

GEOGRAPHIC ENERGETICS OF THE ANDEAN MOUSE, *ABROTHRIX ANDINUS*

FRANCISCO BOZINOVIC, JORGE A. LAGOS, AND PABLO A. MARQUET

Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

We measured basal metabolic rate, thermal conductance, body temperature, and temperature differential of three populations of the Sigmodontine-rodent *Abrothrix andinus* in three different habitats of the Andean range of northern Chile. Individuals from the three habitats were good thermoregulators, were capable of maintaining a high mass-independent temperature differential, and were able to survive the cold ambient temperatures during the night. We compared our data with previously published information on seasonal energetics of another population of *A. andinus* in the Andean range of central Chile and with species of the genus *Abrothrix* in a Mediterranean climate. Energetics of *Abrothrix* did not vary in response to different climatic conditions, which favored the hypothesis that it was a fixed character probably reflecting a common ancestor of Andean origin or radiation along the Andes Mountains.

Key words: *Abrothrix*, South American rodents, Andes Mountains, energetics, thermoregulation, rigid endothermy

Intraspecific geographic variation has been demonstrated for a plethora of physiological and life-history traits (Roff, 1992). This is in part a result of natural populations exposed to geographical gradients in environmental variables of varying intensities (Parson, 1994, 1995). Some organisms can increase their resistance to extreme environmental variables by genetic or phenotypic variation in energy exchange. At a species-specific level, it has been demonstrated that small mammals have evolved physiological mechanisms to cope with cold environments (Schmidt-Nielsen, 1990). Thermoregulatory capabilities of an endotherm at different environmental temperatures depend on the balance between rates of heat production and loss. A high basal metabolic rate (BMR) and low thermal conductance (C), which implies a continuous regulation of body temperature (T_b) regulation, are likely to be advantageous for survival in cool to cold habitats (McNab, 1992).

The study of populations from the same geographical region, but from different hab-

itats, should provide an effective tool for understanding the variability of thermoregulatory traits that allow survival in high-elevation, cold environments. Almost no studies have been carried out in South American habitats with consideration of energetic and thermoregulatory variability among populations in different habitats within a species geographic range (Bozinovic et al., 1995; Mares, 1985). Our objective was to examine spatial and temporal variability of standard energetics of the Andean mouse (*Abrothrix andinus*) from different populations along an elevational gradient of different habitat characteristics. Energetics of small mammals appears to be correlated with features of animal design and characteristics of the habitat in which they live. In fact, McNab (1988) showed that mammalian energetics are sensitive to several ecological and physiological factors, including body mass (m_b), precision of thermoregulation, food habits, climate, and activity patterns.

We tested for differences in m_b , BMR, C, and thermoregulatory capabilities in individ-

uals from three populations of *A. andinus* along an elevational gradient in northern Chile from 2,500 to 4,200 m above mean sea level (geographic variability) and compared our observations with previously reported data on seasonal changes in energetics of *A. andinus* in the Andes Mountain of central Chile (temporal variability). Because the minimal temperature differential between body and ambient (ΔT_m) is equal to BMR/C ($^{\circ}C$) = $3.42 m_b^{0.25}$ (McNab, 1979), we predicted that low values of mass-independent C (high thermal insulation) coupled with high mass-independent values of BMR may contribute to a higher thermoregulatory capacity by allowing heat conservation in *A. andinus*. That prediction is especially important for this small-sized species because cost of continuous endothermy is higher at small body mass and the *A. andinus* inhabit cool to cold environments.

MATERIALS AND METHODS

Laboratory animals.—*Abrothrix andinus* were captured during September 1997 with Sherman traps in several localities of the Andes Mountains of northern Chile and transported to the laboratory. Capture localities were: Parinacota ($n = 7$) at 4,500 m above mean sea level ($18^{\circ}33'S$, $69^{\circ}15'W$, mean annual temperature and precipitation = $1.4^{\circ}C$ and 383 mm, respectively), Río Coya ($n = 6$) at 3,850 m ($22^{\circ}56'S$, $68^{\circ}12'W$, mean annual temperature and precipitation = $4.1^{\circ}C$ and 51.2 mm, respectively), and Chiuchiu ($n = 5$) at 2,529 m ($28^{\circ}18'S$, $68^{\circ}38'W$, mean annual temperature and precipitation = $12.2^{\circ}C$ and 5.4 mm, respectively). Energetic variables of animals from those habitats were compared with a population from the Andes in central Chile ($33^{\circ}21'S$, $70^{\circ}20'W$; 2,200 m above sea level, mean annual temperature and precipitation = $7.3^{\circ}C$ and 400–550 mm, respectively) in which seasonal changes in energy expenditure have been reported (Bozinovic et al., 1990).

In the animal room, *A. andinus* were maintained on rabbit-food pellets (energy content = 16.96 ± 0.02 kJ g^{-1}). During 1 week, enough time to avoid laboratory acclimatization (Nespolo and Rosenmann, 1997) and before the experiments started, they received water ad lib. and experienced a photoperiod of 12L:12D. All

animals seemed healthy because they maintained body mass and were very active. After experiments, animals were killed and were deposited in the National Museum of Natural History, Santiago, Chile.

Metabolic rate.—Metabolic rate (M) was measured during at least 1 hour in a computerized (Datacan V) open-flow respirometry system (Sable Systems) in metabolic chambers of 900 ml at different ambient temperatures (T_a). The metabolic chamber received dried air at a rate of 800 ml min^{-1} from mass flow controllers (Sierra Instruments, Monterey, CA), enough to ensure adequate mixing of the chamber. After and before being placed in the chambers, air was passed through CO_2 absorbent granules of Baralyme ($Ba(OH)_2$) and H_2O absorbent granules of Drierite ($CaSO_4$) and was monitored every 5 s by an Applied Electrochemistry O_2 analyzer model S-3A/I (Ametek, Pittsburgh, PA). Ambient temperature was held constant within $\pm 0.5^{\circ}C$ by maintaining the metabolic chamber in an incubator. Oxygen consumption was calculated by equation 4a of Withers (1977:122), taking the lowest values that did not change more than 0.01% in O_2 concentration and was corrected automatically standard temperature and pressure (STPD). All metabolic trials were completed between 0800–1600 h. Body mass and T_b were measured before and after each metabolic trial with an electronic balance and a Cole-Parmer thermometer and copper-constantan thermocouples, respectively. Basal metabolic rate was assessed as the minimal rate of O_2 -consumption when showed independent of T_a . Thermal conductance was calculated below the thermoneutral zone by the equation $C = M/(T_b - T_a)$ for each measurement. The lower critical temperature (T_{lc}) was obtained from the intersection between BMR and C. The classical equations of Kleiber (1961): $BMR = 3.42 m_b^{-0.25}$ of Morrison and Ryser (1951): $C = 1.0 m_b^{-0.5}$, and of McNab (1979): $\Delta T_m = 3.42 m_b^{0.25}$, with m_b in grams, were taken as standard references.

Statistics.—Variables were tested with non-parametric Kruskal-Wallis ANOVA tests (Steel and Torrie, 1980). Data are given as $\bar{X} \pm SD$.

RESULTS AND DISCUSSION

Energetic variables of *A. andinus* from different localities are shown in Table 1. Measurements of body mass were taken

TABLE 1.—Geographic and seasonal energetic variables of *Abrothrix andinus* in different localities in the Andes Mountains. Each value represents a mean \pm SD.

Locality	m_b (g)	BMR ($\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$)	% ^a	C ($\text{ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot \text{°C}^{-1}$)	% ^b	T_b ($^{\circ}\text{C}$)	T_{lc} ($^{\circ}\text{C}$)	ΔT_m $^{\circ}\text{C}$	% ^c	Reference
Parinacota	22.3 \pm 2.06	1.82 \pm 0.17	115.7	0.144 \pm 0.020	68.1	36.8 \pm 2.06	24.0	12.6	170.0	This study
Río Coya	18.8 \pm 1.98	1.76 \pm 0.37	107.1	0.141 \pm 0.024	61.1	37.1 \pm 1.02	24.6	12.5	175.5	This study
Chiuichiu	19.7 \pm 1.69	1.93 \pm 0.12	118.9	0.143 \pm 0.028	63.4	37.0 \pm 0.62	23.4	13.5	187.4	This study
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Summer	34.9 \pm 2.9	1.77 \pm 0.20	125.8	0.150 \pm 0.011	88.6	37.7 \pm 1.2	25.9	11.8	141.9	Bozinovic et al. (1990)
Autumn	29.2 \pm 5.4	1.80 \pm 0.29	122.3	0.151 \pm 0.010	81.6	37.6 \pm 1.2	25.7	11.9	149.7	Bozinovic et al. (1990)
Winter	25.1 \pm 4.8	1.58 \pm 0.18	104.1	0.138 \pm 0.016	69.1	37.8 \pm 1.1	26.4	11.4	148.9	Bozinovic et al. (1990)
Spring	23.9 \pm 4.9	1.78 \pm 0.22	124.7	0.132 \pm 0.004	75.7	37.5 \pm 0.8	24.0	13.5	178.5	Bozinovic et al. (1990)

%^a = $\text{BMR}/3.42 m_b^{-0.25}$ (Kleiber, 1961); %^b = $\text{C}/1.00 m_b^{-0.50}$ (Morrison and Ryser, 1951); %^c = $(\Delta T_m = T_b - T_{lc})/3.42 m_b^{0.25}$ (McNab, 1979).

during the physiological records. We found significant differences in m_b among populations (Kruskal-Wallis test, $H = 7.638$, $d.f. = 18$, $P = 0.020$). Because all variables studied were allometric functions of body mass (Peters, 1983), and we found differences in body mass, we conducted analysis of mass-independent BMR, C and ΔT_m (i.e., deviations from allometric standard equations) among populations. However, differences were non-significant in mass-independent BMR values ($H = 2.197$, $d.f. = 36$, $P = 0.333$), in mass-independent C values ($H = 2.927$, $d.f. = 49$, $P = 0.231$), or in mass-independent ΔT_m values ($H = 2.224$, $d.f. = 36$, $P = 0.343$).

Classically, studies in comparative ecological physiology emphasize analyses of species as a unit. Little attention has been given to physiological variability between populations of the same species inhabiting different habitats within a geographic area. Because energetics of small mammals appears to correlate with animal-design features and characteristics of habitat, our goal was to determine the geographical and temporal standard energetics of *A. andinus* from different populations in a high-elevation Andean gradient differing in habitat characteristics.

Individuals from different populations that we studied showed, in general, higher mass-independent BMR and lower mass-independent C, with little intraspecific variation in the level at which T_b was regulated (Table 1). No evidence of torpor or natural hypothermia are known for *Abrothrix* (Bozinovic and Rosenmann, 1988).

The minimal temperature differential between body and ambient (ΔT_m) is equal to BMR/C ($^{\circ}\text{C}$) = $3.42 m_b^{0.25}$ (McNab, 1979). Thus, because the cost of continuous endothermy is higher at small body sizes and because the Andean mouse inhabits cool to cold environments, we predicted low mass-independent C values (high thermal insulation) coupled with high mass-independent BMR. We observed that ΔT_m values were, on average, 178% higher than expected (Ta-

ble 1). As a consequence, individuals from the three habitats were good thermoregulators, capable of maintaining a high mass-independent temperature differential, and able to endure cold temperatures during the night. In fact, at the locality of Coya (3,850 m above mean sea level), we used Sherman traps with cotton inside to capture individual small mammals during 3 nights with nocturnal ambient temperature of ca. -10°C . During that period, all eight *A. andinus* that were captured survived overnight inside the traps. However, only one of six sympatric *Phyllotis xanthopygus* survived overnight in the same trapping grids.

In the Andes Mountains in central Chile, Bozinovic et al. (1990) reported that *A. andinus* exhibited seasonal acclimatization with temporal changes in energy expenditure and energy conservation. In fact, body mass exhibited a significant decrease during winter. Body temperature and C did not show changes throughout the year; nevertheless, mass-independent C was lower during winter. The BMR also was always higher than expected (Table 1). As observed among populations of *A. andinus* in northern Chile, ΔT_m was higher than expected throughout the year (Table 1).

Based on our evidence we can conclude that *A. andinus* is characterized by well-regulated thermoregulation, a higher than expected BMR, and a low C that might be expected from their distribution in harsh thermal Andean environments. At present, we do not know if the "rigid endothermy" (sensu McNab, 1992) observed in this species is fixed genetically or represents thermal acclimatization to cold habitats. Previous studies indicate that *Abrothrix* at 520 m above mean sea level in central Chile (Mediterranean climate, mean annual temperature and precipitation = 13.9°C and 356 mm, respectively) also exhibited a rigid endothermy (Bozinovic and Rosenmann, 1988). These authors reported a BMR equivalent in *Abrothrix longipilis* ($m_b = 42$ g) of 101% of the expected rate according to Kleiber's (1961) relation, a C value

equivalent to 87% of the expected rate according to Morrison and Ryser's (1951) equation, and a ΔT_m equal to 23% higher than expected. Similarly, Bozinovic and Rosenmann (1988) documented a BMR in the sympatric *Abrothrix olivaceus* ($m_b = 27$ g) of 122% of the expected value according to Kleiber's (1961) relation, a C value equivalent to 80% according to Morrison and Ryser's (1951) equation, and a ΔT_m equal to 122%. This evidence suggests that energetics of *Abrothrix* do not vary in response to different climatic conditions, favoring the hypothesis that it is a fixed character probably reflecting a common ancestor of Andean origin or radiation along the Andes Mountains (Reig, 1987).

ACKNOWLEDGMENTS

We thank C. Cornelius and V. Olmos for their valuable assistance in field collection. Funded by a Fondo de Desarrollo Científico y Tecnológico FONDECYT 960011 from Programa Sectorial Biomas y Climas Terrestres y Marinos del Norte de Chile.

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Submitted 10 March 1998. Accepted 20 May 1998.

Associate Editor was C. Renn Tumlison.

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