Mammalian Biology 80 (2015) 81–86

Contents lists available at ScienceDirect

Mammalian Biology

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

Original Investigation

Acclimating to thermal changes: Intraspecific variation in a small mammal from the Andes Mountains

Paola L. Sassi*, Agustina Novillo

Grupo de Investigaciones de la Biodiversidad, CONICET, Instituto Argentino de Investigaciones de las Zonas Áridas, CCT-Mendoza, Argentina

ARTICLE INFO

Article history:
Received 6 August 2014
Accepted 17 December 2014
Handled by Jennifer Burns
Available online 23 December 2014

Keywords:
Thermal landscape
Elevation cline
Energy balance
Phenotypic variation
Small mammals

ABSTRACT

Ambient temperature strongly affects an ecosystem's characteristics as well as the attributes of individuals, eventually determining the distribution of populations and species. Phenotypic plasticity plays a central role in the administration of energy under thermal variation through traits underlying energy acquisition and expenditure. A powerful approach to assess acclimation ability to environmental variation is studying relevant traits along natural geographic gradients. Our goal was to assess and quantify in the small rodent *Phyllotis xanthopygus*, changes in traits relevant to energy balance in response to its thermal landscape. We compared energy intake and digestibility by animals from sites at different elevations under different temperatures in the laboratory. Results showed an increase in energy acquisition rates by the lower-elevation individuals to cope with low temperatures, while high-elevation animals appeared unaffected by this treatment. After acclimating to warmer conditions, all individuals showed a similar decrease in energy intake, irrespective of their origin site. We also assessed thermal conductance in individuals from different elevations and found that animals from higher sites exhibited lower heat loss rates. Our evidence suggests that heat conservation differences could in part account for differences among high and low elevation animals in the ability to cope with low temperatures. The lack of plasticity under the warm thermal treatment conforms to recent reports of high conservatism on the upper limit of the thermoneutral zone. *P. xanthopygus* displays intraspecific variation in the response to temperature, and we propose that this is highly relevant to model its chances in a warming environment.

Introduction

Ambient temperature is a major determinant of an organism's life history traits. It influences resource availability, morphology, physiology, and behavior of individuals, eventually determining the distribution of populations and species. In animal species, this is reflected in the energy balance and thermal range achieved within a given habitat (Pörtner et al., 2006). Studying the variation of physiological traits along environmental gradients (Piersma and Lindström, 1997) allows the examination of a species overall thermal tolerance and its acclimation ability (Hammond et al., 2001; Chown et al., 2004). Understanding the physiological aptitude of species is crucial for developing sound biodiversity conservation strategies in the face of rapid climate change (Arlettaz et al., 2000).

Phenotypic plasticity is the ability of a species to produce different phenotypes under different environmental and trophic conditions (Pigliucci, 1996). Preferred traits to evaluate organisms' plastic responses should be intrinsically variable and relevant to environmental factors, such as temperature is relevant to energy balance (Bradshaw, 2003). Thus, phenotypic plasticity plays a central role in the administration of energy under environmental variation, through characters related to the acquisition and expenditure of energy. An elevation gradient represents an appropriate context for the assessment of plastic responses in energy balance relevant traits since it encompasses conspicuous thermal changes across relatively short distances.

Over the last years, ecological and evolutionary physiology has emphasized the importance of studying intraspecific variation as a substrate for natural selection (McNab, 2002). *Phyllotis xanthopygus* is a good animal model to accomplish this because it has a widespread geographic distribution in South America, which covers a steep elevation range in the Andes Mountains as well as a broad climatic cline (Steppan et al., 2007). The genus *Phyllotis* has been thoroughly studied under this approach showing both phenotypic plasticity and genetic variability. Main findings include a

---

* Correspondence to: Av. Ruiz Leal s/n, Parque Gral. San Martín, CC 507 (5500) Mendoza, Argentina. Tel.: +54 261 5244117.
E-mail addresses: psassi@mendoza-conicet.gob.ar, paola.sassi@gmail.com (P.L. Sassi).

http://dx.doi.org/10.1016/j.mambio.2014.12.005

genetic basis for some traits linked to energy balance (Nespolo et al., 2003), a relationship between metabolic rate and habitat productivity (Bozinovic et al., 2007), an effect of ambient temperature and energy demands on digestive functions (Naya et al., 2005), and responses to changes in ambient temperature and diet (Bozinovic and Nespolo, 1997; Rezende and Bozinovic, 2001). Particularly for *P. xanthopygus*, phenotypic plasticity plays an important role in cold acclimation through changes in thermogenic capability (Nespolo et al., 1999). This is favorable in seasonal environments, where the species reduces energy expenditure in warmer periods (Stearns, 1989), and could also explain its wide range of distribution.

Heat generation ability and acclimation temperature are negatively correlated (Nespolo and Rosenmann, 1997). Likewise, heat conservation ability (i.e. thermal conductance) would be influenced by the thermal landscape. According to Sibly (1981) the digestive strategy maximizing net energy acquisition rate will be favored by natural selection. Thus, the interplay between food intake, digestive processing capacity and energy loss is expected to be coupled with demands. Based on this, here we analyzed how diverse experimental temperatures affect energy balance related traits in individuals of *P. xanthopygus* collected at different sites along an elevation cline. We hypothesize that animals adjust energy intake and energy digestibility to meet their requirements; thus we expect that before acclimation to the laboratory, individuals captured in higher elevations will show higher energy intake and assimilation of digestible energy, than individuals from lower elevations. On the other hand, acclimating to a particular environment (usually thermal) provides an organism with advantages within that environment (Leroi et al., 1994). Therefore, we hypothesize that subsequent thermal regimes in the laboratory will lead to changes in the cited energy acquisition traits. More specifically, individuals will increase rates of energy intake and assimilation under cold experimental conditions, compared to warm thermal treatments. Nevertheless, animals from different elevations could respond differently in spite of uniform experimental conditions, due to ontogenetic-based traits raised under diverse thermal regimes in the field. Regarding thermal conductance, we expect, under the same theoretical framework, that animals from higher elevations will show lower heat loss rates than lower elevation ones. A better understanding of a species performance and responses along thermal gradients enables modeling its chances of persistence, migration or resilience to climate change.

Material and methods

Study area

The study area is located at El Manzano Histórico Reserve, Mendoza Province, Argentina. We established sampling sites at 1700, 2300 and 3100 m a.s.l. along an elevation transect. Sites were 3 to 4 km apart, encompassing gradual changes in the landscape. According to Méndez (2011), these sites belong to different phytogeographic regions: sites at 1700 and 2300 m a.s.l. correspond to the Andina ecoregion and at 3100 m a.s.l. to the Alto Andina ecoregion.

In order to characterize the environmental temperature range we set up three dataloggers – Extech® USB Temperature Dataloggers, range −40 to 70 °C, resolution 0.1 °C, accuracy ± 1.0 °C (−10 to 40 °C) –,one at each elevation site, recording temperatures at 3 h intervals for a period of one year (13 January 2013 to 06 Febrary 2014). Each datalogger was previously calibrated in the laboratory and set at ground level (beneath the rocks, within cracks possibly used by the mice) in the field.

Animals and acclimation

In order to test for geographic related variability, a Common Garden Experiment (Garland and Adolph, 1991) was performed, comparing individuals from different sites acclimated to common experimental situations in the lab. Thirty non reproductive adult *P. xanthopygus xanthophygus* (10 from each site) were captured using Sherman traps (Möller® $8 \times 9 \times 24\,\text{cm}^3$) between February and March 2013. All animals belonged to the same subspecies, with a sex ratio of 1/1. Genetic analyses on the individuals showed no genetic differentiation and high gene flow levels among animals from all sites (Ojeda et al., 2013).

In the laboratory, animals were maintained on chinchilla food pellets and water *ad libitum*. Individuals were housed individually in $30 \times 30 \times 40\,\text{cm}^3$ size cages and maintained on 12L: 12D photoperiod and at 25 °C ambient temperature (standard laboratory conditions—Bozinovic and Nespolo, 1997; Nespolo et al., 1999).

To estimate Thermal Conductance, 15 non reproductive adult individuals (five from each site) were collected between February and March 2013, and housed individually under maintenance conditions until the trial.

Experiments

The first experiment consisted of measuring energy intake, digestibility and weight on each individual subsequently exposed to four treatments. The first measurement was carried out immediately after the animals' capture at 25 °C (treatment I), in order to detect the residual effect of distinct thermal conditions endured by them in the field. Subsequently, individuals were acclimated during 8 weeks to 25 °C, 16 °C and 31 °C; treatments two (II), three (III) and four (IV) respectively. Energy intake, digestibility and body weight were measured after the acclimation period to each temperature in order to assess the effect of thermal treatments on animals from distinct elevations.

Experimental temperatures were chosen considering two elements. First, initial field estimates evidenced an ambient temperature differential of 12 °C between the most extreme sites along the elevation cline considered. In fact, mean ambient temperatures during the month of animal captures were 24.29 ± 4.14 °C (1700 m a.s.l),18.96 ± 2.33 °C (2300 m a.s.l), and 12.73 ± 2.34 °C (3100 m a.s.l), which was used as preliminary information on the thermal range in the field. Finally, baseline studies on *Phyllotis*, searching for thermal related responses have acclimated animals at 15 and 30 °C, these alternative temperatures corresponding to relatively high and low energy demanding conditions, respectively, with typical laboratory maintenance temperatures at 25 °C (Bozinovic and Nespolo, 1997; Nespolo et al., 1999; Canals et al., 2009).

Measurements of energy intake and energy digestibility from food (Chindiet®) were performed over the course of four days, which is a standard period for obtaining representative estimates with sufficient resolution (Sales and Janssens, 2003, and references therein). Each day, samples of leftover food and feces were dried at 60 °C in a dry heat sterilizer for a week and weighted in a precision balance (resolution = 0.01 g). Food intake was measured as the difference between the amount of dried food offered and left per day. The energy content per gram in feces and leftover food was measured using a Parr Bomb Calorimeter which was multiplied by the dry weight of samples. Energy intake which was calculated per day for each individual under each treatment according to Qi–Qe, where Qi is the daily rate of energy in food intake and Qe is the daily rate of energy wasted in feces. Digestibility is the extraction efficiency of energy, dry matter or other nutrients from food, calculated as $[(Qi-Qe)/Qi] \times 100\%$. This method underestimates digestive efficiency because it includes the contribution of metabolic wastes, non-reabsorbed secretions of the digestive system and microorganisms (Naya and Bozinovic, 2006). Body weight was measured at the beginning of each four-day trial to detect differences from the acclimation thermal conditions.