Food availability regulates energy expenditure and torpor in the Chilean mouse-opossum *Thylamys elegans*

La disponibilidad de alimento regula el gasto energético y el sopor en el marsupial chileno *Thylamys elegans*

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ABSTRACT

We tested the effect of food availability on energy expenditure and torpor in the Chilean mouse-opossum *Thylamys elegans* (Didelphidae), which inhabits the Mediterranean environments of central Chile. Animals maintained with low food availability showed a higher frequency of torpor bouts in comparison to animals with high food availability, which never entered into torpor. A saturation curve between torpor bout length and digestible energy intake was obtained. With the lowest food availability, torpor bout length increased until a threshold was reached, whereafter it decreased. We postulate that the reduction of energy expenditure achieved with torpor states by *T. elegans* is regulated through food availability.

Key words: torpor regulation, food availability, metabolic rate, Chilean marsupial.

RESUMEN

Estudiamos el efecto de la disponibilidad de alimento sobre el gasto de energía y el sopor en el marsupial chileno *Thylamys elegans* (Didelphidae), que habita los ambientes mediterráneos de Chile central. Los animales mantenidos con baja disponibilidad de alimento mostraron una alta frecuencia de eventos de sopor en comparación a los mantenidos con alta disponibilidad, los que nunca entraron en sopor. Se obtuvo una curva de saturación entre la duración de los eventos de sopor y la ingesta de energia digerible. Bajo la condición de mínima disponibilidad de alimento la duración de los eventos de sopor aumentan hasta un límite para después disminuir. En base a nuestras observaciones, postulamos que el balance de energía y los estados de sopor en *T. elegans* son regulados por la disponibilidad de alimento.

Palabras clave: regulación del sopor, disponibilidad de alimento, tasa metabólica, marsupial Chileno.

INTRODUCTION

Understanding an animal's energy balance regulation in time and space, within an integrative physiological, behavioral and ecological framework is a challenge to both physiological and behavioral ecologists. These researchers attempt to understand where are the limits and what are the physiological and behavioral mechanisms associated to the energy use and its ecological consequences. Physiological dormancy in small endotherms (e.g. torpor) is a well-studied example of energy budget regulation. Daily torpor is an energy-conserving mechanism used by many species of small endotherms during periods of low environmental temperature and food shortage (Schmidt-Nielsen 1987, Holloway & Geiser 1995, López-Calleja et al. 1997). Torpor is characterized by a decrease in body temperature and a decline in metabolism of ca. 90%, in comparison to euthermy (Geiser 1994, Ortmann & Heldmaier 1997). This relationship between torpor and feeding behavior has been documented. For example, Hainsworth et al. (1977) suggests that daily torpor is used by hummingbirds exclusively when food is scarce. Extensive use of torpor by a population should also be advantageous when food is scarce. For example, food supply appears to be an important factor influencing the annual period of inactivity of the rodent *Perognathus longimembris*, which may indicate torpor (Kenagy 1973).

The mean duration of individual episodes of torpor increases for kangaroo mice when food supply is reduced (Brown & Bartholomew 1969).

We examine the influence of food availability on the regulation of the energy budget and torpor in the Chilean mouse-opossum *Thylamys elegans* (Didelphidae) which inhabits Mediterranean environments of central Chile. Occurrence of torpor bouts in this species depends on food quality (Sabat et al. 1995, Bozinovic & Méndez 1997), but how is torpor regulated by different amounts of food? We postulate that if animals are exposed to decreasing amounts of food, they will maintain torpor states for longer times, until they reach a maximum length. On the other hand, with high availability of food, animals should not enter into torpor (Buffenstein 1985, Caviedes-Vidal et al. 1990). Regarding the long-term level of average metabolic rate during euthermy and torpor, we expected a saturation curve with food availability until a stable minimum (which cannot be exceeded) is reached. In contrast, with high amounts of food, the animals should attain a stable maximum.

MATERIALS AND METHODS

Nine individuals of *T. elegans* were captured with Sherman traps during May 1998 in Quebrada de la Plata, central Chile (70°50'W, 33°31'S). Animals were transported to the laboratory and maintained with puppy chow pellets (20.3 kJ/g) and water *ad lib*. To determine digestible energy intake (DEI) we recorded apparent digestibility (D). All animals were individually housed in metabolic cages of 50 x 40 x 40 cm with metal trays underneath to collect excreta. We conducted feeding trials, offering to each animal a known amount of food. After 72 hours, collected excreta and remaining food were weighed, dried up at 60 °C to constant weight, and stored. Apparent digestibility was calculated as: D = [(Qi − Qe)/Qi] x 100%, where Qi = food intake (g/day) and Qe = feces production (g/day). Digestibility is apparent because this method underestimates digestion by

contribution of metabolic wastes and non reabsorbed secretions of the digestive system. Apparent, digestible energy intake was calculated as: DEI = Qi x D, Qi in kJ/g. DEI is apparent because the energy content of feces was not obtained.

To test the effect of food availability on energy expenditure and torpor regulation, animals were transferred to an outdoor laboratory, where photoperiod was natural and ambient temperature ranged 9 to 21 °C. Animals were randomly assigned and individually maintained to different amounts of food (from 2 to 18 pellets/day), ranging 12.2 to 109.5 kJ/day. Each individual was measured under two different and contrasting experimental conditions after allowing a minimum of 12 days of acclimation between experiments.

The physiological state of animals (torpor or euthermia) was recorded daily and their body mass (m_b) measured every two days. After, acclimation the metabolic rate of each individual was measured during 24 hours in a computerized (Datacan V) open-flow respirometry system (Sable Systems) in metabolic chambers of 900 ml at 15 °C. The metabolic chamber received dried air at a rate of 500 ml/min from a mass flowmeter (Sierra Instruments). Before and after the metabolic chamber, air was passed through granules of Baralyme [$Ba (OH)_2$] and Drierite [$CaSO_4$] to absorb CO_2 and H_2O, respectively. Oxygen consumption was monitored every 10 seconds by an Applied Electrochemistry O_2 analyzer model S-3A/I (Ametek). Ambient temperature was held constant ($\pm$ 0.5 °C) by maintaining the metabolic chamber in an incubator. Oxygen consumption values were calculated by equation 4a of Withers (15), taking the lowest values that did not change more than 0.01% in O_2 concentration, and were automatically corrected to STPD (standard temperature and pressure). Body mass and body temperatures (Tb) were measured before and after each metabolic trial with electronic balance and copper-constantan thermocouples, respectively. We recorded the following variables: metabolic rate during euthermia (ME), metabolic rate during torpor (MT), torpor bout length, and average daily energy

expenditure (ADEE). All values are shown as arithmetic mean ± 1SD.

RESULTS AND DISCUSSION

Mean body mass varied between 28.20 ± 0.05 g and 19.70 ± 0.05 g for individuals with low food availability (10-50 kJ/day), and between 39.00 ± 0.05 g and 38.00 ± 0.05 g for individuals with high food availability (40-110 kJ/day). Body temperature during torpor at 15 °C was 17.8 ± 0.4 °C while during euthermia it was 32.9 ± 2.2 °C.

Animals eating puppy chow had an apparent digestibility (D) of 80.42 ± 4.40% which is higher than that for animals with a diet of insects (Sabat et al. 1995); DEI was 70.8 ± 20.4 kJ/day. When animals were offered more than 59 kJ/day they did not consume all of it (Fig. 1), which indicates that above this value food availability was not limiting. Animals continuously maintained with low food availability showed a higher frequency of torpor bouts in
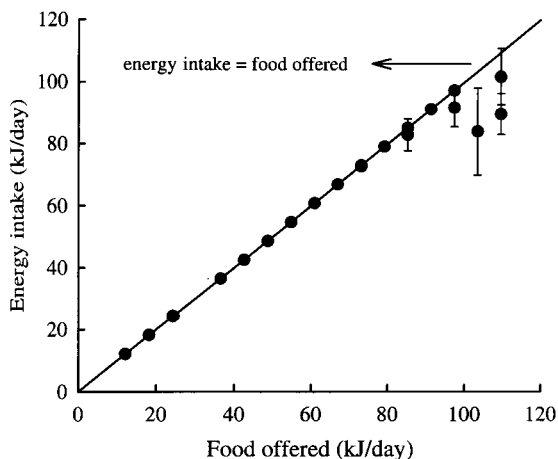

Fig. 1. Relationship between energy intake and food offered. In many cases standard deviation bars are within each point. Some individuals were randomly measured under two different conditions after an acclimation period of 12 days.

Relación entre la ingesta de energía y el alimento ofrecido. Cada punto representa un individuo. En varias ocasiones las barras de desviacion estándar caen dentro de los puntos. Algunos individuos se midieron azarosamente en dos condiciones diferentes después de un período de aclimatación de 12 días.
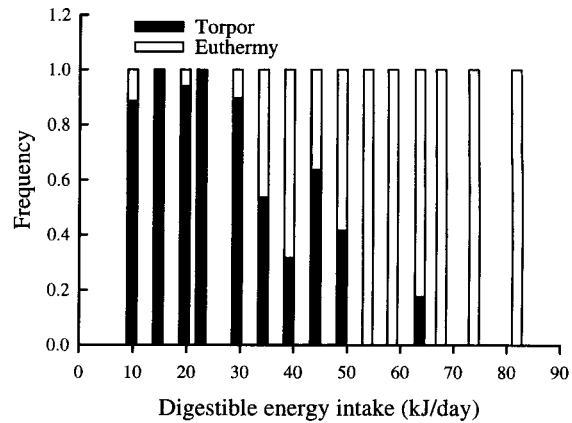

Fig. 2. Effect of daily energy intake on the frequency of daily torpor and euthermia in *Thylamys elegans*. Some individuals were measured under two different conditions after an acclimation period of 12 days.

Efecto de la ingesta diaria de energía sobre la frecuencia estandarizada de sopor diario y eutermia en *Thylamys elegans*. Algunos individuos se midieron azarosamente en dos condiciones diferentes después de un período de aclimatación de 12 días.

comparison to animals maintained with high food availability (Fig. 2). Under intermediate amounts of food (DEI = 35–50 kJ/g), the frequency of torpor events was similar to the frequency of events of euthermia. Animals with a DEI above 58 kJ/day (72 kJ/day of food offered), never became torpid. A saturation relationship between torpor bout length and DEI was obtained. That is under intermediate amounts of food, torpor bout length reached a maximum, decreased under extremely low food availability, and dropped to a minimum when food was always available. Also a saturation relationship between ME and DEI was obtained and represented by the following equation: $y = 0.179/[1 + e^{-((x - 15.55)/3.48)}]$, $r = 0.81$, $P = 0.04$. In addition, MT follows a similar pattern of response to DEI and is represented by: $y = 0.006/[1 + e^{-((x - 12.63)/2.74)}]$, $r = 0.83$, $P = 0.05$; representing approximately a 5% of ME.

Torpor bout length increased when the amount of food decreased. MT and ME decreased to a minimum, but with the highest amount of food, MT and ME increased again. Besides, ADEE followed the same pattern as MT and ME. The equation that describes this relationship is: $y = 0.126/[1 + e^{-((x - 18.07)/3.83)}]$, $r = 0.83$, $P = 0.0001$.

On the other hand, ADEE had a positive parabolic tendency with torpor bout length. Our results show that the frequency of torpor in *T. elegans* varied with food availability. That is, with amounts of food that exceed daily energy requirements, animals never were torpid in opposition to animals confronted to lower availability of food. Moreover, the relationship between the length of torpor bouts and DEI indicates that food availability influences not only the frequency of torpor but also its length. In fact, Holloway & Geiser (1995) indicate that the amount of energy saved during torpor is dependent not only on the level of metabolic rate, but also on the duration of torpor as well as on the amount of energy required for rewarming. We postulated that the reduction of energy expenditure achieved by a torpid animal is due by food availability, — i.e. regulation by supply (*sensu* Ricklefs 1996). With high availability of food animals were never torpid or the length of torpor bouts was short. Torpor bout length increased with a decreased

in DEI. This process continued until a maximum stable value is reached, after that, torpor bout length diminished again when food availability was low.

Under the lower food availability, animals decreased torpor bout length. This observation suggests a trade-off between the energy saved by the animal when in torpor and the necessity to obtain energy through foraging. Thus, under low food availability, animals must spend less time in torpor because they need to search for food. Besides, it has been shown that nutrient absorption in the digestive tract of torpid endotherms decreased when body temperature drops (Holloway & Geiser 1995). Then, in terms of energy savings, it would be risky to maintain torpidity for long periods, given the low absorption of nutrients that it implicates.

Energy savings during torpor are achieved by a considerable reduction in metabolic rate. In the case of *T.elegans* at 15 °C this reduction corresponds to 95% of ME, which translates into an energy saving from 0.39 kJ/g h, when the highest DEI values were recorded in torpid animals, to 0.62 kJ/g h, when the lowest DEI values were noted. The observed saturation relationships between metabolic rate and food availability indicates that there is a constraint that cannot be trespassed. In spite of an increase in food availability, animals did not increase energy expenditure, probably because such augmentation results in extra energy costs. On the other hand, when food availability was low, animals decreased metabolic rate to a minimum that must be maintained even under the lowest food availability. Apparently, there is a physiological constraint set by the energy needed for arousal, which represents the greatest energy cost within the torpid cycle (Opazo et al. 1998)[1].

On the other hand, the relationship between metabolic rate and torpor bout length during euthermia or in torpor was a positive parabolic function instead of linear. In fact, metabolic rate increased
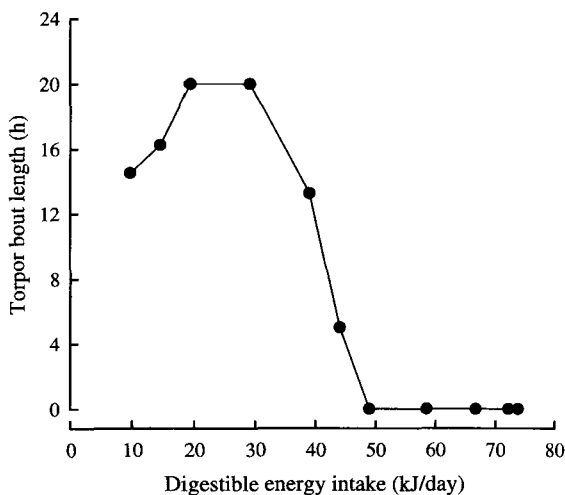

Fig. 3. Relationships between digestible energy intake and torpor bout length in *Thylamys elegans*. Each point represents one individual. Some individuals were measured under two different conditions after an acclimation period of 12 days.

Relación entre la ingesta de energía digerible y el largo de los eventos de sopor en *Thylamys elegans*. Cada punto representa un individuo. Algunos individuos se midieron azarosamente en dos condiciones diferentes después de un período de aclimatación de 12 días.

[1] OPAZO JC, RF NESPOLO & F BOZINOVIC (1998) Salida del sopor en el marsupial chileno *Thylamys elegans*: ¿Juega algún rol la termogénesis sin tiritar? XLI Reunión Anual Sociedad de Biología de Chile. Noticiero de Biología, R-65.

during the longest episodes of torpor. Apparently, under lower food availability not only the duration of torpor diminished but also metabolic rate increased. It could be that animals faced with low food availability need to raise their metabolic rate in comparison to animals experiencing high levels of food availability, to assimilate the few available nutrients. Perhaps under these conditions, animals are making the best of a poor situation.

Regarding how torpor is regulated by food availability in *T. elegans*, we postulate that there is a trade off between the need to satisfy energy requirements through foraging and the necessity to increase energy savings through torpor. Thus, under minimal food availability, animals must spend less time in torpor because they need to search for food. Secondly, there may be a digestive constraint on the energy budget. Because animals cannot raise their metabolic rate during torpor and maintain a high level of activity for a long time, they are unable to absorb the few available nutrients, which could compromise survival in the face of food scarcity.

ACKNOWLEDGMENTS

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