Body mass and water economy in the South American olivaceous field mouse along a latitudinal gradient: Implications for climate change

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ABSTRACT

We compared geographic trends in body mass in a number of populations of the olivaceous field mouse (Abrothrix olivaceus,) along a latitudinal gradient in Chile, and tested the expected neutral tendency resulting from the opposite influences of environmental temperature and aridity across the gradient. Also, we studied water economy through physiological measurements of total evaporative water loss and urine osmolality in individuals from populations inhabiting two contrasting habitats (northern semiarid shrubland and southern temperate rainforest) and acclimated during six months to the same conditions. No change in male body mass with latitude was found across 39 populations. Evaporative water loss in rodents from the semiarid shrubland was significantly lower than that of individuals from the temperate rainforest, and urine osmolality was significantly higher in rodents from the semiarid habitat. We found a better tolerance of water shortage in the rodent population from the xeric habitat, thus suggesting the occurrence of local adaptation to the prevailing habitat conditions. The mechanisms by which rodents regulate their water economy in face of spatial and temporal fluctuations in environmental conditions constitute an essential component of the physiological flexibility that is necessary to cope with challenging climate change scenarios.

1. Introduction

Patterns of within-species phenotypic variation along environmental gradients —or lack thereof— are significant starting points to formulate general hypotheses and/or undertake mechanistic studies aiming at understanding the ecology and evolution of species (Endler, 1986; Conover et al., 2009). Furthermore, this knowledge may be useful to predict the ecological and evolutionary responses of populations or species to current and predicted climate change. On one hand, the commonly found pattern of increased body size with latitude in endotherms (Bergmann's rule) has often been explained considering that the lower surface/volume ratio of larger organisms allows them a reduced heat loss rate in colder environments (McNab, 1971; Atkinson and Sibly, 1997). On the other hand, along an aridity gradient in small endotherms, larger individuals are found in the driest regions (Storz et al., 2001 and references therein),

presumably because conservation of metabolic water is maximized when the evaporative surface/volume ratio is minimized (James, 1970). Therefore, if the temperature gradient inherent to any latitudinal gradient is coupled to an aridity gradient of increased aridity at lower latitudes, no noticeable pattern of phenotypic variation in body size would be expected, at least for small endotherms. To our knowledge, this prediction has not been tested.

In Chile a marked aridity gradient exists from the desert in the north to the semiarid winter-rainfall ecosystems and Mediterranean-type regions in the center to the rainforests in the south. Thus the Chilean latitudinal gradient constitutes the scenario of contrasting environmental influences on body size, and likely neutral outcome, depicted above. Furthermore, there is evidence of a trend of increased aridity across Chilean ecosystems (Pezoa, 2003; Fuenzalida et al., 2007). The effects of predicted climate change on species cannot be assessed only from the type, magnitude or time scale of the perturbation, or from past data of species distribution and climate. The effects must be evaluated in the target organisms, whose success in maintaining homeostasis under stressful conditions determines the survival of individuals and its

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demographic consequences (Pelletier et al., 2007). In fact, physiological adaptation to climate change has been addressed quantitatively (Parmesan, 2006). Small mammals from arid and semiarid habitats often face the challenge of water economy because availability of free water and food is limited and variable (Degen, 1997; Diaz and Ojeda, 1999; Bozinovic et al., 2003; Gallardo et al., 2005; Bozinovic and Gallardo, 2006). Low energy expenditure linked to reduced evaporative water loss is considered adaptive for energy and water conservation in rodents from xeric environments because it results in lower food requirements and reduced water turnover in variable and unproductive habitats (Bozinovic and Gallardo, 2006). In addition, osmoregulatory traits of small endotherms show clinal variation resulting in functional adjustments to the environment (Sabat et al., 2009).

The present study had two main goals. First, we compared body size in a number of rodent populations along a broad latitudinal gradient in Chile, testing the expected neutral trend resulting from the opposite influences of temperature and aridity across the gradient. Second, we studied rodent water economy through measurements of total evaporative water loss and standard urine osmolality in individuals from populations inhabiting two contrasting habitats (northern semiarid shrubland and southern temperate rainforest) and acclimated during six months to the same experimental conditions. Results are discussed in the context of predicted climate change in Chilean ecosystems. We used as study model the South American olivaceous field mouse *Abrothrix olivaceus* (Muridae) because it has a very wide geographic distribution range in Chile: from nearly 20 °S in the Atacama desert to approximately 53 °S in temperate rainforest and Patagonian steppe (Silva, 2005; Iriarte, 2008).

2. Material and methods

2.1. Latitudinal pattern in rodent body mass

We sampled 39 populations of *A. olivaceus* from 26.1 to 53.6 °S along Chile. Trapping was conducted using Sherman traps (8 × 9 × 23 cm) for three nights at each site, and the bait used was a mixture of oat and vanilla. We followed the American Society of Mammalogists Guidelines during the collection and handling of animals used in this work (Gannon et al., 2007).

After capture, animals were weighed in situ (±0.5 g). We averaged body mass of adult males and only those localities where the number of captured rodents was higher than 10 individuals. To reduce age effects and reproductive status we used only adult males and juveniles. Specimens were deposited in the Colección de Flora y Fauna Profesor Patricio Sánchez Reyes (SSUC), Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago, Chile, and the Museum of Southwestern Biology, University of New Mexico, USA.

2.2. Water economy in two contrasting populations

We used adult males and non-reproductive females of the olivaceous field mouse *A. olivaceus* (Muridae). Using Sherman live traps, we captured 12 animals (8 males and 4 females) in Illapel, a semiarid shrubland in northern Chile (31.5°S; 71.1°W, 310 m a.s.l), and 12 animals (5 males and 7 females) in Tomé, a rainy temperate coastal forest in southern Chile (36.6°S; 7.9°W, 35 m a.s.l), from January to April 2008. All individuals were ear-tagged and transported to the laboratory within a week of capture. Animals were individually maintained for six months in rat cages with rabbit food pellets, water ad libitum and a bedding of hardwood chips. Ambient temperature was 25 °C and photoperiod was L:D = 12:12. Rodents were randomly assigned to our treatments.

The distance between the localities is 634 km and environmental conditions are contrasting in terms of temperature and precipitation (Table 1). We also calculated the De Martonne aridity index (DMi; Sabat et al., 2009) for each habitat. This index is the ratio between mean annual precipitation (PP, in mm) and mean air temperature (TA; in °C) plus 10 °C (DMi = PP/[TA + 10]). Lower values of DMi reflect drier environments. A DMi < 20 corresponds to a Mediterranean habitat; a DMi < 10 is a "desert-like" habitat or a semiarid grassland, and a DMi < 5 corresponds to extreme aridity or desert (Oury, 1965; Ahmed, 1997; Cavieres and Sabat, 2008).

We measured total evaporative water loss (TEWL), i.e., the sum of cutaneous and respiratory water loss, in all individuals. TEWL is considered an important physiological trait involved in water balance, thermoregulation and hence survival, being an important avenue of water loss in endotherms (Walsberg and Wolf, 1995; Walsberg, 2000). All trials were completed between 0900 and 1700 h, when individuals were resting, by flow-through water vapor analyzer (Sable Systems, Henderson, Nevada). First, rodents were weighed using an electronic balance (±0.1 g), placed in a metabolic chamber (1 L) and inside a controlled temperature cabinet at 30 ± 0.5 °C. We calculated absolute humidity (kg/m3) of air entering and leaving the chamber as ρout = P/T Rw, where P is water vapor pressure of the air, T is the dew-point temperature and Rw is the gas constant for water vapor (461.5 J/kg °K). The ρin was determined using the average value of the vapor pressure of the air entering the empty chamber (i.e., the baseline period of 15 min) before and after each experiment with a dew-point hygrometer (RH- 200, Sable System, Henderson, Nevada). TEWL was calculated as: (Ve ρout - Vi ρin); ρout and ρin are the absolute humidity of the inlet air and the outlet air, respectively, Vi is the flow rate of the air entering the chamber as given by the mass flow controller (800 mL min^{-1}), and Ve is the flow of exiting air. Ve was calculated following Williams and Tieleman (2000). Output from the H2O and oxygen analyzers (%) was digitized using a Universal Interface II (Sable Systems) and recorded on a personal computer using data acquisition software (EXPEDATA, Sable Systems). Our sampling interval was 5 s. Rodents remained in the chamber for at least 3 h. We averaged water vapor pressure of the excurrent air stream over a 20 min period after steady-state was reached. The day before, animals were anesthetized with sodium pentobarbital (60 mg/kg, ip) and Uosm was measured in samples obtained by bladder puncture. Urine osmolalities were measured by freezing point depression (Advanced Instruments, MA, USA). A linear regression analysis was used to estimate the relationship between rodent body mass and latitude across populations. Rodent mass and physiological traits were compared between populations using Student *t*-test. Data fulfilled the assumptions of the tests. Statistical analyses were performed using STATISTICA® 6.0.

3. Results

No change in body size with latitude was found across the 39 populations of *A. olivaceus* sampled in Chile (r = 0.14, P = 0.39;

Table 1
Localities of studied animals, de Martonne index (DMi), and climatic conditions (in parenthesis, the range of environmental temperatures). Lower values of DMi reflect drier environments. Climatic data were obtained from www.worldclimate. com and di Castri and Hajek (1976).

	Illapel	Tomé
Coordinates	31.5 °S; 71.1 °W	36.6 °S; 7.9 °W
Habitat description	Semiarid shrubland	Temperate rainforest
DMi	6.9	50.4
Annual rainfall (mm)	170	1200
Mean temperature (°C)	14.7 (9.2−23.5)	13.8 (7.2−18.8)

Fig. 1). Rodent body mass was similar in the two populations studied ($t = 1.361$, df $= 22$, $P = 0.18$, Fig.2a). However, TEWL in rodents from the semiarid shrubland was significantly lower than that of individuals from the temperate rainforest ($t = 26.696$, df $= 22$, $P < 0.01$, Fig. 2b). Likewise, although we were unable to obtain urine samples from all of the experimental animals, we found that Uosm was significantly higher in rodents from the semiarid habitat ($t = 2.577$, d.f. $= 5$, $P = 0.05$, Fig. 2c).

4. Discussion

Body size has a fundamental impact on animals. Size constraints almost every aspect of morphology and physiology, and influences the nature of most ecological relationships. Body size of the oliva-ceous mouse *A. olivaceus* did not vary along a very long latitudinal gradient spanning over 3000 km. A possible explanation for the lack of a latitudinal pattern in body size for this small mammal is that aridity and temperature covary, i.e., the colder habitats are the more humid, and vice versa. Consequently, the relative advantages of larger bodies, i.e., lower surface/volume ratios, in colder climates and in drier habitats, probably cancel out. Alternatively, such a lack of phenotypic variation along the latitudinal gradient might be related to countergradient variation (Conover and Schultz, 1995). This pattern may arise if genetic influences at the local scale, e.g., selection pressures of biotic origin acting on body size, oppose environmental effects on this trait (see Conover et al., 2009 for a review of cases). However, further experimental approaches are needed to evaluate this possibility.

The mechanisms by which animals regulate their water economy in face of spatial and temporal fluctuations in environmental conditions constitute an essential component of the physiological flexibility that is necessary to cope with challenging climate change scenarios (McNab, 2002). We found interesting results after comparing water economy mechanisms of semiarid shrubland and temperate rainforest populations of the olivaceous field mouse, which showed similar body mass. We observed a better tolerance of water shortage in the rodent population from the xeric habitat, thus suggesting the occurrence of local adaptation to the prevailing habitat conditions. Bozinovic et al. (1995) reviewed studies dealing with renal performance and maximal urine osmolality among Mediterranean rodent species inhabiting semixeric (and xeric) regions of Chile, the southwestern United States and Australia. For the five species inhabiting semixeric and xeric habitats in Chile, the
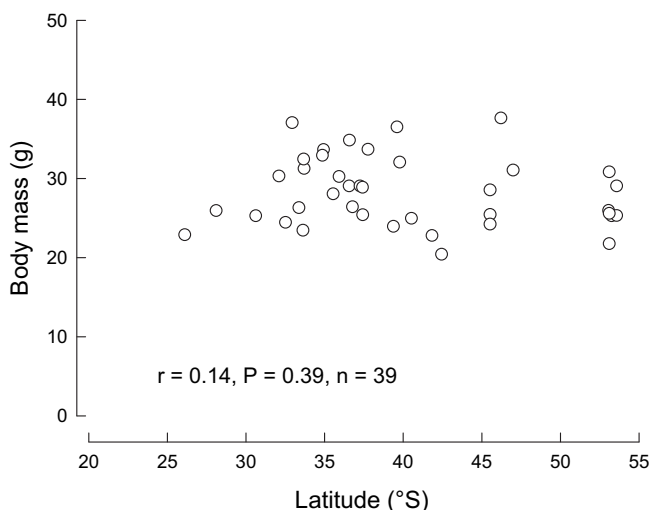

Fig. 1. Relationships between body mass with latitude across the 39 populations of *A. olivaceus* sampled along Chile.
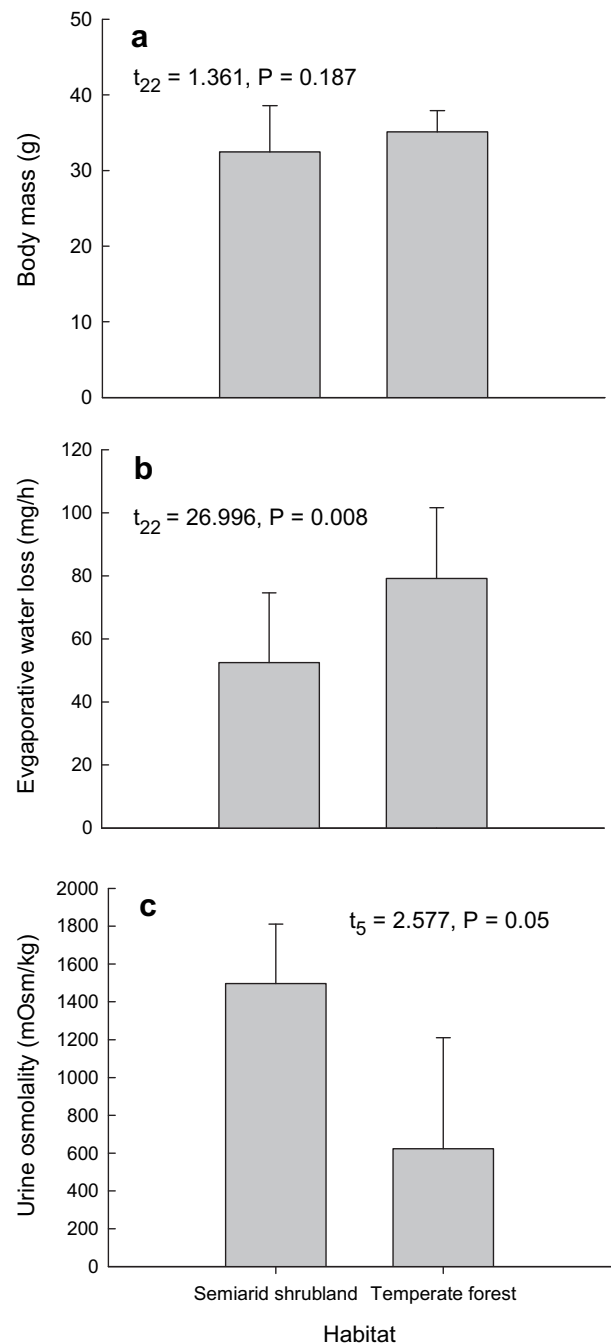

Fig. 2. a) Body mass in the two studied populations of *Abrothrix olivaceus*; b) total evaporative water loss in rodents from the semiarid shrubland and in individuals from the temperate rainforest and c) Comparisons of urine osmolality between rodents from both studied populations.

maximal capacity to concentrate urine (recorded under laboratory conditions) ranged from about 3300 mOsm/kg to nearly 4500 mOsm/kg. The mean value for the species inhabiting the semiarid habitat was 4138 mOsm/kg, a value similar (3930 mOsm/kg) to that found for nine western North American rodent species. Also, Bozinovic et al. (2007a,b) and Tirado et al. (2008a,b) assessed through a field study, the putative effects of the El Niño Southern Oscillation climatic phenomena (ENSO) at the water physiological homeostasis level among six species of small mammals in semiarid Chile. They observed a seasonal rhythm of water economy of these mammals during wet years which is consistent with that observed among

North American desert heteromyds (MacMillen, 1972; MacMillen and Grubbs, 1976), but differs from that of Indian desert gerbils (Goyal, 1988). The trends of seasonal Uosm values during contrasting years (wet and dry years) were a consequence of associated changes in abundance of plants and insects, because they constitute the major sources of food and water for mammals in the study site (Meserve, 1981). The local productivity of plants and insects is determined by the amount of rainfall (Gutiérrez et al., 1993; Gutiérrez, 2001). The insectivorous habit of the marsupials Thylamys elegans allows a larger water intake during wet seasons or years but it also implicates a higher excretion of nitrogen products such as urea. This increases osmotic diuresis, which can be compensated by an increase in Uosm. Consequently, together with the local adaptation at the physiological level observed in this study, water physiological homeostasis regulation among desert dwelling small mammals shows remarkable flexibility in both time and space (Cortés et al., 1994; Bozinovic et al., 2003; Bozinovic and Gallardo, 2006). As far as we know, no information is available concerning the relative importance of regulatory mechanisms versus physiological adaptation in South American desert dwelling rodents. In the context of impending climate change, it has been discussed whether plastic responses or genetic differentiation would be the prevailing mechanism of adaptation of organisms to environmental challenges (Visser, 2008).

There is compelling evidence of climatic change at a global scale (Walther et al., 2005; IPCC, 2007) and likely associated shifts in species distribution and phenology (Parmesan, 2006). However, organisms and populations do not respond to global averages of climatic conditions, but to their regional or local environment (Walther et al., 2002). There is a trend of increased aridity along Chilean ecosystems (Fuenzalida et al., 2007). Our results suggest that no noticeable change in body mass is expected, at least for small mammals such as A. olivaceus. More importantly, results of the present study indicate that, in a scenario of increased desertification, rodent populations would be able to show adaptive physiological flexibility in water economy, thus leading to increased capacity to conserve water (high Uosm and low TEWL) and ultimately to successfully cope with a drier environment. Spicer and Gaston (1999) pointed out a key question in studies of physiological diversity: How well do between-species patterns in physiological diversity predict patterns across populations? This study may help to answer this question since we observed that rodent populations exhibited patterns of physiological adaptations in water economy similar to those exhibited by desert dwelling species of rodents (Degen, 1997). Finally, our results may contribute to understand the sensitivity of the fauna of semiarid ecosystems to foreseen climate changes, considering that drier conditions are expected (Jaksic, 2001).

Acknowledgements

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