Comparative Biochemistry and Physiology, Part A 190 (2015) 32–38

Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa

Intraspecific variation in the energetics of the Cabrera vole

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ARTICLE INFO

Article history:
Received 8 June 2015
Received in revised form 17 August 2015
Accepted 19 August 2015
Available online 28 August 2015

Keywords:
Cabrera vole
Ecophysiology
Global change
Iberomys cabrerae
Intraspecific variability
Oxygen consumption
RMR
Thermoregulation
TNZ

ABSTRACT

Basal metabolic rate (BMR) is an intensively topic studied in ecophysiology for the purpose of understanding energy budgets of the species, variations of energy expenditure during their diary activities and physiological acclimatization to the environment. Establishing how the metabolism is assembled to the environment can provide valuable data to improve conservation strategies of endangered species. In this sense, metabolic differences associated to habitats have been widely reported in the interspecific level, however little is known about the intraspecific view of BMR under an environmental gradient. In this study, we researched the effect of the habitat on metabolic rate of an Iberian endemic species: *Iberomys cabrerae*. Animals were captured in different subpopulations of its altitudinal range and their MR was studied over a thermal gradient. MR was analyzed through a Linear Mixed Model (LMM) in which, in addition to thermal effects, the bioclimatic zone and sex also influenced the metabolism of the species. The beginning of thermoneutrality zone was set on 26.5 °C and RMR was 2.3 ml O_2 g^{-1} h^{-1}, intermediate between both bioclimatic zones. Supramediterranean subpopulations started the T_{lc} earlier (24.9 °C) and had higher RMR than the mesomediterranean ones (26.9 °C). The thermal environment together with primary productivity conditions could explain this difference in the metabolic behaviour of the Cabrera voles.

1. Introduction

Macrophysiological patterns and its variability in time and space are of vital importance to gain insight about evolutionary and ecological theories (Chown and Gaston, 2008; Naya et al., 2013; Bozinovic et al., 2014). In addition, the relatively recent trend in niche modelling literature has evolved from correlative models relating the presence of species to niche conditions to mechanistic models based on physiological data (Kearney and Porter, 2009). Despite the correlative approach is widely used (e.g. Anderson and Raza, 2010; Zeng et al., 2015) it shows low predictive power when is used to predict abundance and distribution over novel environmental conditions and it cannot explain the fundamental causation of geographical distribution (Kearney and Porter, 2004), which could be satisfied with the mechanistic approach. Mechanistic models integrate behavioural, morphological and physiological traits of the organism with the habitat features using energy and mass balance equations to determinate the species' range (Barve et al., 2014). In this field, the energetic metabolism is an intensively studied topic (e.g. Rezende et al., 2004; Agosta et al., 2013), owing to some of its traits as the metabolic rate responses directly to climate conditions; it can be related to the fundamental niche and then be used to model distribution and abundance or predicting potential changes linked to novel climate conditions.

Among various physiological measurements of ecological relevance, basal metabolic rate (BMR) represents the minimum rate of energy necessary to maintain homeostasis and allostasis. BMR has been used as a standard to assess the costs of different components of organism energy budgets, to analyze species-specific as well as intraspecific variations in energy expenditure during maximal and sustained activities, and to understand physiological adaptations to the environment (McNab, 2002). The dependence of metabolic rates on body mass (M_b) has long been recognized (Kleiber, 1961). Nevertheless, M_b alone does not fully explain variation in BMR (McNab, 1992). There are several hypotheses that attempt to explain how biotic and abiotic conditions affect mass-independent BMR in mammals (McNab, 2002), namely, food quality, food availability and/or unpredictable, direct climate effects, aridity, among others. For instance, several interspecific studies have analyzed the effects of food availability and predictability on mass-independent BMR by demonstrating that mass-independent BMR is higher in mesic habitats when compared with xeric habitats

Abbreviations: BMR, *basal metabolic rate*; Cm, *minimal thermal conductance*; M_b, *body mass*; MR, *metabolic rate*; NDVI, *normalized difference vegetation index*; NPP, *net primary productivity*; RMR, *resting metabolic rate*; ΔTm, *minimal (body-ambient) thermal differential*; Ta, *environmental temperature*; Tb, *body temperature*; T_{lc}, *lower critical temperature of thermoneutrality*; TNZ, *thermoneutrality zone*; Vo_2, *rate of O_2 consumption*; Po_2, *partial pressure of oxygen*.

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http://dx.doi.org/10.1016/j.cbpa.2015.08.011
1095-6433/

(Lovegrove, 2000; Mueller and Diamond, 2001; McNab, 2002; Rezende et al., 2004; Bozinovic et al., 2007). Among rodent species it has been largely reported the clear association between the mass corrected-metabolism rate and several key abiotic factors, such as: latitude (Speakman, 2000; Lovegrove, 2003; Rezende et al., 2004), altitude (Hayes, 1989), or climate (McNab, 1970; Hulbert et al., 1985; Bozinovic and Rosenmann, 1989). Most of these studies evaluated the effect of the environment on BMR from an interspecific level approach, considering that the traits are fixed and thus the BMR value is unique for each species. Nevertheless, some genetic or plastic variability can exist so the analysis of the metabolism rates focuses on the intraspecific level which allows approximating the factors responsible for variations in BMR and the ability of the species to adapt to the environment (Cruz-Neto and Bozinovic, 2004). Therefore, studies on changes in BMR across environmental gradients can help to predict the potential response of the species to anthropogenic changes in the environment and then to design better strategies for their conservation.

We investigated here the effects of geographic variations in habitat on the energetics (i.e. RMR, minimal thermal conductance (Cm) and minimal temperature differential between body (Tb) and environment (Ta) = ΔTm) of rodents originated from different populations. We used as study model populations of *Iberomys cabrerae* (*Microtus cabrerae* see Cuenca-Bescós et al., 2013) which is an endemic vole of the Iberian Peninsula, classified as Near Threatened in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Fernandes et al., 2008). The species has a highly fractured distribution area that is restricted to the centre, northeast and southeast of the Peninsula (Garrido-García et al., 2013). The Cabrera vole is a specialist species of scenopoetic variables with very restrictive habitat preferences. It has a patchy distribution in open areas with high water table and covered by formations of perennial grasses and rush beds. The subpopulations are distributed along an altitudinal range from 250 to 1500 m, although they are more common in meso- and supramediterranean bioclimatic zones, between 500 and 1200 m (Fernández-Salvador, 1998). Because of its habitat specificity and limited geographical distribution, the species is highly vulnerable to anthropic activities such as agriculture, farming or human infrastructures (Landete-Castillejos et al., 2000). Furthermore, predictions on climate change in the Iberian Peninsula expect an increase in the xericity (Pachauri et al., 2014) which could change the suitability of Cabrera voles' habitats compromising its conservation and persistence.

Mathias et al. (2003) and Santos et al. (2004) have explored the energetic metabolism of *I. cabrerae* but ignoring the intraspecific approach of this physiological trait. Consequently, our main aim is to evaluate the energetics of Cabrera vole at an intraspecific level in the Cabrera vole and to test for interpopulation differences associated to bioclimatic conditions.

2. Materials and methods

2.1. Experimental animals

This study is made up of 15 adults of *I. cabrerae*, from different subpopulations of two bioclimatic zones: mesomediterranean (subpopulations between 480 m and 710 m a.s.l.) and supramediterranean (subpopulations between 900 m and 1050 m a.s.l.) in Madrid, Spain (Fig. 1). A total of 8 animals were captured for mesomediterranean bioclimatic zone (5 females and 3 males) and 7 in the supramediterranean (4 females and 3 males). Cabrera voles were captured using Sherman live traps supplied with apples, during the day because this species shows diurnal and nocturnal activity (Fernández-Salvador, 1998). Due to the randomness of trapping, it was not possible to obtain equal number of male and female from each bioclimatic range. *I. cabrerae* is a Near Threatened species (Fernandes et al., 2008), thus we had to reach a compromise between selecting a representative number of voles and not affecting negatively to the sampled subpopulations, so we had to use a reduced sample of experimental animals.

Trapping was conducted in four different subpopulations in the supramediterranean zone and in six subpopulations in the mesomediterranean, during June and July of 2013 (Fig. 1). The annual average temperature in subpopulations of the supramediterranean zone varies between 11.1° and 11.9 °C; with maximum temperatures in July between 21.2° and 21.9 °C; minimum temperatures in January ranging from 2.8° to 3.4 °C; the minimum rainfall values occurring in

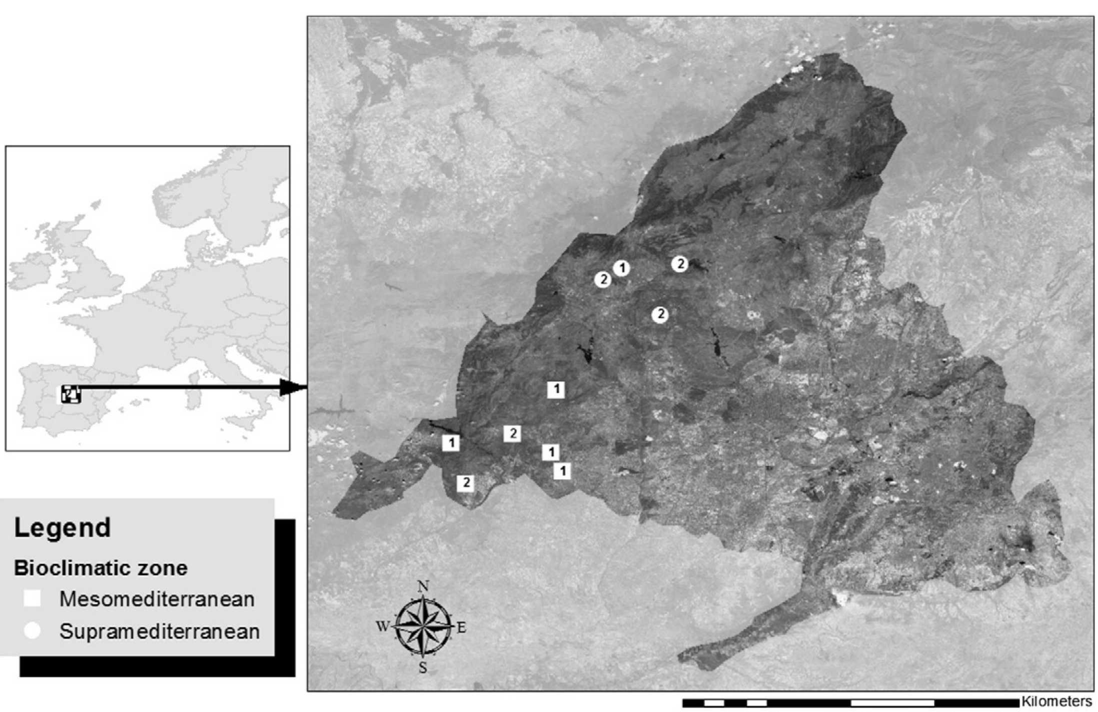

Fig. 1. Geographical localization of the subpopulations where the Cabrera voles were taken for the study. Numbers in the symbol are individuals captured in the respective subpopulation.