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 (Tb) in fasted hamsters. To test this hypothesis we (i) randomly exposed fasted summer-acclimated hamsters to ambient temperatures (Ta) ranging from 5 to 30 °C or (ii) supplied them with different rations of food at Ta 23 °C. All desert hamsters showed heterothermy with the lowest mean Tb of 31.4 ± 1.9 °C (minimum, 29.0 °C) and 31.8 ± 2.0 °C (minimum, 29.0 °C) when fasted at Ta of 23 °C and 19 °C, respectively. Below Ta 19 °C, the lowest Tb and metabolic rate increased and the proportion of hamsters using heterothermy declined. At Ta 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 Ta. During heterothermy, TaS below 31 °C with metabolic rates below 25% of those during normothermia were detected in four individuals at Ta 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 TaS 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.

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1. Introduction

Torpor is defined as a state of profound but controlled reductions of metabolic rate and body temperature (Tb) 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 (Ta) or low food availability (McNab, 2002; Geiser, 2004). Torpor is traditionally divided into two categories: daily torpor and hibernation. Compared to the midday 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, graminivorous 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 Tb below 30.0 °C in fasted hamsters at Ta 23 °C under long photoperiod (Chi and Wang, 2011). Similarly, Ushakova et al. (2012) reported substantially decreased TaS 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...
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 \( T_a \). 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 \( T_a \) and \( T_s \) and investigated the effects of food availability at \( T_b \), 23 °C, at which the maximum decreases of \( T_b \) were previously detected and the hamsters were routinely maintained. \( T_s \) 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′E, 116°10′N, minimum \( T_b \) = −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 mini circuitry and Use Committee of Institute of Zoology, the Chinese Academy of Sciences.

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 LHR-250, Shanghai, China) was used to maintain constant ambient conditions within the animal chamber during the measurement intervals at a series of \( T_a \)s 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:

\[
\text{VO}_2 = \frac{\text{FR} \times (\text{FiO}_2 - \text{FeO}_2)}{\text{F}_{\text{O}_2}} - \text{FR} \times \text{FeO}_2 \times (\text{FeCO}_2 - \text{FiCO}_2) \quad (1 - \text{FeO}_2)
\]

(\( \text{FR} = \text{mass flow rate}, \text{FiO}_2 = \text{input fractional concentration of O}_2 \) to the chamber, \( \text{FeO}_2 = \text{excurrent fractional concentration of O}_2 \) from the chamber, \( \text{FiCO}_2 = \text{input fractional concentration of CO}_2, \text{FeCO}_2 = \text{excurrent fractional concentration of CO}_2 \) from the chamber) (Hill, 1972; Withers, 1977). We took the 5-min least variable and lowest \( \text{VO}_2 \) 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 \( T_s \) in fasted hamsters

To investigate the effects of \( T_s \) 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 \( T_s \) mentioned above. Animals were completely deprived of food from 1700 h for 24 h at each \( T_s \), during which \( T_b \) and metabolic rate were monitored.
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 $\leq 0.05$ 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 $T_a$s
All fasted hamsters expressed heterothermy at $T_a$ of 19 °C and 23 °C with the lowest $T_b$s ranging from 34.0 °C to 29.0 °C. The number of individual hamsters expressing heterothermy decreased at $T_a$s 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 $T_b$s and mean photophase $T_b$s 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 $T_b$s were detected at $T_a$s 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 $T_b$s showed an increasing trend 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 $T_b$s 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 $T_b$s, representative of the combined effects of $T_a$ on the depth and duration of heterothermy, had a similar trend to those of the lowest $T_b$s with minima reached at $T_a$s of 19 °C, 23 °C and 26 °C. Mean photophase $T_b$s 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 $T_a$s 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 there was no difference among individuals was detected ($F_{18,25} = 1.211$, $P = 0.323$). As $T_a$ decreased from...
30 °C to 5 °C, normothermic RMR significantly increased from 2.21 ± 0.31 ml O2 g⁻¹ h⁻¹ at 30 °C to 6.37 ± 0.46 ml O2 g⁻¹ h⁻¹ at 5 °C (P < 0.01). RMR during heterothermy was also significantly affected by Ta (F3,9 = 6.762, P < 0.05) while there was no difference among individuals (F6,84 = 46.136, P = 0.01). The RMRs during heterothermy at 11 °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 RMR. The RMRs during heterothermy was also significantly affected by amount of food supply (F5,70 = 49.098, P < 0.01) ≤ 40% DFR, the reduction in mean photophase Tb reached significant levels (P < 0.01) (Fig. 5A). The mean photophase Tb was also significantly affected by amount of food supply (F5,70 = 49.098, P < 0.01). At food rations of ≤40% DFR, the reduction in mean photophase Tb reached significant levels (P < 0.01). The mean photophase Tb at 0% DFR showed a significant linear relationship with food supply (Ta = 3.1931(\%DFR) + 32.488; R² =0.512, n=15; P < 0.01) (Fig. 5A). The lowest photophase Tb was also significantly affected by amount of food supply (F5,70 = 33.620, P < 0.01). At food rations of ≤40% DFR, the reduction in the lowest photophase Tb reached significant levels (P < 0.05). The lowest photophase Tb 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 Tb showed a significant linear relationship with food supply (Ta = 3.1931(\%DFR) + 32.488; R² = 0.512, n = 15; P < 0.01) (Fig. 5A). The lowest photophase Tb showed a significant linear relationship with food supply (Ta = 3.1931(\%DFR) + 32.488; R² = 0.512, n = 15; P < 0.01) (Fig. 5A).

4.2.2. Food restriction and Tb

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

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 Ta of 19 °C and 23 °C, fasted hamsters inevitably reduced their Tb and had the lowest Tb at 29.0 °C compared to that at other Tbs. In comparison to normothermic Tb maxima (37.9 ± 0.2 °C), these...
hamsters reduced $T_b$ by almost 9 °C. This suggests that $T_s$ from 19 °C to 23 °C is a temperature range in which hamsters most readily display torpor.

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 $T_s$ in those four torpid hamsters fell below this arbitrary boundary ($T_s < 30 °C$) 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 of 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; Körntner 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). 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). The lowest $T_b$ in fasted 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 $T_b$ of ~30 °C during most of the fasting period. In our study, fasted hamsters at $T_b$ 30 °C also remained normothermic with the least body mass reduction compared to those at other $T_b$. It seems that hamsters reduced their energy expenditure by selecting high $T_b$ 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 $T_b$s 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

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**Table 2**

Changes of body mass in desert hamsters during food restriction at $T_b$ 23 °C.

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

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

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