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IS TORPOR ONLY AN ADVANTAGE? EFFECT OF THERMAL ENVIRONMENT ON TORPOR USE IN THE SIBERIAN HAMSTERS (*PHODOPUS SUNGORUS*)

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The aim of our study was determine torpor use in the Siberian hamsters (*Phodopus sungorus*) tested in a wide gradient of ambient temperatures (T_a). Experiments were done on fed and food-deprived animals acclimated to winter-like and summer-like conditions. We found that neither fed nor unfed hamsters acclimated to winter-like or summer-like conditions selected low T_a's and entered torpor. Instead, food deprivation led to selection of higher T_a's and slight lowering of body temperature (T_b), especially during the rest-phase of the day. Our calculations show that this strategy may lead to higher energy savings than torpor would. We argue that torpor use is not a fixed strategy but is determined primarily by a thermal conditions available in the environment.

Key words: *torpor, Siberian hamster, Phodopus sungorus, temperature selection, energy conservation*

INTRODUCTION

Both daily and seasonal torpor bring about significant energy savings to heterothermic animals. Episodes of seasonal, hibernation torpor are significantly longer and deeper than episodes of daily torpor, resulting in larger energy savings (1, 2). It is mainly due to a considerable lowering of body temperature (T_b) and parallel reduction of metabolic rate. The most important for energy savings during torpor seems to be a reduction of the gradient between T_b and ambient temperature (T_a) (3 - 5), however, the significant role of metabolic depression in torpor was also found in several mammalian taxa (2, 6). Nevertheless, the T_b-T_a difference

determines the rate of heat loss to the environment, both in normothermic and torpid animals (7) affecting the energy expenditure.

However, there is also evidence of significant physiological and ecological costs of entering torpor (8). Torpor may lead to an accumulation of sleep debt (9), as well as to reduced synaptic efficacy or to oxidative stress resulting from large T_b variations between torpor and normothermy (10, 11). Animals entering torpor are also more susceptible to predation (12, 13), and frequent episodes of torpor in bat females can result in prolonged pregnancy and slowed growth of young, which may decrease their fitness (14, 15). In addition, a considerable energy expenditure during arousal from torpor must be taken into account (5, 16). The arousal is the most energy consuming phase of torpor and if torpor episode is too short then energy expenditure can surpass energy savings. Torpor can be regarded as energy saving mechanism only if its total costs (entrance, maintenance and arousal) are lower than costs of being normothermic during corresponding time under the same conditions.

In nature torpor is a response to a complex action of at least several factors, like weather, food or water availability or both, which are often correlated with particular season and corresponding day length (17). For many insectivorous or nectarivorous species food availability correlates with T_a and weather (17 - 19). Thus, it is not surprising that changes in T_a, which signal changes of food availability, determine the length and depth of the torpor episodes (5). However, food resources of granivorous species usually do not undergo such large daily and seasonal variations. Thus, one might expect different mechanisms involved in the control of torpor use in animals which diets differ. Hence, we analysed changes in body and selected ambient temperatures in response to food deprivation in a heterothermic, granivorous rodent, the Siberian hamster (*Phodopus sungorus*).

There are at least two potential scenarios available for a hamster to reduce the costs of survival under unfavourable conditions: i) entering torpor at selected T_a, where torpor episodes can ensure significant energy savings, and ii) selecting a proper thermal environment, if such is available, and remaining normothermic. Since *Phodopus sungorus* are known to enter torpor readily on the daily basis even when exposed only to short photoperiod, we predicted that when placed in the thermal gradient, hamsters acclimated to winter-like conditions will regularly enter torpor. Food-deprivation, in turn, would result in selection of lower T_a's for longer and deeper torpor to maximize energy savings.

MATERIALS AND METHODS

Animals

The Siberian hamster, *Phodopus sungorus*, is a dwarf hamster inhabiting steppes and semi-steppes of western Siberia, eastern Kazakhstan, and Krasnoyarsk Region of Russia (20). Adult animals weigh between 19 and 45 g and their body mass (m_b) is always lower in winter than in

summer. They are mainly granivorous, but in summer they supplement their diet with insects. *P. sungorus* is a highly photosensitive species and uses daily torpor only in winter. At that time, lowered body mass is paralleled by regressed gonads, white pelage and increased thermogenic capacity of brown adipose tissue (BAT). In captivity *P. sungorus* require several weeks of acclimation to short photoperiod to change to their winter status.

Hamsters used in these studies were adult, at least 4-month old males (10 animals acclimated to summer-like and 8 to winter-like conditions) from our own breeding colony. Before as well as between experiments animals were housed individually in standard laboratory cages (33 × 20 × 18 cm) with food (assorted grains, flakes and fruit) and water available *ad libitum*.

Experimental procedure

About 3 months before the first set of experiments, hamsters were acclimated to summer-like days (long photoperiod 16L:8D; lights on: 0600-2200 h and T_a of 25 °C). After completing the first set of experiments, each animal was transferred to a climate chamber with winter-like conditions (short photoperiod 8L:16D; lights on: 1000-1800 h, and T_a of 10 °C). After 3 months of acclimation the animals were sampled again. To monitor changes in m_b, all hamsters were weighed to ± 0.1 g at the beginning and at the end of the acclimation, as well as before and after each experiment.

After acclimation to summer and winter-like conditions, fed and fasted *P. sungorus* were tested in a thermal gradient system that consisted of an aluminum trough (120 × 12 × 10 cm) divided by half-width partitions into 16 compartments of the same size, and covered with Perspex® to permit light entry. Heating of the system at one end and cooling at the other, resulted in a linear gradient of T_a ranging between 5 and 45 °C. The construction of the gradient did not restrict animal movements during the experiments. Infrared photoemitter-photodetector pairs detected location of an animal while T_a was measured automatically with thermocouples placed in the floor of each compartment. A narrow slit in the gradient's lid allowed movement of the thermocouple suspended above the gradient with an elastic band that let animals to move freely inside the gradient. All electronic temperature measuring devices were calibrated in a water bath against a mercury thermometer with accuracy ± 0.1 °C.

At least one week before experiments, each hamster was implanted, under Sevorane (Abbott Laboratories Ltd., UK) anaesthesia, with a polyethylene cannula (φ = 0.8 mm; PORTEX Ltd., England). The cannula was inserted subcutaneously through a small incision at the back of the neck, and fixed with a surgical thread and adhesive to the skin. During experiments, the cannula served as a guide for a type T thermocouple (W-TW-36 P2; Physitemp Instruments Inc., USA). Each experiment lasted for 72 h, starting in the late morning. At the beginning of each experiment, the thermocouple was inserted into the cannula at the depth of the interscapular BAT deposits and taped in place. We decided to measure T_b in BAT since it is the major site for nonshivering thermogenesis, and thus gives direct information on changes in T_b (21). Then the hamster was left undisturbed to enable its habituation. During experiments on fed hamsters food was placed equidistantly along the trough to avoid the effect of food searching on T_a selection. Unfed hamsters, both acclimated to summer and winter conditions were food deprived for the 72 h of the experiment. During all experiments water was always available *ad libitum*.

T_b and selected T_a were sampled simultaneously at 1 second intervals and saved on disk. The apparatus was set up in a room with the photoperiod adjusted to summer or winter-like conditions.

Data analysis

The first 24 hours of each experiment were excluded from analysis. Since there was no difference in T_b or selected T_a between the second and the third day of experiments, the data were

pulled together in each animal. If hamsters chewed their thermocouple lead wires, the break was immediately repaired. During lead repair, animals were handled for no more than 10 minutes. Data collected for one hour after the repair were discarded from analysis. In each hamster, all data recorded within 48 h of experiment were averaged in 1-min intervals, and then daily mean values of T_b, selected T_a as well as T_b - T_a difference (ΔT_b - T_a) during the day (light phase) and night (dark phase of the day) were calculated.

The effect of acclimation (winter or summer), time of day (day or night) and food availability (fed or unfed) on T_b, selected T_a and ΔT_b - T_a were analysed with 3-way ANOVA. When ANOVA results showed significant effects, a post hoc Tukey HSD test was used for comparisons. We defined torpor as a state of an animal when its T_b was ≤ 32 °C. Differences were considered statistically significant at $P < 0.05$. All values are presented as mean ± SE.

RESULTS

After acclimation to winter-like conditions (short photoperiod and cold) hamsters reduced their m_b, on average by 30 % (F(1.36)=89.76, P < 0.001; *Fig. 1*). Together with the appearance of white fur, the decrease in m_b indicates their winter status.

Surprisingly, neither fed nor fasted hamsters entered daily torpor. When tested in the thermal gradient, all hamsters, both summer- and winter-acclimated, were normothermic and followed clear daily rhythm of T_b. However, fed winter acclimated animals had significantly lower T_b than fed summer acclimated ones, both by day and by night (F(1,66)=138.25; P < 0.001; *Fig. 2*).

Food deprivation significantly affected T_b of hamsters, both in summer and in winter. In summer, daily rhythm of T_b was maintained (F(1,72)=69.78; P < 0.001), but during the day mean T_b was higher in fed than in fasted individuals (F(1,72)=10.41; P < 0.002; *Fig. 2*). After acclimation to winter-like conditions, food deprivation also led to the decrease in mean T_b (F(1,55)=4.29; P < 0.05), and in both fed and unfed animals T_b was higher by night than by day (F(1,55)=21.91; P < 0.001; *Fig. 2*).
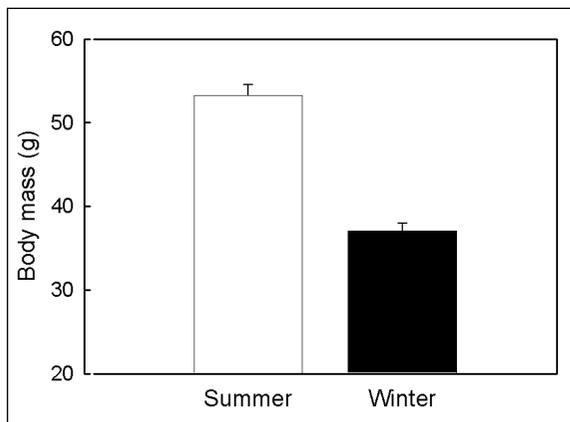
Fig. 1. Body mass (mean ± SE) of *Phodopus sungorus* acclimated to summer-like (T_a = 25°C, 16 h of light - open bar) and winter-like (T_a = 10°C, 8 h of light - black bar) conditions. Values were different at P < 0.001.

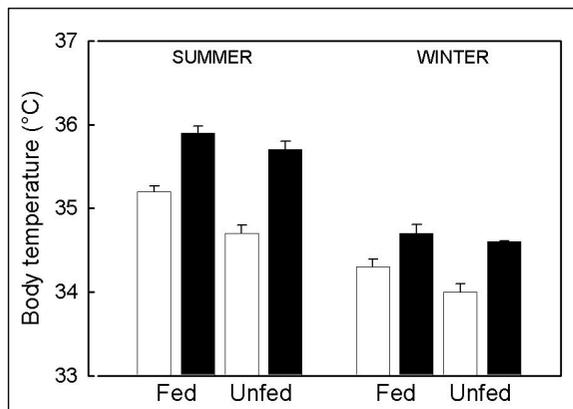*Fig. 2.* Mean (± SE) day (open bars) and night (black bars) body temperatures (T_b) of fed and unfed *Phodopus sungorus* after acclimation to summer- and winter-like conditions. All animals maintained higher T_b at night than at day (P<0.001). Acclimation to winter-like days and food deprivation resulted in lower T_b (P < 0.001 and P < 0.001, respectively).

Selection of T_a depended on the acclimation regime. Mean selected T_a was higher in animals acclimated to winter than to summer-like conditions (F(1,65)=9,08; P < 0.0037; *Fig. 3*). Both winter and summer acclimated hamsters selected T_a's within the range of thermoneutrality and avoided low T_a's. In fed hamsters, significant differences between T_a's selected by day and by night were recorded only in summer while in winter these T_a's did not differ (F(1,65)=5,21; P < 0.03).

Food deprivation in summer affected T_a selection. Preferred T_a was higher by day than by night, both in fed and fasted hamsters (F(1,71)=13.66; P < 0.001) but fasting led to selection of higher T_a's at rest, during daytime and of lower T_a's by night, when hamsters were active (P < 0.004; *Fig. 3*). In winter, both in fed and unfed animals there were no significant daily variations in selected T_a (day 30.7 ± 0.3 °C and night 31.5 ± 0.5 °C, respectively; *Fig. 3*).

Selection of high T_a's combined with a slight drop in T_b resulted in considerable variations in the Δ T_b-T_a. Acclimation to cold and short photoperiod resulted in the lowering of T_b-T_a difference in fed hamsters (F(1,67)=18,14;
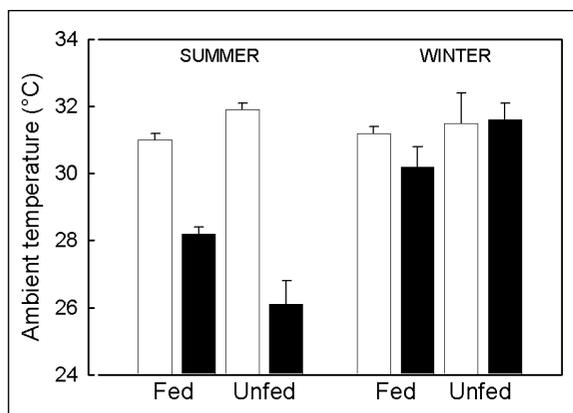

Fig. 3. Mean (± SE) ambient temperatures (T_a) selected during day (open bars) and night (black bars) by fed and unfed *Phodopus sungorus* in the thermal gradient after acclimation to winter- and summer-like conditions. On average, acclimation to winter-like conditions resulted in increase of selected T_a (P < 0.004). Food deprivation affected T_a selection only in summer (P < 0.001).
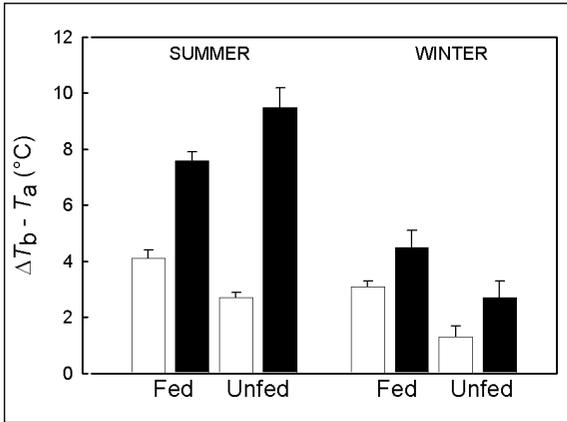
Fig. 4. Mean (± SE) differences between body and ambient temperatures (ΔT_b-T_a) by day (open bars) and night (black bars) in fed and unfed *Phodopus sungorus*, acclimated to winter- and summer-like conditions. Acclimation to winter-like conditions resulted in the lowering of ΔT_b-T_a difference and dampened its daily variations (P < 0.001). Food deprivation led to decrease of ΔT_b-T_a during the rest phase pf the day.

p<0.001) and dampened its daily variations. Significant differences in Δ T_b-T_a between day and night were recorded only in hamsters acclimated to summer-like days (F(1,65)=7.26; P < 0.01; *Fig. 4*). Also season affected the effect of food deprivation on T_b-T_a difference. In summer, fasting led to reduction of Δ T_b-T_a by day (P < 0.05) while to its increase by night (P < 0.01), when compared to fed animals. In summer acclimated fasted individuals daytime T_b-T_a difference was as low as 2.7 ± 0.2 °C while at night it reached 9.5 ± 0.7 °C (*Fig. 4*). In winter, ΔT_b-T_a was larger in fed than in food deprived individuals (F(1,54)=13,64; P < 0.0005). The highest ΔT_b-T_a was recorded in fed hamsters by night (4.5 ± 0.6 °C) while the lowest in fasted animals by day (1.3 ± 0.4 °C; *Fig. 4*).

DISCUSSION

In nature *Phodopus sungorus* uses daily torpor only in winter to overcome harsh environmental conditions and low food availability. In the process of acclimatization they strongly rely on changes in day length. Under laboratory conditions, several week exposure to short days elicits all symptoms of winter acclimation including torpor use even in hamsters fed *ad libitum* and kept at T_a only slightly lower than thermoneutral (22, 23). This is why we expected, that winter acclimated hamsters, when placed in the thermal gradient, would select low T_a's and enter daily torpor. However, although the hamsters were in their winter status (reduced m_b, white pelage), they never selected low T_a's, lowered their T_b < 32 °C and entered torpor. Instead, even when food deprived for 72 h they remained normothermic and selected relatively high T_a's in the thermal gradient.

One could argue that there must have been an effect of the stress related to experimental conditions or the fact that animals used in these experiments were born and bred in captivity. However, similar sized bats (5) as well as other heterothermic mammals, like rodents (24, 25) and marsupials (26, 27) also do not

select low T_a's and do not enter torpor when placed in the thermal gradient in which wide spectrum of T_a's is available. However, when the range of available temperatures is limited and resembles the natural spectrum of T_a's, bats enter prolonged torpor (28). In our previous studies on the *Myotis myotis* we proposed that avoidance of low T_a's in the thermal gradient is a result of "an error" in the environmental signal (5). For insectivorous bats high T_a, both in summer and in winter, signals potential food availability. Hence, when fasted bats experience high T_a in the gradient, they await the day (without food) in shallow torpor, or even remain normothermic, at T_a slightly lower than T_b. As a result, the small gradient between body and ambient temperatures minimizes energy expenditure. This strategy allows *M. myotis* for higher energy savings than in animals entering deeper torpor at lower T_a's. This is because entry into and arousal from shallow torpor are less expensive than in the case of deeper torpor. The latter becomes more profitable only when it is longer. Similar explanations were offered by Song *et al.* (26, 27). Short and shallow torpor would be favoured because of the disadvantages of long-lasting hypothermia and benefits resulting from being normothermic (8, 25, 26).

However, the above reasoning concerns mainly the avoidance of torpor in insectivorous or nectarivorous animals, in which food availability is temperature-dependent. The *P. sungorus* is a granivorous species, and its food availability depends on the weather to much lesser extent. This is why in their natural environment hamsters can arouse every dusk and forage during the night (29). In this light, torpor seems to be rather a strategy of avoiding excessive energy loss during the rest phase of the day than of a response to food deficit. Such strategy was observed in several animal taxa, like birds (30 - 32), bats (33) and primates (34). If so, then the selection of high T_a would reflect the natural tendency to minimize energy loss to the environment while remaining normothermic. In contrast, torpor would be the way to reduce the gradient between T_b and T_a in the cold environment.

If this is true, then one would expect that energy savings, resulting from being normothermic at high T_a, would be higher or at least comparable to energy savings resulting from entering torpor in the cold. To test it, we did simplified calculations of the energy costs of torpor in a hamster and compared it to the cost of staying normothermic at high T_a, where the difference between T_b and T_a was small.

To calculate the energy expenditures of a normothermic and torpid hamsters we used the data obtained in the present experiments. In winter acclimated hamsters the rest-phase T_b was 34.5 °C and selected T_a was 31.2 °C. Hence, the mean T_b-T_a difference was 3.3 °C. We assumed that T_b in torpor was 15°C (23) and T_a was 11.7°C (ΔT_b-T_a = 3.3 °C, i.e. equal to that observed in normothermic animals). We also assumed that the maintenance phase of torpor lasted 6 h (23). Metabolic rate (MR) was calculated according to the equation: MR = h (T_b-T_a), where h is heat loss coefficient (7, calculated following 22). To account for the reduction in metabolic rate resulting from the Q_{10} effect, we assumed its value at 2.5, which is the average for most physiological processes (35). Costs of arousal from torpor

were calculated following McKechnie and Wolf (36) and the duration of the arousal from torpor was calculated using equations from Geiser and Baudinette (37). Calculations were made for hamster's m_b of 37 g (the average m_b of winter acclimated hamsters).

Total cost of remaining normothermic for 6 h at $T_a = 31.2$ °C equals 2.5 kJ. During 6 h of steady-state metabolic rate in torpor at $T_b = 15$ °C and at $T_a = 11.7$ °C a hamster consumes 0.4 kJ, however, total cost of this torpor, including the cost of ~30 min-long arousal equals 4.2 kJ. These results clearly show that although the energy consumption in torpor is significantly lower than in normothermy, its total cost, including the cost of arousal is almost two times higher than the energy consumption in normothermic hamster which selects T_a lower by 3.3 °C than T_b. Accordingly, it is not surprising that the *P. sungorus* remains normothermic when the environment offers appropriate thermal conditions.

Based on above we argue that the thermal environment plays a key role in determining torpor use in heterothermic mammals. Frequent torpor episodes observed in the laboratory, in hamsters acclimated to short photoperiod (22, 23) appear to be a response to even moderately unfavourable thermal environment rather than a fixed or preferred strategy for winter survival. Under short days, either food deprivation or drop in T_a, or both, prolong and deepen torpor episodes (38). Under these conditions staying normothermic would be too expensive. Keeping high T_b at low T_a in the face of food shortage would lead to fast energy depletion due to high rate of shivering and nonshivering thermogenesis. Hamsters would have to forage intensely to cover the energy loss resulting from large gradient between T_b and T_a. This in turn, would increase a risk of predation and would disturb normal sleep-wake cycle. However, if an animal may choose T_a's within the thermoneutral zone it will do so and remain normothermic, only slightly reducing the gradient between T_b and T_a. This strategy would ensure not only necessary energy savings but would also enable avoiding additional costs of torpor, like sleep debt, oxidative stress or potential risk of being predated.

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