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Metabolism and thermoregulation in the Cabrera vole (Rodentia: *Microtus cabreræ*)

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Abstract

Metabolism and thermoregulation were studied for the first time in the Cabrera vole (*Microtus cabreræ*), an endemic and threatened rodent of the Iberian Peninsula. Low values of resting metabolic rate (RMR) were registered ($1.13 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1}$) at the lower limit of the thermoneutral zone (TNZ) (around $33.5 \text{ }^\circ\text{C}$). Body temperature increased near the TNZ up to $37.3 \text{ }^\circ\text{C}$ but remained stable, around $36 \text{ }^\circ\text{C}$, at ambient temperatures below $25 \text{ }^\circ\text{C}$. Values of thermal conductance remained quite stable at ambient temperatures of $10\text{--}25 \text{ }^\circ\text{C}$ ($0.144\text{--}0.160 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}$) and increased to $0.301 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}$ at $33.5 \text{ }^\circ\text{C}$. Data revealed that *M. cabreræ* developed a highly adaptive ability of conserving energy and lowering the metabolic cost of thermoregulation at high ambient temperatures, allowing the body temperature to approximate that of the environment and exhibiting low resting metabolic rate and high conductance.

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1. Introduction

The Cabrera vole (*Microtus cabreræ*, Thomas, 1906) is an endemic and threatened rodent for the Iberian Peninsula (SNPRCN, 1990; Blanco and González, 1992), distributed over central Portugal to the Iberian Prepyrenees, through Central and South-Eastern Spain, apparently avoiding areas of increasing aridity such as the South of Portugal and the Mediterranean coast of Spain (Ventura et al., 1998; Mathias, 1999; Mitchell-Jones et al., 1999). Within their range, voles preferentially occur in areas of tall grasses or dense herbaceous vegetation, sometimes associated with oaklands (Soriguer and Amat, 1988; Fernández-Salvador,

1998; Mathias, 1999). Human impact over these habitats has apparently contributed to a fragmented distribution of populations, which has been considered a major threat for the survival of the species (Fernández-Salvador, 1998; Mathias, 1999; Landete-Castillejos et al., 2000).

Species with a narrow geographical range and specific habitat requirements that are always found in small populations require habitat protection and, possibly, habitat management to maintain their few fragile populations (Primack, 1993). However, more information on natural history of threatened species is needed for the implementation of effective conservation efforts and the identification of factors that place them at risk (Gilpen and Soulé, 1986; Simberloff, 1988).

Little is known about the general biology and life history of *M. cabreræ*. In particular, physio-

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logical data are lacking, such as thermoregulatory abilities that may have critical ecological and evolutionary significance (e.g. Jakobson, 1978; Christian, 1981; Sparti and Genoud, 1989; Haim et al., 1991). The main aim of the present study was to provide the first measures on metabolism and thermoregulation in the Cabrera vole. By doing this we were hoping to contribute to the investigation of *M. cabrae* basic physiological needs and, thus to the increase of the scarce biological knowledge on the species.

2. Materials and methods

2.1. Experimental animals

Nine adult non-reproductive Cabrera voles (five females and four males) were captured in Alentejo, Central Portugal, between June and September 2001, in two different sites, 116 km apart. One female and one male were caught near Alandroal (38°40' N, 7°23' W), while the remaining came from near Grândola (38°05' N, 8°35' W). During this period, minimum and maximum air temperatures registered varied, respectively, between 11–16.7 °C and 27.8–35.5 °C, with the mean temperatures lying between 20.1 and 23.5 °C. In the same period, total rainfall was 86.2 mm with a minimum value of 0.2 mm, in August, and a maximum value of 70 mm, in September (data from the Meteorological National Institute: Évora meteorological station, the nearest station from both capture sites).

Both Alandroal and Grândola sites were associated to drainage and/or temporary watercourses, which provided fresh grass over most of the year. In the Alandroal site, brambles (*Rubus* sp.), rushes (*Juncus* sp.), grasses and herbs constituted the dominant vegetation over an area of ca. 450 m² occupied by voles, being surrounded by cereal crops and pastures. At Grândola, typical vegetation consisted of scrubs (*Cistus salvifolius*, *C. monspeliensis*), rushes (*Juncus* sp.), grasses and herbs over an area of ca. 1500 m², surrounded by oakland (*Quercus suber*).

Voies were housed in individual cages (0.41×0.30×0.20 m) on natural light conditions and ambient temperature averaging 24–26 °C during the period of experiments (end of June–beginning of October).

They were fed a composite diet of apples (Golden delicious), carrots, corn and sunflower seeds

and water ad libitum. This selection of food items was based on preferences of voles, as judged by previous studies on baits attraction (S. Santos, pers. obs.; J. Ventura, pers. comm.).

At capture, body mass of voles ranged from 32.89 to 55.45 g (mean±S.D.: 43.03±6.78 g). No significant changes in individual body mass were recorded during the period of captivity (difference between initial and final mean individual body weights: Student's *t*-test, $t = -1.177$; $P > 0.05$).

All the nine animals were released at the end of experiments.

2.2. Experimental procedures

2.2.1. Protocol

Oxygen consumption (VO_2) was measured separately, in each of the nine voles, in an open-circuit respirometry system, in natural atmosphere at ambient temperatures (T_a) of 10, 15, 25, 30 and 33.5 °C, using a Servomex oxygen analyzer (Series 1100; Servomex International Limited), as described elsewhere (e.g. Hayes et al., 1992). Because the Cabrera vole is a threatened species, it was decided not go further than 33.5 °C to avoid the possible death of animals.

Voies were put into cylindrical Perspex chambers (0.19-m length×0.1-m diameter) that restricted their locomotory activity, which were then placed inside an incubator (Sanyo, Limited) allowing temperature control (± 0.1 °C). The inner part of chambers contained a wire-mesh grid to avoid the contact of voies with urine and faeces. A flow of dried air passed through the metabolic chambers at a rate of 500 ml/min. Analogue signals of the O_2 content in the air leaving the chambers were digitized using the 'Labtech: data acquisition and process control' software.

Each vole was monitored twice, for 2 h, in two consecutive days at different periods of the day (between 09.00 h and 17.00 h) to minimize the effects of potential endogenous rhythms of metabolism (e.g. Hayes et al., 1992; Halle and Stenseth, 1994; Bennett and Spinks, 1995), starting with the lowest temperature and ending with the highest. Animals were not fasted prior to measurements but no food or water was available in the chambers, such that at the end of runs they had not fed for at least 2 h. Body masses of voies (to 0.1 g accuracy) were recorded before and after the VO_2 measurements. Body temperatures (to 0.1 °C

Table 1

Mean values \pm S.D. of metabolic rates (VO_2), body temperatures (Tb) and thermal conductances (C) measured in Cabrera voles at different ambient temperatures (Ta)

Ta (°C)	n	VO_2 (mlO ₂ g ⁻¹ h ⁻¹)	Tb (°C)	C (mlO ₂ g ⁻¹ h ⁻¹ °C)
10	9	3.69 \pm 0.50	35.6 \pm 1.3	0.144 \pm 0.02
15	9	3.11 \pm 0.45	35.6 \pm 1.1	0.151 \pm 0.02
25	9	1.74 \pm 0.29	35.9 \pm 0.4	0.160 \pm 0.03
30	9	1.32 \pm 0.20	36.7 \pm 0.6	0.197 \pm 0.03
33.5	9	1.13 \pm 0.21	37.3 \pm 0.6	0.301 \pm 0.07

accuracy) were measured rectally at depth around 6 mm with a thermocouple K probe (MI-K-Miniz-1.0-100) connected to a Digitron thermometer (2088T, Sifam Instruments Limited) at the end of each 2 h-period of measurements.

2.2.2. Data analysis

Oxygen consumption was calculated as the average of the lowest ten measurements of stable sections of each respirometry run. VO_2 measurements were obtained after Depocas and Hart (1957) as $VO_2 = V_2(F_1O_2 - F_2O_2)/(1 - F_1O_2)$, where V_2 is the flow rate measured after the metabolic chamber, and F_1O_2 and F_2O_2 are the oxygen concentrations before and after the metabolic chamber. All VO_2 measurements were corrected to standard temperature and pressure (STPD).

For the five different ambient temperatures, means and S.D. of metabolic rate values (VO_2) were calculated, using the mean values of the two sessions.

Conductance was calculated below the lower critical temperature from individual measurements of VO_2 using the formula $C = VO_2/(Tb - Ta)$, where C is conductance, Tb is the body temperature of the animal and Ta the ambient temperature (e.g. Armitage et al., 1990; Bennett and Spinks, 1995). There were no statistical differences in individual body temperatures between the two sessions at the same ambient temperatures (Student's t -test = 1.5700, $P > 0.05$) and so, a mean value could be used for thermal conductance calculations. Parametric tests were only used after assumptions of normality (Kolmogorov–Smirnov test) and homogeneity of variances (Levene test) were satisfied. A Pearson's correlation coefficient was computed to measure the relationship of VO_2 and body temperature with ambient temperature. Repeated measures ANOVAs and Student's t -tests were

computed to search for significant differences between mean values. For multiple comparisons, the Tukey honest significant difference test was used (Sokal and Rohlf, 1995).

3. Results

Mean values of oxygen consumption (VO_2) over the selected range of temperatures for Cabrera voles varied from 1.13 mlO₂ g⁻¹ h⁻¹ at $Ta = 33.5$ °C to 3.69 mlO₂ g⁻¹ h⁻¹ at $Ta = 10$ °C (Table 1).

Significant differences in VO_2 were found between all ambient temperatures, except between the two highest temperatures ($F(4,32) = 194.22$, $P < 0.0001$; all Tukey tests $P < 0.01$, except between 30 °C and 33.5 °C, $P = 0.463$). VO_2 decreases with increasing Ta and can be represented as $VO_2 = 4.778 - 0.114 \times Ta$ ($r^2 = 0.891$, $n = 45$, Student's t -test = -18.760, $P < 0.0001$).

Mean body temperature of voles ranged from 35.6 °C at $Ta = 10$ °C (33.8–37.1 °C) to 37.3 °C at $Ta = 33.5$ °C (36.4–38.5 °C) (Fig. 2; Table 1). Within the measured range of Ta 's, body temperature of voles slightly increased when the ambient temperature became higher (body temp = $34.641 + 0.700 \times$ ambient temp; $n = 45$, $r^2 = 0.334$, Student's t -test = 4.644, $P < 0.0001$). However, the body temperature of Cabrera vole remained almost constant from 10 to 25 °C ambient temperatures, with a mean value of 35.7 ± 0.9 °C ($n = 27$). Above 25 °C the body temperature of individuals increased to 37.0 ± 0.6 °C ($n = 18$) (Fig. 2). Mean thermal

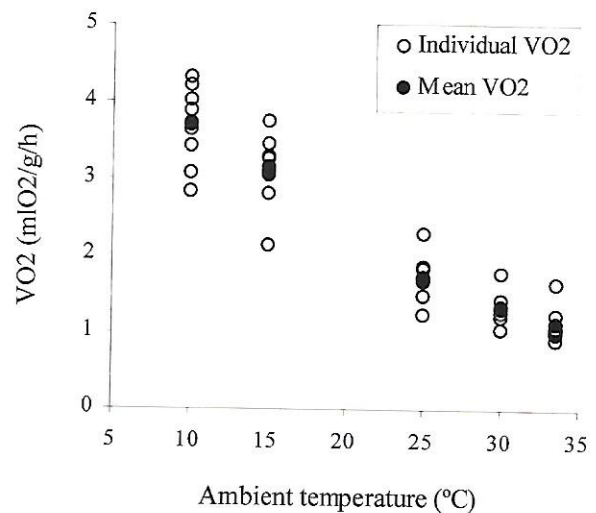


Fig. 1. Individual and mean resting metabolic rates (VO_2) of Cabrera voles as a function of ambient temperature.

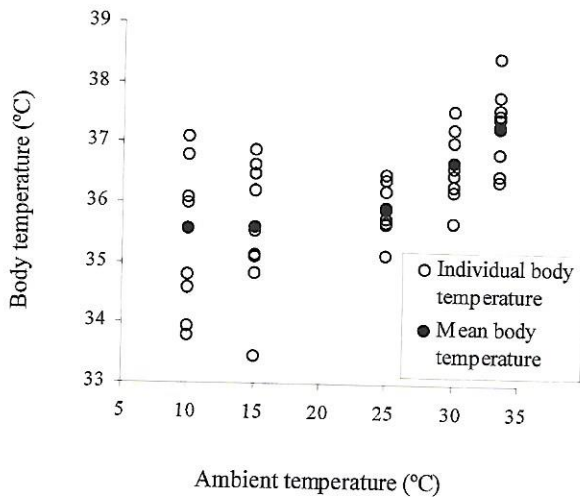


Fig. 2. Individual and mean values of body temperature of Cabrera voles as a function of ambient temperature.

conductance of Cabrera voles ranged from $0.144 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}$ at the lowest ambient temperature tested to $0.301 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}$ close to the lower critical thermoneutral temperature ($33.5 \text{ }^\circ\text{C}$) (Fig. 3, Table 1). Mean values of thermal conductance from 10 to $30 \text{ }^\circ\text{C}$ are significantly lower than at $33.5 \text{ }^\circ\text{C}$ ambient temperature ($F(4,32) = 45.634$, $P < 0.0001$; Tukey tests significant for pairs 10– $30 \text{ }^\circ\text{C}$, 10– $33.5 \text{ }^\circ\text{C}$, 15– $30 \text{ }^\circ\text{C}$, 25– $33.5 \text{ }^\circ\text{C}$ and 30– $33.5 \text{ }^\circ\text{C}$, $P < 0.05$).

4. Discussion

Most of the variation in basal rate of metabolism in eutherians can be accounted by the combined influences of body mass, food habits, behavior and climate (McNab, 1986). The Cabrera vole is distributed over the supra and mesomediterranean bioclimatic regions, as defined by Rivas-Martinez (1981). Hot dry summers and mild winters characterize these regions.

The lower limit of the thermoneutral zone (TNZ) of Cabrera voles was defined from the values of VO_2 plotted as a function of T_a (Fig. 1). This shows that at the two highest measured ambient temperatures the resting metabolic rate tends to stabilize. Because the Cabrera vole is a threatened species, it was decided not to go further than $33.5 \text{ }^\circ\text{C}$ to avoid the possible death of animals. Therefore, the lower limit of the TNZ was estimated at approximately $33.5 \text{ }^\circ\text{C}$ and the upper limit could not be determined. This value is higher

than the corresponding value reported in other microtines from temperate regions: $28.9 \text{ }^\circ\text{C}$ in *M. pennsylvanicus*, $29.8 \text{ }^\circ\text{C}$ in *M. breweri* (Kurta and Ferkin, 1991) or $28 \text{ }^\circ\text{C}$ in *M. oeconomus* (Wang and Wang, 2000). Resting metabolic rate (RMR) at thermoneutrality was $1.13 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1}$, which was assumed to approximate the basal metabolic rate (BMR) (e.g. Grodzinski and Wunder, 1975; Górecki and Kania, 1986; Górecki et al., 1990; Withers, 1992). Compared to other *Microtus* species, this value is quite low (e.g. *M. breweri*: $1.39 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1}$; *M. pennsylvanicus*: $1.81 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1}$; *M. montanus*: $1.90 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1}$) (Tomasi, 1985; Kurta and Ferkin, 1991; Wang and Wang, 2000) but still within the BMR range of grazers (Elgar and Harvey, 1987). It corresponds to 79% of that predicted on the basis of the allometric equation for 11 grazing rodents of Chile ($\text{BMR} = (6.04 \pm 1.53) \times Wb^{-0.382 \pm 0.094}$, where Wb is body weight; Bozinovic, 1992). Low values of VO_2 at the thermoneutral zone have been referred as an adaptation to minimize total heat production in arid and xeric environments (e.g. Yahav et al., 1988; Armitage et al., 1990), which are common at Mediterranean climates.

Because thermoregulation has a high metabolic cost, Cabrera voles may also save energy allowing body temperatures to approximate those of the environment at high ambient temperatures, behaving as heterotherms during hot stressful periods. The smaller the gap between environmental and body temperature, the lower the rate of heat flow between the environment and the body (Vaughan,

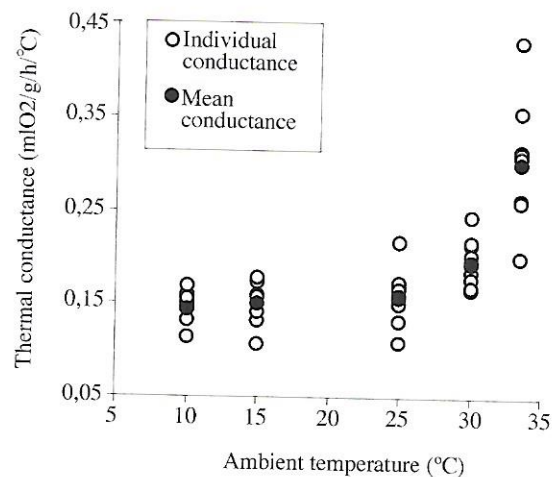


Fig. 3. Individual and mean values of thermal conductance of Cabrera voles as a function of ambient temperature.

1986; Eckert, 1988). This pattern of regulation is of critical adaptive importance, by facilitating metabolic economy (Grodzinski and Wunder, 1975; Vaughan, 1986; Withers, 1992). Conductance values in *M. cabreræ* in ambient temperatures below the TNZ ($0.163 \pm 0.024 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}$) were slightly higher (106%) than that predicted from the equation of Bartholomew (1977) for small mammals ($C = 0.154 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}$, when $C = 1.05 \times Wb^{-0.51}$, Wb -body weight) and the equation of Bradley and Deavers (1980) for 180 mammalian species ($C = 0.153 \text{ mlO}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}$, when $C = 0.76 \times Wb^{-0.426}$). Tomasi (1985) also found similar differences (105%) for *M. montanus*. High conductance at the critical thermoneutral temperature, in association with low RMR, suggests a physiological adaptation to reduce the overheating at high ambient temperatures.

The experiments in this study were performed between July and October, the hotter period of the year. Haim et al. (1991) showed that *Saccostomus campestris*, a fossorial rodent, had lower values of RMR at the thermoneutral temperature, higher conductance and lower body mass during the summer-acclimatized period. Similarly, a study on *M. guentheri* held at long photoperiod regime revealed an increase in the high critical temperature and a decrease in the metabolic rate (Haim et al., 1998). A recent study on *M. cabreræ* from Spain reported values of individual body weight varying on average between 44 and 67 g in May and October, respectively (Ventura et al., 1998), indicating that the voles in this study had slightly lower body masses ($43.03 \pm 6.78 \text{ g}$). Lowering metabolic rate may lead to enhanced digestive efficiency allowing voles to maintain their energy/matter budget when food availability and quality are poorer (Busch, 1989; Veloso and Bozinovic, 1993; Holloway and Geiser, 2001) or foraging cost is expensive (Busch, 1989). Besides lowering the metabolic cost of thermoregulation during the hot and dry season, and considering the reduced thermoregulatory abilities, the success of voles may also be based in their ability to avoid extremely high temperatures rather than to cope with them. In fact, Cabrera voles built their burrows and nests usually beneath the shade of low-growing vegetation and, besides, the thick fur facilitate insulation. In addition, experience had shown that, during summer, trapping success was higher during the milder periods of the day (S. Santos and M.L. Mathias, pers. obs). Ventura et al. (1998), also

based on captures and on signs of presence (e.g. fresh latrines), reported a reduced activity of voles in summer over autumn. Nevertheless, there are no reports of torpor in Cabrera voles, either on a seasonal basis or for shorter periods (Fernández-Salvador, 1998; this study) thus, they must always expend energy for thermoregulation. Apparently voles take advantage of periods of moderate temperatures, associated with a higher humidity which is confirmed by peaks of reproduction in the beginning of spring and in autumn, separated by a decrease in the breeding activity at the end of spring into summer (Ventura et al., 1998). It is expected that the lower critical temperature and the RMR would be slightly lower and higher, respectively, in winter-acclimatized Cabrera voles (e.g. Haim et al., 1998).

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