

Energetics, thermoregulation and torpor in the Chilean mouse-opossum *Thylamys elegans* (Didelphidae)

Energética, termorregulación y sopor en la yaca *Thylamys elegans* (Didelphidae)

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ABSTRACT

In this paper we studied the energetics and thermoregulation of the Chilean mouse-opossum *Thylamys elegans* (Didelphidae) a nocturnal small marsupial, endemic of southern South America. We studied their standard energetic and determined whether they exhibit shallow daily torpor or deep prolonged torpor as a function of ambient temperature and food availability. *Thylamys elegans* partially supports the hypothesis that Neotropical marsupials have somewhat a higher basal metabolic rate (BMR) and thermal conductance (C_m) than Australian ones. In fact, BMR was higher but C_m was lower than expected for their body mass. The higher mass-independent BMR of the Chilean mouse-opossum may be explained by its insectivorous food habits and its low C_m by its temperate habitats. Euthermic Chilean mouse-opossum showed daily fluctuations in body temperature being significantly higher during night time. In addition *T. elegans* entered in daily torpor and aroused spontaneously only when food was absent. That is, this species displays a facultative type of daily torpor because propensity to enter in torpor was dependent of the combination of food absence and low ambient temperature. No torpor was observed when food was available. During torpor ambient temperature was slightly above ambient temperature between 0.3 to 0.5 °C. Torpor in this species as well as in marsupials in general, appears to be a flexible and an opportunistic response to unpredictable environmental conditions.

Key words: South America, Chile, marsupials, energetic, thermoregulation, facultative torpor.

RESUMEN

Estudiamos la energética y termorregulación de *Thylamys elegans* o “yaca” (Didelphidae) un marsupial pequeño y endémico de Sudamérica. Estudiamos su energética estándar y determinamos si presentan estados de sopor superficial o profundo en función de la temperatura ambiente y la disponibilidad de alimento. *Thylamys elegans* apoya de manera parcial la hipótesis que sostiene que los marsupiales neotropicales poseen tasas metabólicas basales (BMR) y conductancias térmicas (C_m) más altas que los australianos. En efecto BMR fue alta pero C_m fue menor que la esperada para la masa corporal. La BMR masa-independiente elevada de la yaca podría ser explicada por sus hábitos tróficos insectívoros y su C_m baja por vivir en hábitat templados. Durante eutermia la yaca muestra fluctuaciones en la temperatura corporal siendo significativamente mayores durante la noche. Además, *T. elegans* entra y sale del sopor diario en forma espontánea solamente en ausencia de alimento. Es decir, esta especie muestra sopor del tipo facultativo pues este dependió de la interacción entre la ausencia de alimento y la temperatura ambiental. No se observaron estados de sopor cuando existió alimento disponible. Durante el sopor la temperatura del cuerpo entre 0,3 a 0,5 °C superior a la del ambiente. El sopor en esta especie así como en marsupiales en general parece ser una respuesta flexible y oportunista a la variabilidad del ambiente.

Palabras clave: Sudamérica, Chile, marsupiales, energética, termorregulación, sopor facultativo.

INTRODUCTION

Torpor in small endotherms is a well-studied example of energy budget regulation. Theoretically, torpor is often hypothesized to be

responsible for allowing some organisms to adjust to changing biotic and abiotic environmental conditions, through increases in survival under harsh environmental conditions (Humphries et al. 2003). Thus, torpor is an

energy and water-conserving mechanism used by many species of small endotherms (Schmidt-Nielsen 1987, Geiser 1994, Holloway & Geiser 1995, Cryan & Wolf 2003). Torpor is characterized by a decrease in body temperature and a decline in metabolism of c.a. 90 %, in comparison to euthermy (Geiser 1994, Ortmann & Heldmaier 1997). This relationship between torpor, ambient temperature and food availability has been well documented for many years. For example, Hainsworth et al. (1977) suggested 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. Indeed, 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). On the other hand, ambient temperature largely explains the reduction of metabolism of daily heterotherms and hibernators (Geiser 1986, 1988, 1994, López-Calleja et al. 1997).

Small eutherian mammals and birds are classical examples of the processes listed above (for a review see McNab 2002). However, it is not well known what happens in other endotherms such as in South American marsupials (but see Bozinovic & Rosenmann 1988a, 1988b, Caviedes-Vidal et al. 1990, Bozinovic & Marquet 1991, for examples in some South American rodents). The physiology of torpor in marsupials is similar to eutherians in several aspects (Hallam & Dawson 1993, Chappell & Dawson 1994, Gibson & Hume 2000, Holloway & Geiser 2001). Nevertheless, with respect to energetics and thermal acclimation, some differences arise. Nespolo et al (2002) demonstrated that the potential for acclimatory response of thermogenic capacity in marsupials is controversial, reporting a significant effect of thermal acclimation on energy metabolism, organ masses and digestive enzyme activity in a Chilean mouse-opossum marsupial *Thylamys elegans* (Didelphidae). In the same species Silva-Durán & Bozinovic (1999) tested the effect of food availability on energy expenditure and torpor (see also Roig 1971). They found that 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, hypothesizing that the reduction of energy expenditure achieved with torpor states by *T. elegans* is regulated through food availability.

In this study we followed the later approach to assess the effects of temperature and food availability on metabolic rate, thermoregulation and torpor bouts in this species which inhabits Mediterranean environments of central Chile.

Thylamys elegans shows conspicuous phenotypic flexibility in activity of intestinal enzymes, both, on a seasonal basis (Sabat & Bozinovic 1994) and in response to diet acclimation (Sabat et al. 1995, Bozinovic & Méndez 1997). In addition to the conceptual relevance of determining the underlying causes of observed differences in performance in a wild endothermic species, the scarcity of knowledge regarding the comparative physiology of South American marsupials will make this effort a valuable one. Consequently, the aim of this work is to determine in *T. elegans* the effect of changes in ambient temperature and food availability on metabolic rate, torpor state as well as on its frequency and regulation.

MATERIAL AND METHODS

Between 1982-1990 we studied a total of fifteen individuals (six males and nine females) with a mean body mass (m_b) of 40.2 ± 9.8 g (SD). Animals were captured in semiarid and Mediterranean scrublands of central Chile. This species feeds primarily on insects (Sabat & Bozinovic 1994), and is strictly nocturnal. Animals were captured with Sherman traps, transported to Santiago, and individually maintained in large plastic cages with a photoperiod of LD = 12:12 and ambient temperature of 20-25 °C. Grapes, apples, eggs, grounded beef meat, worms and water were provided ad libitum.

Metabolic rate was measured during at least 1.5 h at different T_a in a computerized closed respirometric system (Morrison 1951). CO₂ and water vapor were absorbed inside the metabolic chamber through granules of Baralyme™ and Drierite™ respectively. Body mass and T_b were measured before and after the metabolic runs through Cu-Constant thermocouples and BAT-

12 digital thermometer. Minimal thermal conductance was calculated from the slope of the regression of VO_2 versus T_a curve below the thermoneutral zone. Extrapolated T_b fell within 1 SD of the average diurnal and nocturnal euthermic measured values of T_b , thus the theoretical classical assumption that $T_a = T_b$ when $\text{VO}_2 = 0$ was satisfied. To determine BMR, animals were fasted for 3 h before beginning the measurements that were conducted in 850-mL steel chambers at 30 and 32.5 °C.

All VO_2 values were corrected for STP (standard temperature and pressure). Body temperature was measured during day and night in euthermic animals as well as in torpid individuals through Cu-Constantan thermocouples connected to a Baily digital thermometer. To test for a shallow or for a deep torpor response, continuous VO_2 records were conducted in different individuals with food as well as, deprived of food (the most usual way to induce torpor, Lyman et al. 1982). Animals were exposed to a LD = 12:12, but at different T_a ranging from 5 to 25 °C. These measurements lasted for a minimum of 24 h. In addition, to determine torpor regulation by effect of temperature, we changed it during VO_2 measurements.

Comparisons between means were made through a one-way ANOVA and a post-hoc Tukey test, also a linear regression analysis was conducted to determine the thermal dependence of VO_2 . Results are reported as mean \pm 1 SD. Statistical analyses were performed using STATISTICA (6.0).

RESULTS

The effect of T_a on VO_2 of *T. elegans* is shown in Fig. 1. The resting VO_2 below thermoneutrality increased in a linear form as T_a decreased being represented by the following linear regression, $\text{VO}_2 = 4.94 - 0.138 (\pm 0.004) T_a$, $r = 0.99$, $P < 0.0001$. The line intersects the abscissa at 35.8 °C a value within the range of diurnal and nocturnal recorded T_b (see below). The slope of the curve ($0.138 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$) represents the minimal thermal conductance (C_m) which was: 87.5 % of the expected value for a similar size (40.2 g) standard mammal (i.e., $C_m = 1.0 m_b^{-0.5}$, Herreid & Kessel 1967).

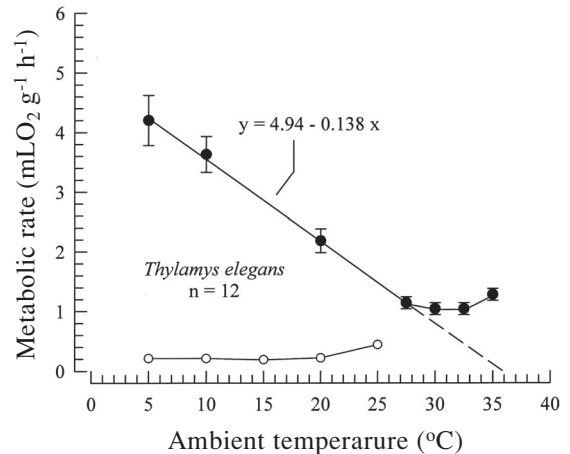


Fig. 1: Relationship between metabolic rate and ambient temperature in *Thylamys elegans* in euthermia (closed circles) and in torpor (hollow circles). Values are a mean of 12 animals (\pm 1 SD). See text for details.

Relación entre la tasa metabólica y la temperatura ambiente en *Thylamys elegans* durante eutermia (círculos cerrados) y sopor (círculos abiertos). Cada punto representa una media de doce animales (\pm 1 DE). Véase el texto para detalles.

The basal metabolic rate was $1.07 \pm 0.01 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ ($n = 12$) which was a 112.3.9 % of the predicted value for a standard metatheria ($\text{BMR} = 2.49 m_b^{-0.26}$) and 85.3 % of the predicted value for a standard eutheria ($\text{BMR} = 3.53 m_b^{-0.28}$) see (McNab 2002). The lower critical temperature of thermoneutrality was 27.5 °C. A slight increase in VO_2 was recorded at 35 °C (Fig. 1). In addition *T. elegans* exhibit torpor between 5 to 25 °C and only when food was absent (Fig. 1). During torpor T_b was slightly above T_a , between 0.3 to 0.5 °C.

Fed Chilean mouse-opossum showed daily euthermic fluctuations in T_b held under LD = 12:12 and T_a of 20 ± 2 °C. During daylight hours mean T_b was 34.5 ± 2.0 °C at 09:30 h and 34.4 ± 1.5 °C at 15:30 h ($n = 12$). At night T_b was significantly higher, being 36.8 ± 0.5 °C at 03:50 h and 36.7 ± 0.4 °C at 21:00 h, $n = 12$ (one-way ANOVA $F_{1,78} = 41262$, $P < 0.00001$). Post-hoc Tukey test only revealed significant differences between diurnal and nocturnal T_b values ($P < 0.0001$).

In an experimental T_a of 15 °C and only when deprived of food, *T. elegans* entered in daily torpor and aroused spontaneously every night (Fig. 2). When in torpor VO_2 falls nearly 1/100th of that during euthermia. Body

temperature during deep torpor was 0.5-1.0 °C ($n = 12$) above T_a . Interestingly when we changed T_a from 15 to 0 °C, torpid animals aroused spontaneously (Fig. 3). Also, torpor bouts length lasted from 7 to 19 h. When T_a was changed to the initial conditions (15 °C) animals become torpid again (Fig. 3). The same patterns of daily torpor in the absence of food were observed during all seasons, revealing a facultative type of torpor.

DISCUSSION

Marsupials in general have lower BMR than eutherian mammals (MacMillen & Nelson 1969, McNab 2002, see McNab 2005 in this volume). Nevertheless McNab (1978) pointed out that Neotropical marsupials have somewhat higher BMR and C_m values than Australian ones. Contrarily, Bozinovic et al. (2004) demonstrated that the South American living fossil *Dromiciops gliroides* does not support the energetic standards for Neotropical marsupials. These authors

hypothesized that this is because *Dromiciops* is a well-differentiated lineage from South American opossums within the Australidelphian radiation of metatherians (Palma 2003). That is, hypothetically its physiological energetics seems to be phylogenetically closer to the Australian marsupials.

Nevertheless, *T. elegans* partially supports McNab's (1978) predictions, because BMR was higher but C_m was lower than expected for their body mass. The higher mass-independent BMR of the Chilean mouse-opossum may be explained by its insectivorous food habits and its low C_m by its temperate habitats (McNab (1978, 2002). In addition, Nespolo et al. (2002) measured thermoregulatory maximum metabolic rate and BMR in *T. elegans*, before and after acclimation to cold or warm conditions. These authors observed no significant effect of thermal acclimation on maximum metabolic rate however; BMR of cold acclimated animals was 30 % higher than that for warm acclimated individuals, suggesting that BMR shows plasticity.

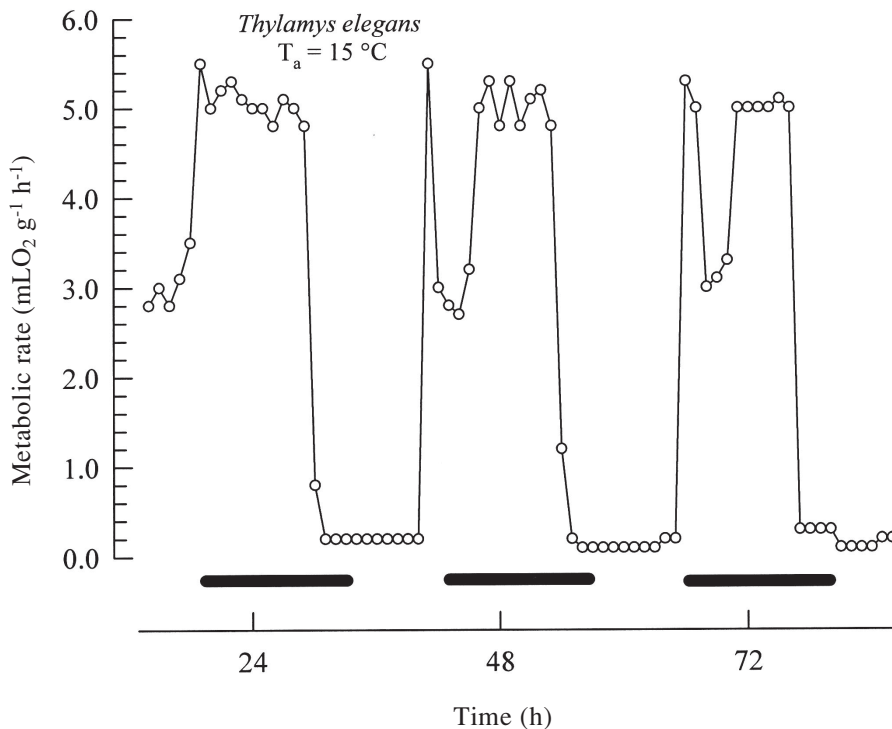


Fig. 2: Daily torpor in a representative individual of *Thylamys elegans* measured over a 3 days period at 15 °C without food. Bars indicated dark hours.

Sopor diario en un individuo representativo de *Thylamys elegans* medido durante 3 días a 15 °C sin alimento. Las barras indican las horas de oscuridad.

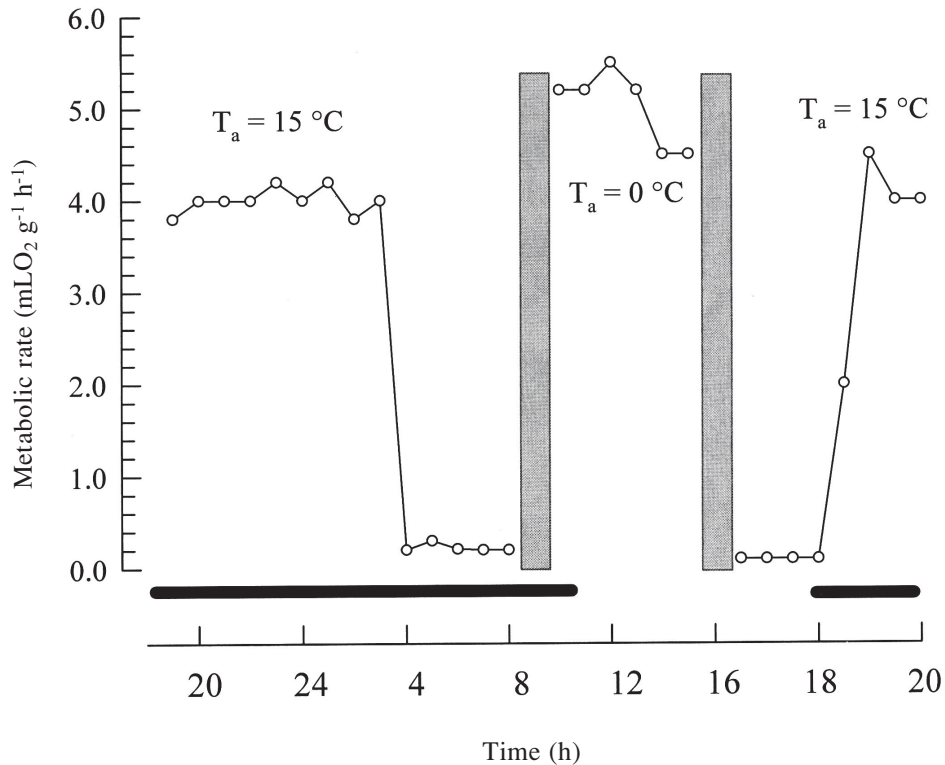


Fig. 3: Continuous changes in metabolic rate (euthermy and torpor) in a representative individual of *Thylamys elegans* at two different temperatures without food. Black bars indicated dark hours while the vertical grey bars indicate the time lag between changes in ambient temperature. Note that animals arouse from torpor at freezing temperature. See text for details.

Cambios continuos en la tasa metabólica (eutermya y sopor) en un individuos representativo de *Thylamys elegans* en dos temperaturas diferentes y sin alimento. Las barras negras indican las horas de oscuridad mientras que las barras grises el tiempo entre cambios de temperatura. Note que los animales sales del sopor a la temperatura de congelamiento. Véase el texto para detalles.

The combinations of high BMR and low C_m by implying a continuous T_b regulation, is likely to be advantageous for survival in temperate habitats (McNab 1992). The minimal temperature differential between body and ambient (ΔT_m) is equal to BMR/C_m (McNab, 1979). Indeed low mass-independent C_m values (high thermal insulation) coupled to high mass-independent BMR values may contribute to a higher thermoregulatory capacity by allowing heat conservation. The predicted ΔT_m for marsupials follow the equation: $2.49 m_b^{0.28}$ (McNab 2002). In *T. elegans* the ratio BMR/C was $7.8 \text{ }^\circ\text{C}$ representing a 111.4 % of the expected value for a 40.2 g standard marsupial. The high thermoregulatory capability of *T. elegans* may explain why this species never became torpid when food is available (Silva-Durán & Bozinovic 1999).

Following Geiser's (1994) classificatory scheme of torpor in marsupials, *T. elegans* seems to display a facultative type of daily torpor. The propensity to enter in torpor was dependent of the combination of food absence and T_a . Torpor in this species as well as in marsupials in general appears to be a flexible and an opportunistic response to unpredictable environmental conditions (Geiser 1987). It is interesting to note that the tendency to become torpid at freezing temperatures was reduced (Fig. 3). We hypothesized that under these environmental conditions, this species should exhibit a controlled daily torpor avoiding physiologically risky conditions. Overall, the thermoregulatory energetic response of *T. elegans* during daily torpor was similar to the one reported for Australian species (Geiser (2003) as well as to that shown by some small

eutherian hibernators (Kayser 1961), representing a fall to 1/100th of the metabolic rate of the euthermic animals.

Silva-Durán & Bozinovic (1999) reported that the frequency of torpor in *T. elegans* varied with food availability. That is, these authors observed that with amounts of food that exceed daily energy requirements, animals were never torpid in contrast to animals confronted to lower availability of food. Moreover, the relationship between the length of torpor bouts and digestible energy intake 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 was 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 induced by food availability, i.e., regulation by energy supply (Ricklefs 1996). Besides, it has been shown that nutrient absorption in the digestive tract of torpid endotherms decreased when T_b 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. Nevertheless, in the absence of food it may allow an economy of energy. In addition, Silva-Durán & Bozinovic (1999) also observed that, 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 should 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. 1999). Interestingly, winter-acclimated Djungarian hamsters (*Phodopus sungorus*) enter torpor spontaneously with food ad lib when their thermogenic capacity is high (Heldmaier & Steinlechner 1981).

The habitat of *T. elegans* may be described as an evergreen scrub, locally known as matorral. The climate is Mediterranean, with an annual mean rainfall of 376.4 mm, concentrated

(65 %) during the winter months. On average, it rains every month of the year, but precipitation is scant during late spring and summer (3 % of the yearly total). Mean temperature is highest from late spring and summer and lowest during the austral winter. The combination of high temperature and low precipitation occurs during summer, thus determining a summer drought. Since this habitat is seasonal in both water and food availability, torpor appears to be important in water and energy economy. Thus, depending of the local environmental conditions, we postulate that there is a trade off between the need to satisfy energy/water requirements through foraging and the necessity to increase energy/water savings through torpor. Furthermore, as postulated by Geiser (1986) torpor appears to have importance in the survival of individuals mainly in a highly seasonal and unproductive habitat (see Humphries et al. 2003).

In summary, the observed flexibility in torpor states dealing with energy and water economy may favour survival and reproduction. News studies dealing with the variability of thermoregulatory strategies during torpor are needed. For example, Cryan & Wolf (2003) demonstrated that during reproduction females of heterothermic bats defend euthermy, presumably to expedite embryonic growth, while males use torpor, presumably to minimize energy and water deficits.

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