Effect of food restriction on energy budget in warm-acclimated striped hamsters

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HIGHLIGHTS

- We examined energetics in response to food restriction in hamsters at 30 °C.
- Hamsters at 30 °C decreased energy spent on thermogenesis compared with 21 °C.
- Exposure to 30 °C attenuated the decrease in body mass of food-restricted hamster.
- Hamster can compensate for limited food supply by decreasing thermogenesis at 30 °C.
- Reductions in thermogenesis at 30 °C increase the capacity to sustain food shortage.

ARTICLE INFO

ABSTRACT

The capacity of small mammals to sustain periods of food shortage largely depends on the adaptive regulation of energy budget in response to the decrease in food supply. In addition to food availability, ambient temperature (T_a) is an important factor affecting the rates of both energy intake and expenditure. To examine the effect of T_a on energy strategy and the capacity to sustain food shortage, striped hamsters were exposed to a warm condition (30 °C) and were then restricted to 70% of *ad libitum* food intake. Body mass, energy intake and expenditure and physiological markers indicative of thermogenesis were measured. Warm exposure had no effect on body mass and digestibility, but decreased energy intake, basal metabolic rate and maximum nonshivering thermogenesis. The mitochondria protein content, cytochrome c oxidase activity and uncoupling protein 1 level of brown adipose tissue were significantly lower in hamsters at 30 °C than at 21 °C. Food restriction induced a significant decrease in body mass, but the decreased body mass was attenuated at 30 °C relative to 21 °C. This suggests that striped hamsters could not compensate for the limited food supply by decreasing daily energy expenditure at 21 °C, whereas they could at 30 °C. The significant reductions in the rates of metabolism and thermogenesis in warm-acclimated hamsters increase the capacity to cope with food shortage. Although, it remains uncertain whether this response represents some generalized evolutionary adaptation, the T_a-dependent adjustment in the capacity to survive food restriction may reflect that warm acclimation plays an important role in adaptive regulation of both physiology and behavior in response to the variations of food availability.

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1. Introduction

The life history of many animals includes extended periods of food scarcity [1]. In rodents, different strategies for coping with food shortage have been described, including the use of torpor, food hoarding and an increase in food foraging activity [2,3]. It has been suggested that the capacity to sustain periods of food shortage may be different between rodent species [2,3,4]. For example, golden spiny mice (*Acomys russatus*)

inhabit rocky deserts and do not store food but have a greater ability to sustain food restriction than Wagner's gerbils (*Gerbillus dasyurus*, Gerbillidae), that burrow under rocks and do store food [2].

The striped hamster (*Cricetulus barabensis*) is a major rodent in northern China and is also distributed in Russia, Mongolia and Korea [5]. The climate is arid and characterized by hot and dry summers with a maximum temperature of 42 °C and cold winters where temperatures can decrease below −20 °C. This species is granivorous and nocturnal and feeds mainly on stems and leaves of plants during the summer, during which they dig their burrows but do not store food [5]. In preparation for winter the striped hamster forages on crop seeds, and accumulates large amounts of seeds in burrows in the

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autumn [5–8]. We previously found that striped hamsters were susceptible to food restriction [9]. This is inconsistent with either golden spiny mice or Wagner's gerbils, or other rodents [2–4,10–13].

The striped hamsters do not go into torpor and have a higher metabolic rate relative to that predicted (145% of that predicted by Hayssen and Lacy [14]; 170% of that predicted by McNab [15]) [8]. This may suggest that the problem of food shortage is more significant in this hamster species than other mammals with low metabolic rate, such as the golden spiny mice [2,16]. This leads to the conclusion that the susceptibility of striped hamsters to food restriction may be partly due to their high rate of metabolism [9]. In addition, the rate of survival of the striped hamster was lower following exposure to cold conditions (5 °C) compared to room condition (21 °C), which might suggest that the ability to sustain food restriction was associated with the ambient temperature (T_a) [9].

It has been well established that the metabolic rate of mammals is affected by T_a, and a decrease in T_a induces elevations of both basal metabolic rate (BMR) and nonshivering thermogenesis (NST) [17–21]. In contrary, mammals usually decrease the energy expended on BMR and NST after they are exposed to warm conditions, and reach a constant lowest rate of energy metabolism when they are in the thermal neutral zone (TNZ) [19,22,23]. In addition to the decreasing energy expenditure, warm-exposed animals usually consume less food, and show lower energy intake than animals maintained at cold temperatures [24,25]. It is therefore presumed that changes in T_a may have significant effects on energy budget in food-restricted animals, and consequently on the capacity to survive periods of food shortage. To examine this hypothesis, in the present study striped hamsters were exposed to a warm condition (30 °C, within TNZ of this species) and then restricted to 70% of ad libitum food intake. Physiological markers indicative of metabolic thermogenesis were measured and compared to ad libitum and food restricted animals housed at 21 °C. We predict that warm-acclimated hamsters show decreases in both energy intake and expenditure, but may have greater capacity to survive the periods of food restriction compared to the food-restricted hamsters housed at 21 °C.

2. Materials and methods

2.1. Animals

Striped hamsters were obtained from our laboratory-breeding colony, which originated from animals that were initially trapped from the farmland at the center of the Hebei province (115°13′E, 38°12′S), North China Plain. This breeding colony was maintained under a 12 L:12D (light:dark, lights on at 0800 h) photoperiod, and room temperature was kept at 21 ± 1 °C. Food (standard rodent chow; produced by Beijing KeAo Feed Co., Beijing, China) and water were provided ad libitum. All experimental procedures are in compliance with the Animal Care and Use Committee of Liaocheng University.

2.2. Experiment protocol

Forty female hamsters were randomly assigned into one of the four groups: a control and a warm-exposed group, which were fed ad libitum at 21 °C and 30 °C (hereafter referred to as the 21 °C-ad, $n = 8$ and 30 °C-ad, $n = 8$), respectively; a food-restricted group (21 °C-FR, $n = 12$), which was fed ad libitum on days 1 to 28, but restricted to 70% of ad libitum food intake on days 29 till 42 at 21 °C, and a warm-exposed and food-restricted group (30 °C-FR, $n = 12$), during which the feeding protocol was the same with that in 21 °C-FR, but hamsters were exposed to 30 °C throughout the experiment. Based on the large set of data in striped hamsters, no gender differences were observed in any energetic parameters in response to food restriction and temperatures, thus only females were used in this study.

2.3. Body mass and food intake

Body mass and food intake were measured every two days from day 1 to day 28, and daily from day 29 until day 42. We previously observed a significant decline in body mass in the hamster after being exposed to food restriction, and food-restricted hamsters had a risk of death when body mass decreased by 22.5% relative to the initial body mass [9]. Here, we observed that three hamsters lowered body mass by 20%, and food restriction was terminated. Food intake was calculated as the weight of food missing from the hopper every day, subtracting orts mixed in the bedding. Ad libitum food intake for each animal at either 21 °C or 30 °C was averaged based on food intake between days 22 and 28, which was taken to calculate 70% of ad libitum food intake.

2.4. Gross energy intake (GEI) and digestibility

GEI, digestive energy intake (DEI) and digestibility were measured over the last three days of experiment (days 40–42), and calculated as follows [26–28],.

Dry matter intake (DMI, g·d^{-1}) = food intake (g·d^{-1}) × [(100% − water content of diet (%)];

GEI (kJ·d^{-1}) = DMI (g·d^{-1}) × energy content of food (kJ·g^{-1});

DEI (kJ·d^{-1}) = GEI − [dry mass of feces (g·d^{-1}) × energy content of feces (kJ·g^{-1})];

Digestibility (%) = DEI/GEI × 100%.

The spillage of food and feces was sorted and separated manually after they were dried at 60 °C to constant mass. The decrease in weight of the diet was used to calculate the water content of diet (%). Gross energy contents of the diet and feces were determined using a Parr 1281 oxygen bomb calorimeter (Parr Instrument, Moline, IL, USA).

2.5. Basal metabolic rate (BMR) and maximal nonshivering thermogenesis (NST_{max})

BMR and NST_{max} were qualified as the rate of oxygen consumption, using an open-flow respirometry system (Sable system, USA). Air was pumped at a rate of 650–750 ml/min through a cylindrical sealed Perspex chamber, which was transferred to an incubator (± 0.5 °C). Gases leaving the chamber were dried (silica gel) and directed through an oxygen analyzer at a flow rate of 150–175 ml/min. The data were averaged and collected every 10 s by a computer connected analogue-to-digital converter (STD-UI2, Sable system), and analyzed using a standard software (Sable system). BMR was measured for at least 2.5 h at 29 ± 0.5 °C (within the thermal neutral zone of this species [8,22]) on day 42. The lowest rate of oxygen consumption over 5 min was taken to calculate BMR.

NST_{max} was measured following BMR measurements. NST_{max} was quantified as the maximal rate of oxygen consumption induced by a subcutaneous injection of norepinephrine (NE) (Shanghai Harvest Pharmaceutical Co. Ltd) at 25 ± 1 °C. A mass-dependent dosage of NE was calculated according to the equation: NE (mg/kg) = 6.6 M_b $^{-0.458}$(g) [29]. The data were averaged and also collected every 10 s, and the highest recordings over 5 min were averaged to estimate NST_{max}. Both BMR and NST_{max} were corrected to standard temperature and air pressure conditions and expressed as ml O$_2$/h [22,23]. All measurements were made between 1000 and 1700 h.

2.6. Body composition

Interscapular brown adipose tissue (BAT) was removed, weighed (to 0.1 mg), and quickly put in liquid nitrogen for BAT cytochrome c oxidase (COX) measurements. The gastrointestinal tracts (stomach, small and large intestines and cecum) were separated and weighed (to 0.1 mg) after the content was removed. The liver, heart, lung, spleen and kidneys were also separated and weighed (to 0.1 mg). The remaining carcass (including the brain, but excluding the thyroid and