



Magnitude of food overabundance affects expression of daily torpor



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HIGHLIGHTS

- We examined the relationship between daily torpor and overabundance of food.
- Different magnitudes of food overabundance did not affect expression of daily torpor.
- Temporal changes in food overabundance did affect expression of daily torpor.
- The mice showed shallower torpor when food availability increased.
- Recognition of changing food availability may be a factor in regulating daily torpor.

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ABSTRACT

Many small mammal species use torpor as a strategy for reducing energy expenditure in winter. Some rodent hibernators also hoard food to provide reserves of energy, and individuals with large hoards express less torpor than those with smaller reserves. These facts imply that animals can recognize levels of food availability, but where food is very plentiful, it is unclear whether torpor expression is affected by temporal changes in the extent of food overabundance. Moreover, the relationship between daily torpor and excess food availability has not been clearly established. The large Japanese field mouse *Apodemus speciosus* caches food for use as a winter energy resource and exhibits daily torpor under artificial winter conditions. The present study examined whether individuals exposed to different magnitudes of overabundant food exhibited differences in expression of daily torpor, and secondly whether torpor expression varied in response to changes in the overall quantity of overabundant food. It was observed that while absolute quantities of overabundant food did not appear to affect daily torpor expression, the mice did respond to changes in food availability, even when food remained overabundant. This suggests that the mice respond to fluctuations in food availability, even where these changes do not place any constraint on energy budgets. Thus recognition of changing food availability cannot be a purely physiological response to shortage or plenty, and may contribute to predictions of future energy availability. The expression of torpor was inhibited in response to increasing food availability, and the mice used shallower torpor when food availability increased to superabundance. These findings suggest that daily torpor may be regulated not only physiologically in response to energy constraints but also psychologically, via recognition of food availability.

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1. Introduction

The capacity of mammals to maintain a virtually constant body temperature (T_b) by endogenous heat production depends on the ability to

balance energy budgets and therefore is essential for survival. Small mammals have greater energy requirements per body mass than larger species because of their relatively large surface-area-to-volume ratio and relatively greater heat loss, and their survival is therefore more likely to be influenced by fluctuations in food availability. In temperate biomes, winter conditions present significant challenges to small mammals, including cold ambient temperatures (T_a) and food scarcity, both of which impact on energy budgets. Some species use torpor as a strategy to reduce energy expenditure and thereby limit their requirements for food [1,2].

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Torpor is a physiological adaptation, which serves to conserve energy and water by spontaneously reducing both metabolic rate and T_b [2,3]. Species using torpor, often referred to as heterotherms, are traditionally categorized into two groups, the hibernators and the daily heterotherms [2].

Hibernators have the capacity to enter prolonged and multiday torpor [2]. They also cache food and/or accumulate fat to provide reserves of energy in winter [4,5]. These energy resources can be not only large but also quite variable, both between individuals and from year to year for the same individual [6]. Humphries et al. [4] predicted a close relationship between energy availability and hibernation, and individuals with large energy reserves have been seen to express less torpor than those with smaller reserves, both in food-hoarding hibernators such as *Tamias striatus* [6–8], and *Perognathus inornatus* [7] and fat-storing hibernators such as *Spermophilus beldingi* [7]. Unlike fat-storing hibernators, food-hoarding hibernators cache energy outside the body and are able to adjust torpor in response to food availability without exhausting these external reserves [6]. Such animals should be able to make quantitative assessments of available food reserves, but it is unclear to what extent torpor expression is influenced by changes in food availability as opposed to absolute abundance of food.

Conversely, the daily heterotherms use daily torpor, which is defined as short-term hypometabolism for periods of up to 24 h [2]. Spontaneous daily torpor as a winter adaptation is induced by short-day photoperiod, irrespective of food availability or T_a , and is therefore strongly seasonal in some species [9,10], but torpor expression is generally facilitated by food restriction and cold [11]. There have been many studies of the relationship between daily torpor and food shortage [11–13], but to our knowledge, the relationship between daily torpor and food overabundance has not been clearly established. The daily heterotherms should be more sensitive to changes in overabundance of food than hibernators because they arouse from torpor to forage regularly. Thus, we predicted that daily heterotherms might adjust the expression of daily torpor in response to food availability even where the change places no constraints on energy budgets. If so, they should respond to temporal changes in overabundance of food as well as different overall magnitudes of overabundance.

The large Japanese field mouse *Apodemus speciosus*, of which body mass ranges from 20 to 60 g, is nocturnal and endemic to Japan [14]. The mouse caches food as a winter energy resource [15,16], and exhibits spontaneous daily torpor during artificial winter conditions [17], making it an ideal food-hoarding daily heterotherm model for investigating the relationship between torpor expression and food overabundance. The present study examined whether individual mice living under artificial winter conditions such as constant short-day photoperiod and cold T_a expressed daily torpor differently when supplied with different quantities of overabundant food, or were able to adjust torpor expression in response to temporal changes in food overabundance. Both experiments were conducted without placing energy constraints on experimental animals, so that results could be clearly attributed to animal's perception of the food situation rather than their physiological response to changing energy budgets.

2. Materials and methods

2.1. Animals

The large Japanese field mice *A. speciosus* used in this study were captured using live traps (Sherman Trap, H.B. Sherman Traps Inc., FL, USA) in Miyazaki Prefecture, Japan from February to June and housed in transparent plastic cages (225 × 338 × 140 mm) with wood chips for bedding under a long-day photoperiod (16L:8D; lights on at 0600 h) prior to the experiment commencing. Commercial rodent diets (Labo MR Stock, Nosan Corporation, Kanagawa, Japan) and water were provided ad libitum. All animal procedures were approved

by the Animal Experimentation Committee of the University of Miyazaki (Permission No. 2005-053).

2.2. Experimental protocols

2.2.1. Experiment 1 – influence of magnitude of food overabundance on expression of daily torpor

Twenty-seven mice, including 13 males and 14 females were used.

The trial was conducted for 22 weeks from June to November, including an 11-week acclimatization period followed by 11 weeks of experimental treatments. To mimic the onset of winter conditions, the mice were maintained at 25.3 ± 0.4 °C (mean \pm SD) for the first 9 weeks of the acclimatization period, then exposed to the cold at 6.0 ± 1.4 °C for the subsequent 13 weeks, including the 11-week experimental period. When the experiment commenced, the photoperiod was shifted to replicate a short day (8L:16D; lights on at 0800 h).

After the mice were shifted to the cold conditions, they were housed individually in larger transparent plastic cages (276 × 445 × 204 mm). A stainless-steel nest box (200 × 110 × 150 mm) with a wooden lid was placed into each cage, and corn diets were provided ad libitum until the experimental period commenced. Water was provided ad libitum throughout. All cages and wood chips were replaced weekly, and food was supplied after the weekly replacement of those.

Individual animals were assigned to one of two groups. The first group of 7 males and 7 females was supplied with 100 g corn diet per week. Given that individual mice consume an average of 6.2 g of food per day under artificial winter conditions [17], or ca. 42 g per week, the corn diets supplied at 100 g/week must have been ample. The second group, comprising 6 males and 7 females mouse, received superabundant corn rations of 1000 g/week.

2.2.2. Experiment 2 – influence of temporal changes in overabundance of food on expression of daily torpor

The trial involved nineteen mice, including 9 males and 10 females, and was conducted for 18 weeks from July to November, including a 12 week acclimatization period followed by 6 weeks of experimental treatments. The mice were maintained at 25.0 ± 0.6 °C of T_a for the first 10 weeks of the acclimatization period and then exposed to the cold at 5.8 ± 0.4 °C for 8 subsequent weeks, including the 6 week experimental period.

During periods of cold exposure, the mice were subjected to same housing conditions used in Experiment 1, and the photoperiod was shifted to replicate a short day (8L:16D; lights on at 0800 h) as above.

At the start of the experimental period, the mice were assigned to one of two groups. Members of Group A, comprising 5 males and 5 females, received corn diets at 100 g/week for the first 2 weeks, after which rations were increased to 1000 g/week for 2 weeks, and then reduced once more to 100 g/week for a final 2 weeks. Group B, comprising 4 males and 5 females, received 1000 g/week corn rations for the first 2 weeks, after which rations were reduced to 100 g/week and then increased to 1000 g/week in the reverse direction to the changes in Group A. All cages and wood chips were replaced weekly, and animals were weighed to the nearest 0.1 g using an electronic balance at the same time. T_b for each mouse was recorded during the last 4 weeks of the experimental period.

2.3. Measurement of T_b

Core T_b of all experimental animals was recorded to the nearest 0.1 °C every 30 min during Experiment 1 and every 15 min in Experiment 2 using data loggers (iButtons, DS1922L, Maxim Integrated, CA, USA) surgically implanted into the abdominal cavity. All data loggers were calibrated to the nearest 0.1 °C in a water bath of known temperature ranging from 20 to 40 °C before the experiments, and again at the end. Before implantation, the data loggers were coated with thin layers of a paraffin-Evaflex (EV220, Du Pont-Mitsui Polychemical Co., Ltd., Tokyo,

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