} ; $T_b = 22.0 \pm 2.6^\circ C$; $T_a = 15.1 \pm 0.8^\circ C$; $C = 0.113 \pm 0.058$ ml O_2 g^{-1} h^{-1} $^\circ C^{-1}$; body mass = 25.1 ± 2.8 g).

Torpor entry was characterized 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 A,B); the maximum cooling rate for T_b during torpor entry over 10 minutes at T_a $15^\circ C$ was $0.173 \pm 0.016^\circ C/min$ ($n=9$). 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 $\sim 03:00$ hours Fig. 3B). Endothermic arousal from the first torpor bout when no radiant heat was provided (Fig. 3A at $\sim 06:00$ hours, Fig. 3B at $\sim 05:00$ hours) 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 hours) 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 $10.5^\circ C$ during radiant heat-assisted rewarming) than during the previous fully endothermic arousal (T_b increase by $8.5^\circ C$ at $\sim 06:00$ hours). 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 hours. Because this hamster remained torpid at T_a $15^\circ C$ even when the heat lamp was switched off at 10:14 hours, the lamp was again switched on at 10:58 hours, but this time the T_a was allowed to increase. On this occasion, the T_b increased with T_a , the TMR increased somewhat but remained below or near BMR, and only after the heat lamp was switched off again and T_a fell, endothermic rewarming was 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 minutes did not differ between endogenous (0.27 ± 0.09 °C/min) and radiant heat-assisted rewarming (0.27 ± 0.12 °C/min).

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 metabolic rate of 100.85 ± 25.98 ml O₂ h⁻¹ (T_b increase 9.6 ± 2.6 °C). Radiant heat-assisted rewarming required an average MR of only 44.92 ± 16.20 ml O₂ h⁻¹ (T_b increase 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. The metabolic rate during radiant heat-assisted rewarming at T_a 15°C was not significantly raised in comparison to times T_a was permitted to rise. The mean total MR (ml O₂ 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).

Discussion

Our study shows that winter-acclimated hamsters provided with access to 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 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/day, but it is known that multiple bouts/day may be used in 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 1991; Diedrich et al. 2015). However, the mean minimum TMR measured here was only 34% of that measured by Heldmaier and Steinlechner (1991), 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 savings afforded by this reduced heat loss is significant at 33 to 39% and will 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 maximize heat gain most hamsters parted 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 likely is 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 is not only 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), and therefore results in 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 maximizes the dorsal heat uptake because of the increased temperature differential, and also minimizes 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 likely explained by the 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 may 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 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 s 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 there seems to be little reason for hamsters to be able to move at low T_b if it is not used for some purpose. Basking behavior 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 criticized because we have only limited information on 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 organization 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 that the species is not only 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, but only if they contributed endogenous heat to the rewarming process. This is likely due to two major factors. *P. 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, likely aided by parted fur, was absorbed for reducing thermoregulatory and rewarming costs. The other important consideration in this regard is of course also 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 provided by 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 et al. 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.

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

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Figures

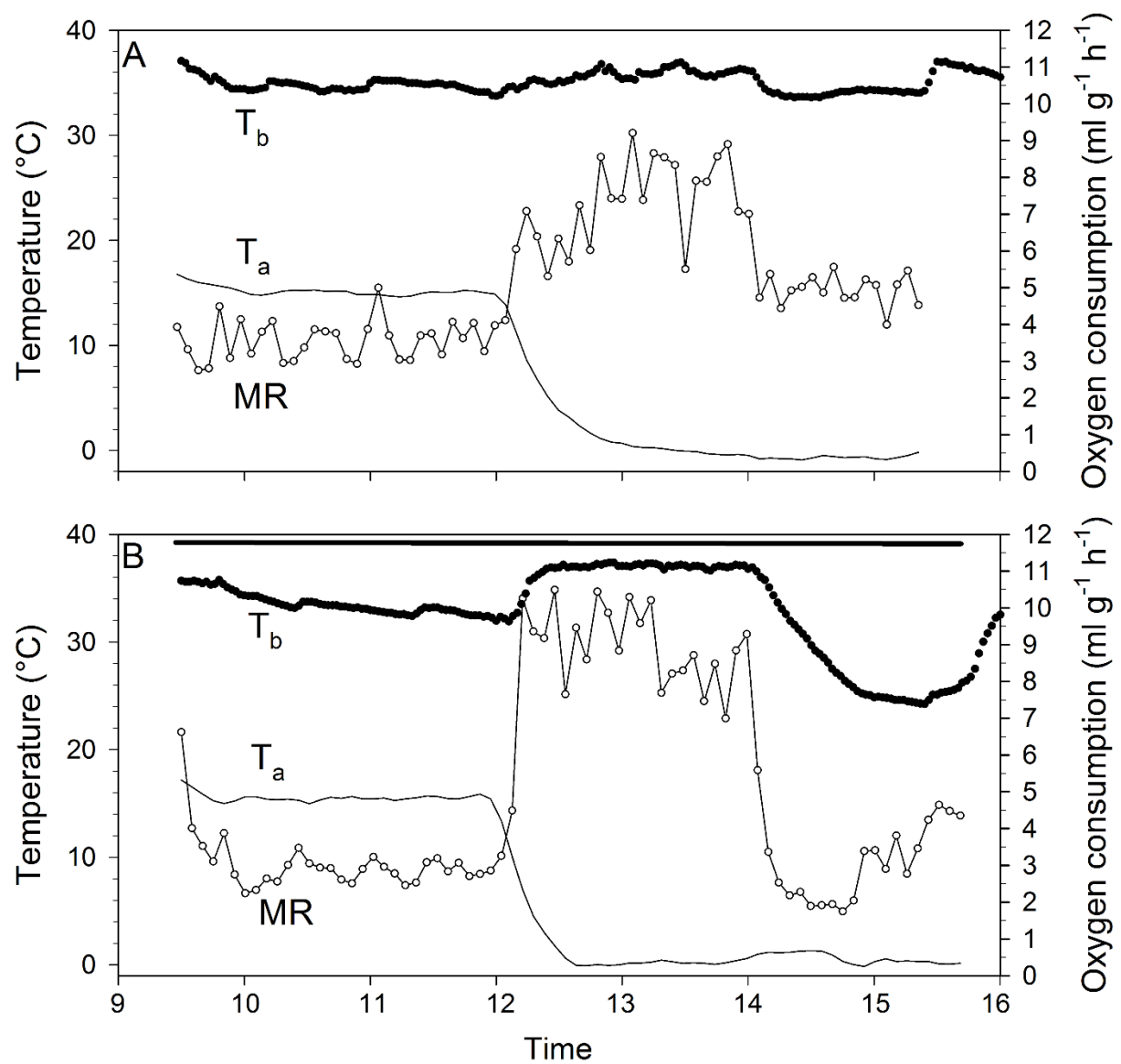


Fig. 1. Body temperature (T_b) and metabolic rate (MR) measured as rate of oxygen consumption, and ambient temperature (T_a) in *P. sungorus* as a function of time during daytime measurements. (A) heat lamp off, (B) heat lamp on for the entire time, as indicated by the bar at the top of the graph.

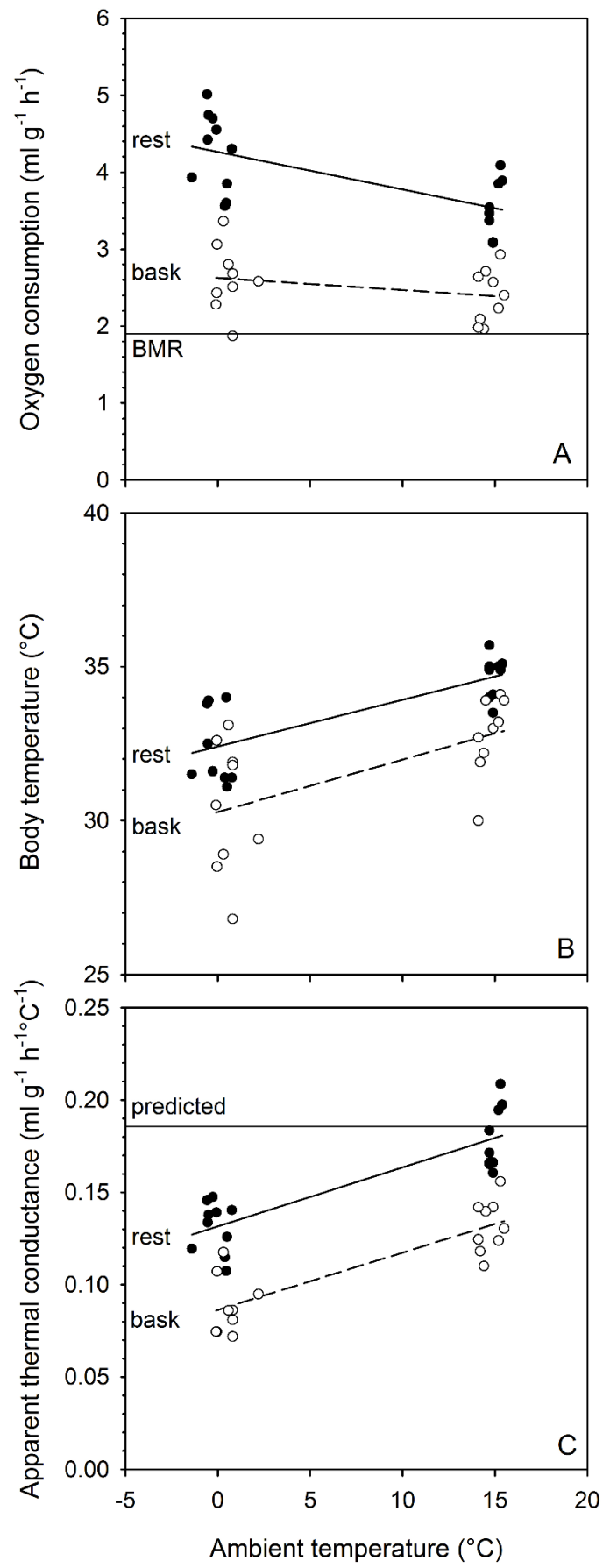


Fig. 2. The rate of oxygen consumption (A), body temperature (B), and apparent thermal conductance (C) as a function of ambient temperature in resting *P. sungorus* with heat lamp off (rest) and resting with heat lamp on (bask). The BMR was obtained from Ruf and Geiser (2015) and the predicted conductance from Bradley and Deavers (1980). Linear regressions were calculated to identify slope and intersect for comparison and the equations were:

A rest: $y=4.26-0.049x$, $r^2=0.44$; A bask: $y=2.626-0.0158x$, $r^2=0.084$

B rest: $y=32.41+0.15x$, $r^2=0.61$; B bask: $y=30.28+0.17x$, $r^2=0.35$

C rest: $y=0.136+0.0032x$, $r^2=0.73$; C bask $y=0.086+0.0031x$, $r^2=0.71$

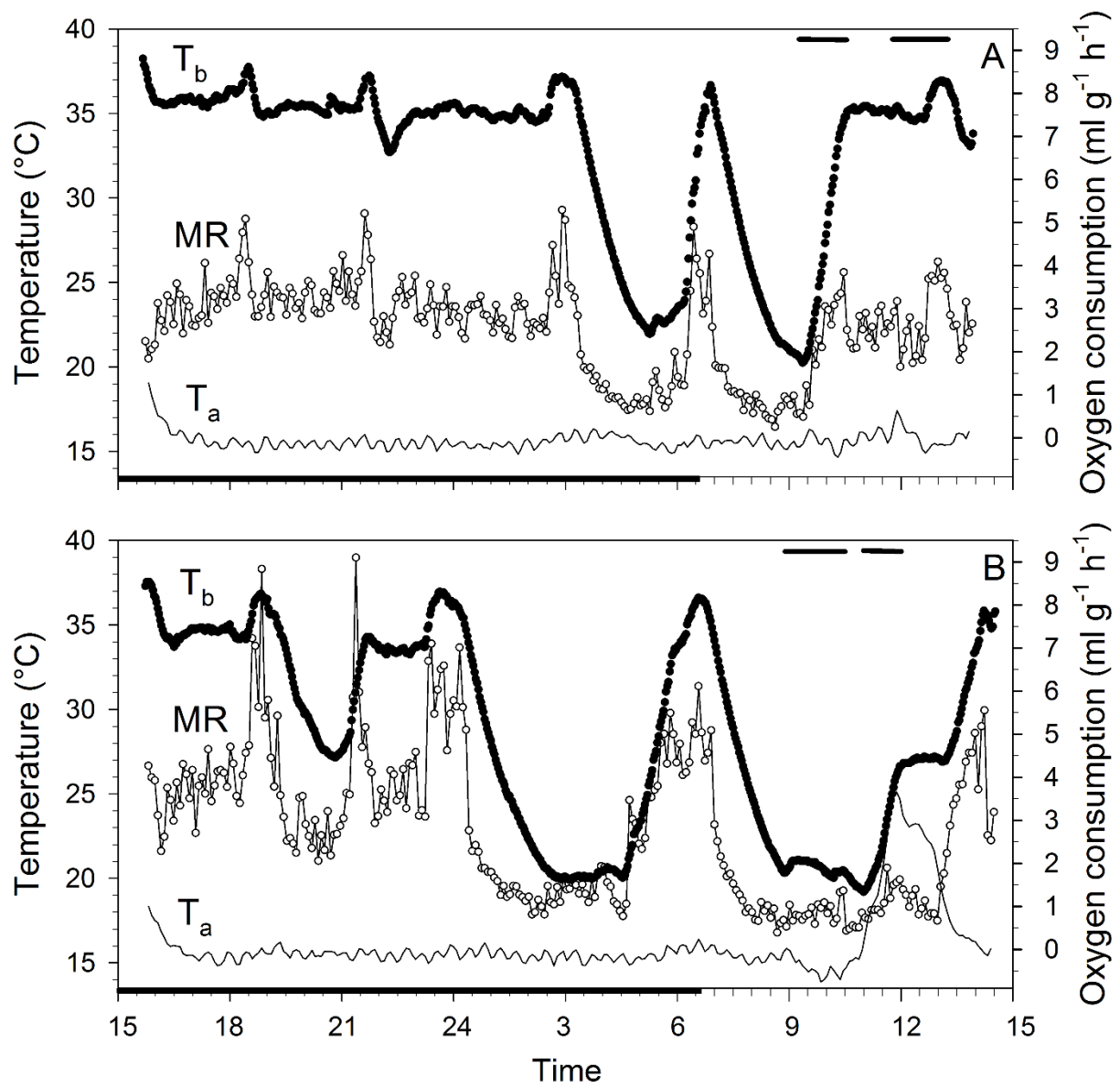


Fig. 3. Body temperature (T_b) and metabolic rate (MR) measured as rate of oxygen consumption, and ambient temperature (T_a) in a female (A top) and male (B bottom) *P. sungorus* measured overnight. The times at which heat lamps were switched on are shown as bars at the top of each graph; night is indicated as black horizontal bars at the bottom of each graph.

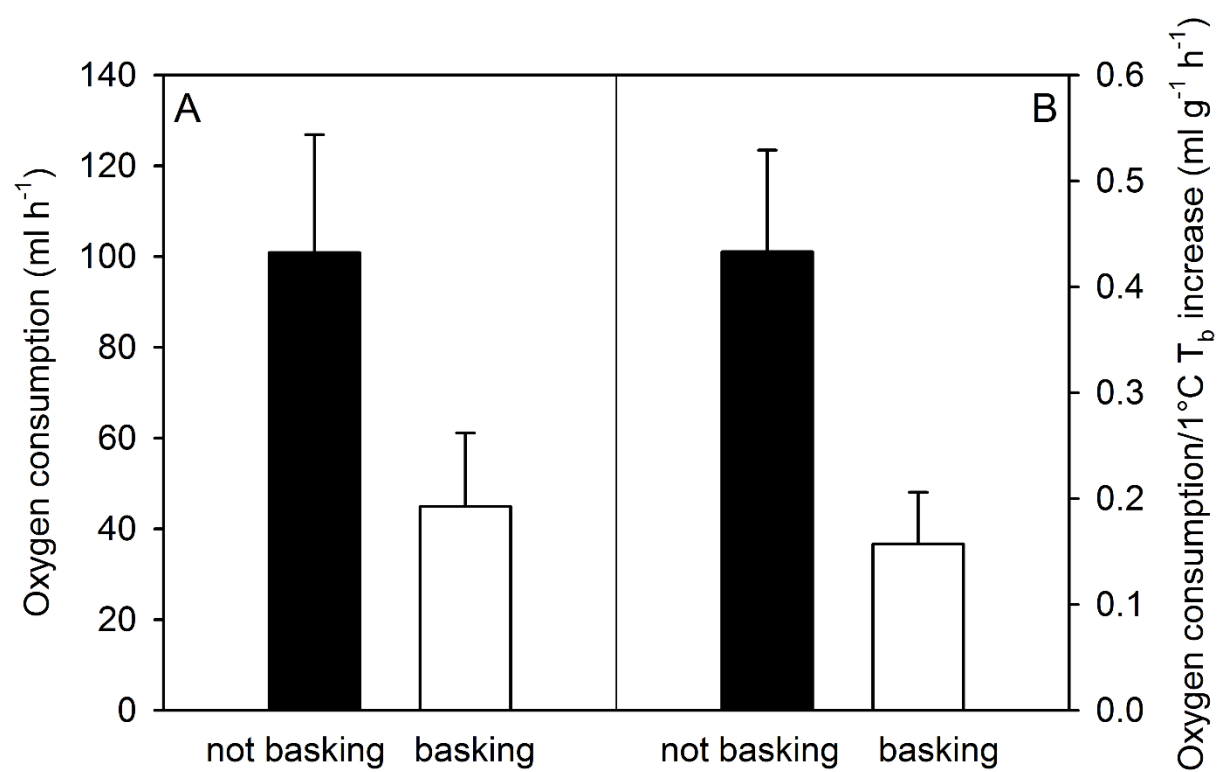


Fig. 4. The average total energy expenditure, measured as the rate of oxygen consumption, required for rewarming from torpor in *P. sungorus* (A left) and the energy required for an increase of T_b by 1°C (B right). Not basking (black bar) and basking (white bar).