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Fasting-induced daily torpor in desert hamsters (*Phodopus roborovskii*)

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ABSTRACT

Daily torpor is frequently expressed in small rodents when facing energetically unfavorable ambient conditions. Desert hamsters (*Phodopus roborovskii*, ~20 g) appear to be an exception as they have been described as homeothermic. However, we hypothesized that they can use torpor because we observed reversible decreases of body temperature (T_b) in fasted hamsters. To test this hypothesis we (i) randomly exposed fasted summer-acclimated hamsters to ambient temperatures (T_as) ranging from 5 to 30 °C or (ii) supplied them with different rations of food at T_a 23 °C. All desert hamsters showed heterothermy with the lowest mean T_b of 31.4 ± 1.9 °C (minimum, 29.0 °C) and 31.8 ± 2.0 °C (minimum, 29.0 °C) when fasted at T_a of 23 °C and 19 °C, respectively. Below T_a 19 °C, the lowest T_b and metabolic rate increased and the proportion of hamsters using heterothermy declined. At T_a 5 °C, nearly all hamsters remained normothermic by increasing heat production, suggesting that the heterothermy only occurs in moderately cold conditions, perhaps to avoid freezing at extremely low T_as. During heterothermy, T_bs below 31 °C with metabolic rates below 25% of those during normothermia were detected in four individuals at T_a of 19 °C and 23 °C. Consequently, by definition, our observations confirm that fasted desert hamsters are capable of shallow daily torpor. The negative correlation between the lowest T_bs and amount of food supply shows that heterothermy was mainly triggered by food shortage. Our data indicate that summer-acclimated desert hamsters can express fasting-induced shallow daily torpor, which may be of significance for energy conservation and survival in the wild.

1. Introduction

Torpor is defined as a state of profound but controlled reductions of metabolic rate and body temperature (T_b) in endotherms. Many small mammals can reduce their energy expenditure by expressing torpor to cope with daily or seasonal fluctuations of environmental conditions like low ambient temperature (T_a) or low food availability (McNab, 2002; Geiser, 2004). Torpor is traditionally divided into two categories: daily torpor and hibernation. Compared to the multiday duration and profound reduction of metabolic rate during hibernation, daily torpor lasts less than one day, is usually less profound and closely related to the circadian rhythm (Ruf and Geiser, 2015). Mammals capable of torpor are widely distributed in most recent mammalian orders and the number of heterothermic species is likely to be higher than known at present (Geiser and Ruf, 1995; Ruf and Geiser, 2015).

Desert hamsters (*Phodopus roborovskii* SATUNIN) mainly inhabit the desert regions of north Asia, characterized by harsh and cold winters (Ross, 1994). They are small, nocturnal, granivorous rodents with body mass around 20 g (Bao et al., 2002; Zhan and Wang, 2004; Wan et al., 2007, 2013). Desert hamsters are active year-round and usually hoard food to cope with the fluctuation of food availability (Feoktistova and Meschersky, 2005; Wan et al., 2007; Müller et al., 2015). They are known to be non-hibernating animals and daily torpor could not be confirmed in a previous study, neither under summer- nor under winter-like conditions (Jefimow, 2007). In contrast, we observed reversible decrease of T_b below 30.0 °C in fasted hamsters at T_a 23 °C under long photoperiod (Chi and Wang, 2011). Similarly, Ushakova et al. (2012) reported substantially decreased T_bs in winter-acclimated individuals under semi-natural conditions. Thus, desert hamsters might be a potentially heterothermic species, but their pattern of torpor has never been quantified.

Siberian hamsters (*Phodopus sungorus*), an intensely studied congener, express spontaneous daily torpor mainly as a response to prolonged short photoperiod exposure even when food is available ad libitum (Heldmaier and Steinlechner, 1981; Kirsch et al., 1991; Ruf and Heldmaier, 1992). In long photoperiod, Siberian hamsters display fasting-induced daily torpor after severe food restriction and a reduction in body mass of about 25% (Ruby and Zucker, 1992; Diedrich et al., 2015). A further congener named Campbell hamsters (*Phodopus campbelli*) was also found to be heterothermic (Ushakova et al., 2012; Müller et al., 2015). In several other heterotherms, such as small rodents and marsupials, daily torpor often occurs when food is restricted under

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moderate cold conditions (Geiser, 2004; Hudson and Scott, 1979; Tannenbaum and Pivorun, 1987; Nespolo et al., 2010; Geiser and Martin, 2013).

Because the profound and reversible decrease of T_b in fasted desert hamsters, we hypothesized that they are able to express daily torpor when facing food shortage at certain T_as. To test this hypothesis and to quantify the thermal energetics of desert hamsters under different thermal and trophic conditions, we exposed fasted hamsters to different T_as and investigated the effects of food availability at T_a 23 °C, at which the maximum decreases of T_b were previously detected and the hamsters were routinely maintained. T_b and/or metabolic rate were monitored continuously during the experiments.

2. Material and methods

2.1. Animals and housing

Adult hamsters (12 to 18 months old) used in this study were offspring of 30 pairs, live-trapped in Hunshandake sandy land (43°11′N, 116°10′E, minimum T_a −30.3 °C, field observation with iButton, Maxim Model DS1922L) of Inner Mongolia. According to our records, the life span of desert hamsters in laboratory conditions was around 36 months. They were raised individually in standard plastic cages (30 cm × 15 cm × 20 cm) with saw dust and wood shavings under photoperiod conditions of 16 h light and 8 h darkness at T_a 23 ± 1 °C. Hamsters had ad libitum access to standard rodent maintenance pellets (crude protein, ≥18%; crude fat, ≥4%; coarse fiber, ≤5%; ashes, ≤8%; moisture, ≤10%) (Beijing HFK Bio-Technology Co. Ltd.) and water. The use of these animals in this study was permitted by the Animal Care and Use Committee of Institute of Zoology, the Chinese Academy of Sciences.

2.2. Surgery

About two weeks before the beginning of the experiments, each of the 34 desert hamsters (16 males and 18 females) was implanted intraperitoneally with a battery-free temperature-sensitive transponder (15.5 mm × 6.5 mm; 1.1 g) (Mini Mitter, Model G2 E-Mitter, made of biocompatible materials). Transponders had been calibrated by the company using a two point calibration (to the nearest of ±0.1 °C) and an accuracy of ±0.15 °C over a temperature range of 20 °C–45 °C was guaranteed. The weight of the transponder falls within the recommended weight of <10% of the body mass in small terrestrial mammals (Rojas et al., 2010). Transponders and surgical apparatus were sterilized prior to surgery with 75% alcohol (≥0.5 h). Animals were anesthetized by injection of pentobarbital sodium salt (Sigma, P3761) (0.5%) with a dose of 30 mg/kg (Chi and Wang, 2011). After sterilizing the skin with iodophor (Nanjing Modern Sanitation and Anti-epidemic Products Co. Ltd), a small ventral incision was made, a transponder was inserted intraperitoneally and the wound was closed with absorbable PGA surgical suture (Jinhuan Model R413, 4/0) and again sterilized with iodophor. During the surgery, a thermal blanket (TSE, Type 908100-OPT-HB) was used to prevent animals from becoming hypothermic. Small mammals can recover from such a surgery in 7 days (Gamo et al., 2013). Hamsters were checked daily and after 10 days, all hamsters had recovered well from the surgery as evaluated by examining the condition of wounds as well as their behavior.

2.3. Body temperature

Each of the animal cages was placed on a receiver board (Mini Mitter, Model ER-4000). Apart from receiving the transponder's signals, the receiver board also worked as an energizer to power the transponder. Receivers were connected to a computer via a RS-232 serial port cable. When the animals had fully recovered from the surgery, continuous T_b recording with the VitalView software (Mini Mitter) began.

2.4. Metabolic trials

Metabolic rates were measured as oxygen consumption with an open flow respirometry system (Sable Systems, TurboFOX Complete Field System, including a mass-flow meter) by placing each animal into a transparent plastic chamber (TSE, type I for mice, Volume 2.7 L) with small pieces of paper to absorb animal wastes. An incubator (Yiheng Model LRH-250, Shanghai, China) was used to maintain constant ambient conditions within the animal chamber during the measurement intervals at a series of T_as from 5 °C to 30 °C (±0.5 °C) (Thermal neutral zone, TNZ, 25–33 °C, Zhan and Wang, 2004). Fresh air from outside was pumped through the chamber at 500–600 ml/min. Before entering the chamber, air passed through a copper coil to ensure that its temperature was adjusted to that inside the incubator. After passing through the chamber, the gas was subsampled and dried using a non-chemical gas drier (Sable Systems, ND-2); approximately 100 ml/min at a stable flow rate was analyzed. Baseline measurements of reference air outside the animal chamber were carried out every 4 h to compensate for the drift of the oxygen sensor during long-term metabolic rate monitoring.

Oxygen consumption was calculated using the equation:

$$VO_2 = \frac{FR \times (FiO_2\text{-}FeO_2) - FR \times FeO_2 \times (FeCO_2 - FiCO_2)}{1 - FeO_2}$$

(FR = mass flow rate, FiO_2 = input fractional concentration of O_2 to the chamber, FeO_2 = excurrent fractional concentration of O_2 from the chamber, $FiCO_2$ = input fractional concentration of CO_2, $FeCO_2$ = excurrent fractional concentration of CO_2 from the chamber) (Hill, 1972; Withers, 1977). We took the 5-min least variable and lowest VO_2 average as resting metabolic rate (RMR) after the animal had been at rest for at least 30 min (Li et al., 2010; Chi and Wang, 2011).

2.5. Body mass and daily food intake determination

Animals were provided with a pre-weighed quantity of food in excess. Uneaten food together with feces was collected after 3 days. Daily food intake was calculated for each animal. Feeding trials always started at around 1700 h and ended at the same time 3 days later. At the beginning and end of each trial, body mass was measured with an electronic balance (Sartorius Model BL1500, to the nearest 0.1 g).

2.6. Torpor definition

In a torpor study of laboratory mice, Hudson and Scott (1979) defined torpor as the state when T_b was below 31 °C and the metabolic rate decreased by 25% or more below the normothermic RMR at the same T_a. We followed these criteria to identify torpor in our study. T_b in desert hamsters showed robust circadian rhythms with a lower mean value during photophase (36.1 ± 0.2 °C, resting) compared to scotophase (37.3 ± 0.4 °C, active) (Wang et al., 2012). Our measurements also revealed that photophase T_b of normothermic hamsters was usually above 35 °C and never fell below 34 °C (with a mean of the lowest value of 35.8 ± 0.1 °C, unpublished data) (Fig. 1). Hence we considered it the initiation of torpor or heterothermy when photophase T_b fell below 34 °C. The duration of torpor was defined as the interval during which T_b remained at <34 °C as described by Ruby and Zucker (1992) in a study of Siberian hamsters.

2.6.1. Experiment 1: thermoregulation as a function of T_a in fasted hamsters

To investigate the effects of T_a on RMR and T_b in fasted hamsters, 9 males and 10 females were fasted randomly at T_a of 5 °C, 10 °C, 13 °C, 16 °C, 19 °C, 23 °C, 26 °C and 30 °C, respectively. It should be noted that each fasted hamster experienced some but not all of the T_as mentioned above. Animals were completely deprived of food from 1700 h for 24 h at each T_a, during which T_b and metabolic rate were monitored

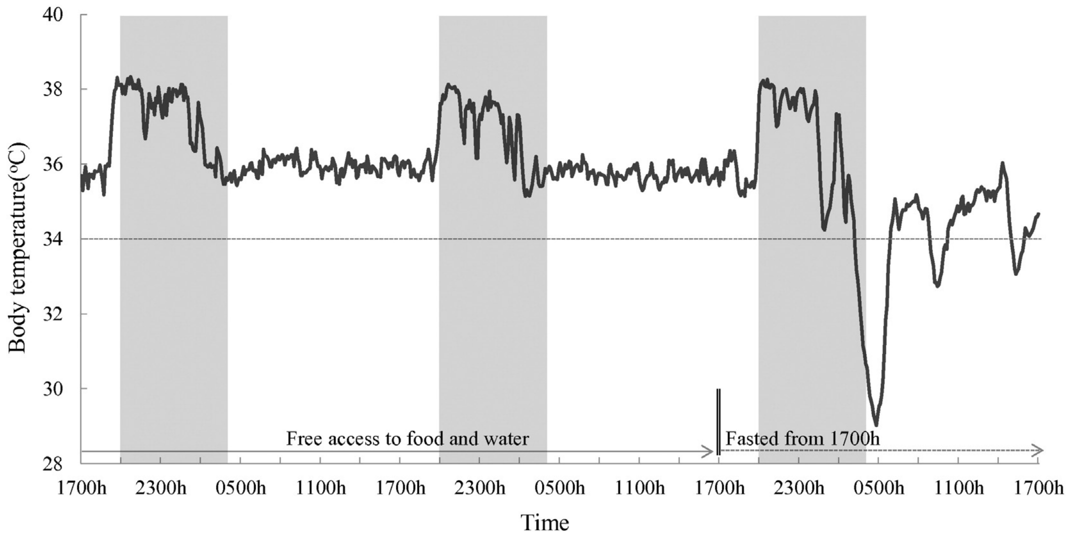

Fig. 1. Body temperatures in a representative summer-acclimated desert hamster measured over three days. The animal had free access to food on the first two days and then was fasted from 1700 h on the third day (gray area indicates the scotophase).

simultaneously at 15-second intervals. Normothermic or heterothermic RMR was identified by referencing the simultaneous records of T_b according to the above criteria of heterothermy. Between any two 24 h treatments, hamsters were allowed to recover from the fasting conditions for 1–2 weeks.

2.6.2. Experiment 2: food restriction at T_a 23 °C

To examine the effects of amount of food on thermoregulation, food restriction trials were conducted in desert hamsters at T_a 23 °C and a photoperiod of 16L:8D. 7 males and 8 females were subjected to 3-day feeding trials for six successive days. Thus, daily food intake was measured twice and averaged as the daily food requirement (DFR) for each animal. Hamsters were then randomly provided with rations of 100%, 80%, 60%, 40%, 20% and 0% (fasted) of their DFR. Each food restriction treatment lasted for 24 h, during which T_b were recorded at 15-second intervals. Between every two successive treatments of food restriction, animals were allowed to recover for one day with free access to food.

3. Statistics

Data analysis was performed using SPSS 17.0. Because fasted hamsters mainly reduced T_b during photophase while they remained normothermic during scotophase, data analyses of T_b were focused on photophase. Effects of T_a on the T_b, RMR, body mass reduction, and differential of lowest T_b and T_a in fasted hamsters were examined by using univariate general linear model with individual coded as a random factor nested within treatment and Tukey post hoc multiple comparisons. Paired sample *t* tests or nonparametric tests were used to analyze energy saving resulting from heterothermy by comparing RMR during heterothermy to that during normothermia. Effects of food restriction on the body mass and T_b were tested using repeated measures ANOVAs and least significant difference (LSD) post hoc multiple comparisons. Linear regression analysis was used to examine the relationship between T_b and the amount of food supply. Since we were unable to detect difference between physiological variables of males and females, data of two sexes were combined. Two-tailed P values of ≤0.05 were considered statistically significant. Numeric values are presented as mean ± SD.

4. Results

4.1. Experiment 1: thermoregulation as a function of T_a in fasted hamsters

4.1.1. Frequency and timing of heterothermy at different T_as

All fasted hamsters expressed heterothermy at T_a of 19 °C and 23 °C with the lowest T_bs ranging from 34.0 °C to 29.0 °C. The number of individual hamsters expressing heterothermy decreased at T_as below 19 °C, but also above T_a 23 °C (Table 1). Only one individual showed heterothermy at T_a 26 °C with the lowest T_b of 33.8 °C. Hamsters expressed heterothermy mainly during photophase with 1–5 V-shaped bouts during fasting trials (Fig. 2).

4.1.2. Effects of T_a on T_b and body mass reduction in fasted hamsters

T_a significantly affected the lowest T_b and mean photophase T_b in fasted hamsters ($F_{7,33} = 3.358$, $P < 0.01$ and $F_{7,33} = 4.549$, $P < 0.01$, respectively) while there was no difference among different individuals ($F_{18,33} = 0.620$, $P = 0.855$ and $F_{18,33} = 0.998$, $P = 0.490$, respectively). Minimum lowest T_bs were detected at T_as of 23 °C and 19 °C with similar values of 31.4 ± 1.9 °C and 31.8 ± 2.0 °C respectively (Table 1). Below T_a 19 °C, the lowest T_b showed an increasing tendency and at T_a 5 °C, the lowest T_b was 35.7 ± 0.6 °C, significantly higher than that at T_a of 19 °C or 23 °C ($P < 0.01$). Above T_a 23 °C, the lowest T_b also showed an increasing tendency and at T_a 30 °C, the lowest T_b (35.1 ± 0.4 °C) was significantly higher than that at T_a of 19 °C or 23 °C ($P < 0.05$, $P < 0.01$) (Table 1).

Changes of mean photophase T_b, representative of the combined effects of T_a on the depth and duration of heterothermy, had a similar trend to those of the lowest T_b with minima reached at T_as of 19 °C, 23 °C and 26 °C. Mean photophase T_b reached a significantly higher level only at T_a 5 °C ($P < 0.05$) (Table 1).

T_a also had significant effects on body mass reduction in fasted hamsters ($F_{7,33} = 3.862$, $P < 0.01$; $P < 0.05$) with the least and greatest body mass reduction at T_a of 30 °C and 5 °C, respectively ($P < 0.05$), while there was no difference among individuals ($F_{18,33} = 0.560$, $P = 0.903$) (Table 1).

4.1.3. Metabolic rate and T_a in fasted hamsters

The normothermic RMR in fasted hamsters was significantly affected by T_a ($F_{7,25} = 82.228$, $P < 0.01$) while no difference among individuals was detected ($F_{18,25} = 1.211$, $P = 0.323$). As T_a decreased from

Table 1
Expression of heterothermy, body temperatures and body mass reduction in fasted desert hamsters at different ambient temperatures.

T_a (°C)	Sample size	Number of hamsters with heterothermy	Mean photophase T_b (°C)	Lowest T_b (°C)	Lowest T_b–T_a differential (°C)	Body mass reduction (g)
5	6	0	36.5 ± 0.4^{a}	35.7 ± 0.6^{a}	30.7 ± 0.6^{g}	4.6 ± 1.0^{a}
10	7	2	35.4 ± 1.1^{ab}	33.8 ± 1.6^{ab}	23.8 ± 1.6^{f}	3.7 ± 0.7^{ab}
13	13	6	35.9 ± 0.6^{ab}	33.2 ± 2.4^{ab}	20.2 ± 2.4^{e}	3.7 ± 1.1^{ab}
16	6	4	35.2 ± 0.8^{ab}	32.7 ± 2.1^{ab}	16.7 ± 2.1^{d}	2.9 ± 0.8^{ab}
19	7	7	34.8 ± 1.4^{b}	31.8 ± 2.0^{b}	12.8 ± 2.0^{c}	3.6 ± 1.2^{a}
23	8	8	35.0 ± 0.7^{b}	31.4 ± 1.9^{b}	8.4 ± 1.9^{b}	2.5 ± 0.3^{b}
26	6	1	34.9 ± 0.4^{b}	34.2 ± 0.6^{ab}	8.2 ± 0.7^{b}	3.7 ± 1.3^{ab}
30	6	0	35.6 ± 0.4^{ab}	35.1 ± 0.4^{a}	5.1 ± 0.4^{a}	2.2 ± 0.5^{b}

Different superscript letters mean significant difference in the same vertical row. For differential of lowest T_b and T_a: effects of T_a, $F_{7,33} = 127.4$, $P < 0.01$; among individuals, $F_{18,33} = 0.859$, $P = 0.625$.

30 °C to 5 °C, normothermic RMR significantly increased from 2.21 ± 0.31 ml O_2 g^{-1} h^{-1} at 30 °C to 6.37 ± 0.46 ml O_2 g^{-1} h^{-1} at 5 °C ($P < 0.05$). RMR during heterothermy was also significantly affected by T_a ($F_{3,9} = 6.762$, $P < 0.05$) while there was no difference among individuals ($F_{9,9} = 1.961$, $P = 0.165$). Heterothermic RMR increased from the lowest level of 2.59 ± 0.23 ml O_2 g^{-1} h^{-1} at 23 °C to 4.29 ± 0.87 ml O_2 g^{-1} h^{-1} at 13 °C ($P < 0.05$). The RMRs during heterothermy at 13 °C ($t = 3.819$, df = 6, $P < 0.05$), 16 °C (nonparametric test, df = 4, $P < 0.05$), 19 °C ($t = 5.840$, df = 6, $P < 0.05$) and 23 °C ($t = 7.954$, df = 5, $P < 0.01$) were 24.2%, 23.6%, 28.0%, and 17.6% lower than normothermic RMRs in fasted hamsters at the same T_as, respectively (Fig. 3).

Among hamsters that showed heterothermy, T_b below 31 °C and RMR <25% of the normothermic value were observed in total four of fasted individuals at T_a of 19 °C and 23 °C. Consequently, daily torpor was conformed in desert hamsters. With regard to their torpid metabolic rate (TMR), with a mean of 2.35 ± 0.20 ml O_2 g^{-1} h^{-1} was similar to basal metabolic rate (BMR) (2.21 ± 0.31 ml O_2 g^{-1} h^{-1}) measured at T_a 30 °C in this study ($Z = 0.730$, $P = 0.495$, n = 4). The duration of torpor bouts in desert lasted 2.8 ± 0.2 h (n = 4).

4.2. Experiment 2: food restriction at T_a 23 °C

4.2.1. Food restriction and body mass

Daily food requirements of hamsters ranged from 3.0 to 4.4 g/day with a mean of 3.5 ± 0.4 g/day. The initial body mass before food restriction was 24.3 ± 2.1 g. Food restriction reduced body mass, however the decrease reached significant level only in fasted hamsters ($F_{6,84} = 46.136$, $P < 0.01$; $P = 0.01$). No significant difference was detected in the body mass among re-fed hamsters (Table 2).

4.2.2. Food restriction and T_b

As in Experiment 1, fasted hamsters also inevitably showed heterothermy and could rewarm spontaneously to normothermia. The lowest photophase T_b tended to decline as the amount of food supply decreased (Figs. 4 and 5).

Food restriction had significant effects on the lowest photophase T_b ($F_{5,70} = 33.620$, $P < 0.01$). At food rations of ≤40% DFR, the reduction in the lowest photophase T_b reached significant levels ($P < 0.05$). The lowest photophase T_b decreased from 35.3 ± 0.2 °C at 100% DFR down to 31.9 ± 1.6 °C of fasting condition ($P < 0.01$). The lowest photophase T_b showed a significant linear relationship with food supply ($T_b = 3.1931(\%DFR) + 32.488$; $R^2 = 0.512$, n = 15; $P < 0.01$) (Fig. 5A). The mean photophase T_b was also significantly affected by amount of food supply ($F_{5,70} = 49.098$, $P < 0.01$). At food rations of ≤40% DFR, the reduction in mean photophase T_b reached significant levels ($P < 0.01$). A significant linear relationship was detected between amount of food and mean photophase T_b ($T_b = 1.3917(\%DFR) + 34.703$; $R^2 = 0.572$, n = 15; $P < 0.01$) (Fig. 5B).

5. Discussion

5.1. Defining torpor in desert hamsters

Our results support the hypothesis that fasted desert hamsters do have the capability to express daily torpor when facing acute food shortage. At T_a of 19 °C and 23 °C, fasted hamsters inevitably reduced their T_b and had the lowest T_bs (29.0 °C) compared to that at other T_as. In comparison to normothermic T_b maxima (37.9 ± 0.2 °C), these

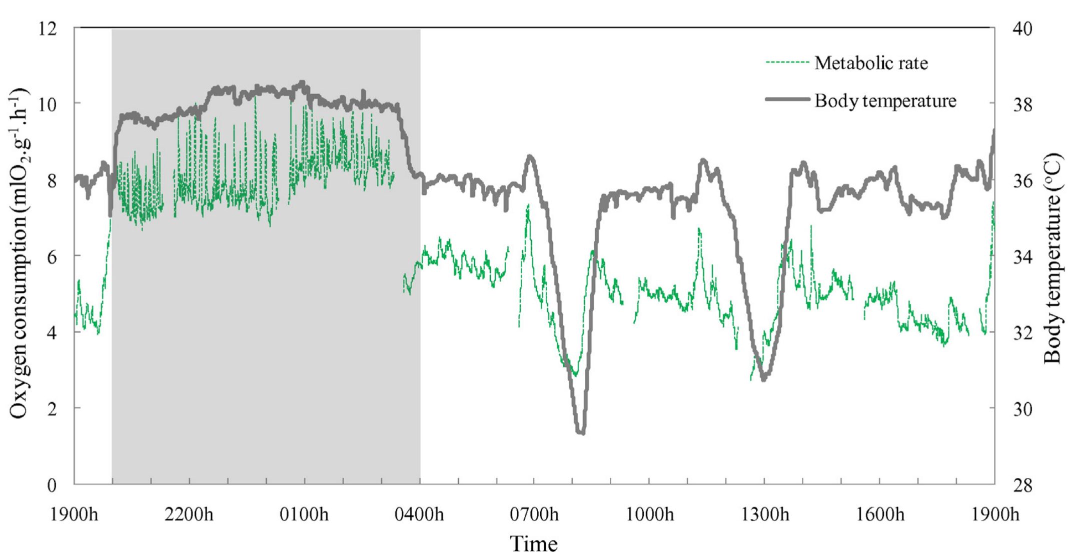

Fig. 2. Changes of body temperature and metabolic rate in a representative fasted desert hamster at T_a 19 °C (gray area indicates the scotophase. Interruptions in the dashed MR line show the 15-min automatic baseline measurements). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

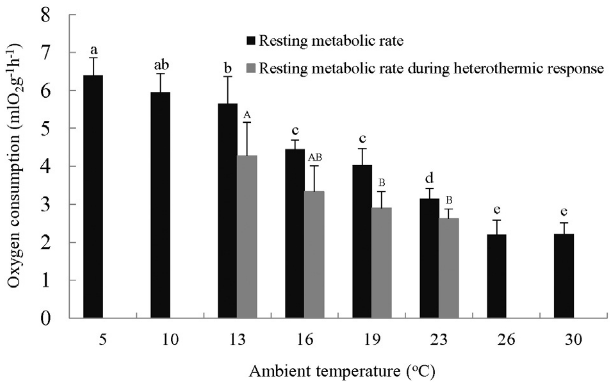

Fig. 3. Resting metabolic rates of fasted hamsters in normothermia or during heterothermy at different ambient temperatures (different letters indicate significant differences in RMRs among different T_as in normothermia (lower case letters) or during heterothermia (upper case letters), respectively).

hamsters reduced T_b by almost 9 °C. This suggests that T_as from 19 °C to 23 °C is a temperature range in which hamsters most readily display torpror.

The T_b during torpor in birds and mammals falls from high normothermic values of ~32 to 42 °C to values between −3 and <30 °C, and the minimum TMR is on average reduced to 5–30% of the BMR (Geiser, 2004) (hibernators included). Our study indicates that T_bs in those four torpid hamsters fell below this arbitrary boundary (T_b < 30 °C) and thus within this range. However, TMR was not lower than BMR in the torpid hamsters. Thus, considering the classic profile of torpor, which is usually associated with profound decreases in metabolic rate lower than BMR, daily torpor in fasted desert hamsters was rather shallow.

5.2. Characteristics of shallow daily torpor in desert hamsters

Although desert hamsters do express fasting-induced torpor, they differ somewhat from most other heterothermic species because of the following reasons: 1) the lowest T_b in fasted desert hamsters is higher than that in other daily heterotherms (minimum T_b ~ 11 to 23 °C) such as some rodents (Ruby and Zucker, 1992; Vogt and Lynch, 1982; Hudson and Scott, 1979; Tomlinson et al., 2007), similar-sized marsupials (Bozinovic et al., 2007; Körtner and Geiser, 2011) and even birds (Bucher and Chappell, 1992; Geiser, 2004; Ruf and Geiser, 2015). The lowest T_b in torpid desert hamsters of 29.0 °C is therefore among the highest minimum T_b in daily heterotherms (see reviews by Heldmaier and Ruf, 1992; Geiser and Ruf, 1995; Ruf and Geiser, 2015). 2) Torpid mammals usually have a thermo-conforming T_a range, in which their T_b–T_a differential is usually 1–5 °C while their metabolic rate decreases with T_a (Geiser, 2004; Chruszcz and Barclay, 2002). In the present study, torpid desert hamsters always kept higher T_b–T_a gradients of >6 °C and also increased metabolic rate and T_b further at T_a < 23 °C (Table 1). 3) The duration of one torpor episode in desert hamsters lasted up to 3.1 h therefore shorter compared to those in most other daily heterotherms, for example about 5 h during spontaneous daily torpor of Siberian hamsters (Ruf and Heldmaier, 1992; Kirsch et al., 1991) and up to 5–6 h in laboratory mice (Hudson and Scott, 1979; Schubert et al., 2010). 4) The preferred T_a for desert hamsters to enter a state of torpor was 19–23 °C, which is higher than that in many other small mammals (e.g. 0–15 °C during spontaneous daily torpor in Siberian hamsters, Ruf and Heldmaier, 1992). Perhaps this is related to the fact that fasted hamsters with T_b below 34.0 °C at T_a of 5 °C, would eventually die because of a continuous falling T_b and would only survive when they were passively re-warmed. The high torpid T_b and T_b–T_a gradients, plus the high preferred T_a to enter torpor should be favorable for it could prevent death during cold spells. T_as around 5 °C were often observed in June of their habitats during our field study.

Finally, torpid desert hamsters sat and curled up adopting a resting posture similar to that in normothermic individuals. They could respond to mechanical stimuli by showing weak noises and impaired locomotor activity. Torpid animals at low T_a often are well aware of their surroundings and even express a number of complex behaviors which likely contribute to maximize survival of the species (Geiser, 2010).

Jefimow (2007) fasted summer- and winter-acclimated desert hamsters in laboratory conditions, but did not detect torpor. The most likely reason for the different result is that her hamsters were maintained in a thermal gradient system (5–45 °C) and chose a higher T_a of ~30 °C during most of the fasting period. In our study, fasted hamsters at T_a 30 °C also remained normothermic with the least body mass reduction compared to those at other T_as. It seems that hamsters reduced their energy expenditure by selecting high T_a and thereby avoided the need for using torpor (Jefimow, 2007). The avoidance of entering torpor maybe related to potential physiological and ecological cost of torpor, e.g. impaired physiological function and reduced mobility (Humphries et al., 2003).

5.3. Food restriction and torpor induction

Although mammalian daily torpor often occurs during winter, periods of food shortage can occur all over the year and thus represent the most common trigger for torpor induction in most heterotherms (Hudson, 1978; Ruf and Geiser, 2015). For example, daily torpor induced by partial food restriction has been shown in summer-acclimated *Peromyscus* spp. and *P. sungorus* (Gaertner et al., 1973; Tannenbaum and Pivorun, 1989; Diedrich et al., 2015). The linear relationships between photophase T_bs and amount of food in desert hamsters suggest that food shortage directly influenced depth and perhaps duration of the heterothermy and thus was the main trigger of daily torpor. Importantly, hamsters in our study were also maintained under summer-like conditions, the thermal biology and related energetic significance of winter-acclimated hamsters might differ. It should also be noted that a 1-day recovery period in Experiment 2 was quite short especially regarding the 0%DFR treatment, thus the influence from last trails should not be ignored.

Our study is the first to demonstrate that shallow daily torpor can occur in fasted desert hamsters when they are acclimated to summer-like conditions. Because of their low energy reserves associated with

Table 2
Changes of body mass in desert hamsters during food restriction at T_a 23 °C.

Food supply	Body mass before food restriction (g)	Body mass after food restriction (g)	Body mass after re-feeding (g)	Body mass reduction (g)
100% DFR	23.5 ± 2.2	23.5 ± 2.1	23.7 ± 2.1	0.0 ± 0.4
80% DFR	23.4 ± 2.5	22.8 ± 2.3	23.3 ± 2.3	0.6 ± 0.2
60% DFR	23.2 ± 2.3	22.2 ± 2.3	23.2 ± 2.2	1.0 ± 0.3
40% DFR	23.7 ± 2.2	22.0 ± 2.1	23.4 ± 2.2	1.7 ± 0.2
20% DFR	24.1 ± 2.1	21.8 ± 2.0	23.3 ± 2.1	2.3 ± 0.3
Fasting	23.6 ± 2.0	20.7 ± 1.7*	22.5 ± 1.8	2.9 ± 0.4

* Indicates body mass significantly reduced compared to the initial value of 24.3 ± 2.1 g.

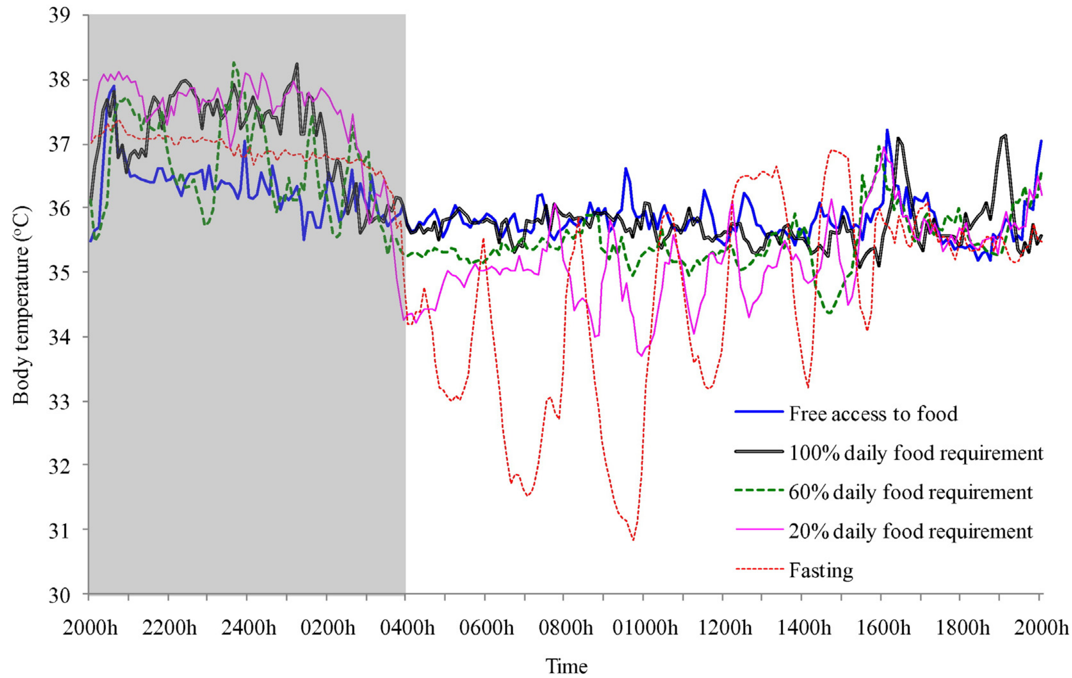

Fig. 4. Body temperature in a representative desert hamster with different amounts of food supply at 23 °C and 16L:8D photoperiod (gray area indicates the scotophase). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

small body size, daily torpor may play an important role in the energy balance especially in their barren, sandy and seasonal habitats of Inner Mongolia. During moderate weather conditions like in early summer when stored food is depleted and foraging success is low, torpor may be expressed.

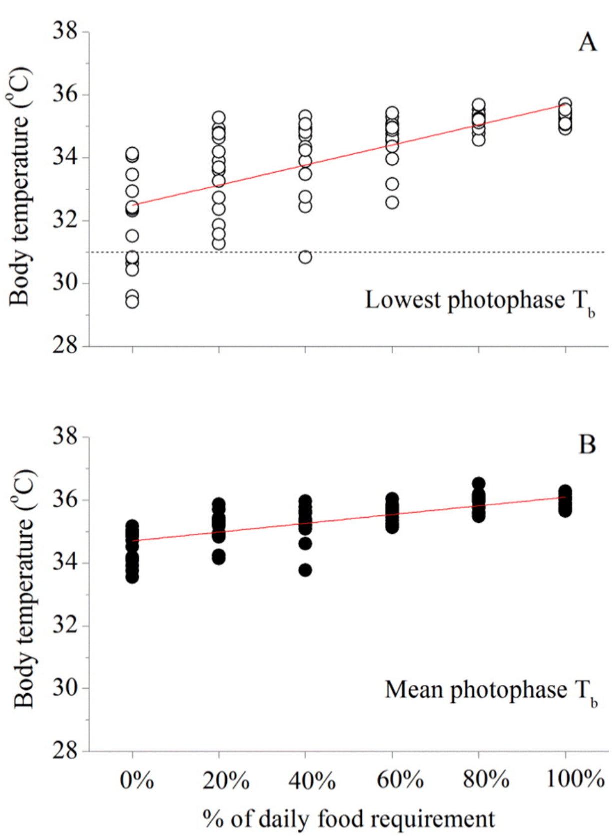

Fig. 5. Minimum photophase T_b as a function of food provided (A, $r^2 = 0.512$) and mean photophase T_b as a function of food provided (B, $r^2 = 0.572$) in desert hamsters at 23 °C and 16L:8D photoperiod (horizontal dashed line at T_b 31 °C shows torpor threshold).

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