ELSEVIER

CBP

A test of the thermal-stress and the cost-of-burrowing hypotheses among populations of the subterranean rodent *Spalacopus cyanus*

Francisco Bozinovic*, Mauricio J. Carter, Luis A. Ebensperger

Center for Advanced Studies in Ecology and Biodiversity and Departamento de Ecología, Facultad de Ciencias Biológicas,
Pontificia Universidad Católica de Chile, Santiago 6513677, Chile

Abstract

Subterranean mammals show lower than–allometrically expected–basal metabolic rates (BMR), and several competing hypotheses were suggested to explain how physical microenvironmental conditions and underground life affect subterranean mammalian energetics. Two of these are the thermal-stress and the cost-of-burrowing hypotheses. The thermal-stress hypothesis posits that a lower mass-independent BMR reduces overheating in burrows where convective and evaporative heat loss is low, whereas the cost-of-burrowing hypothesis states that a lower mass-independent BMR may compensate for the extremely high energy expenditure of digging during foraging activity. In this paper we tested both hypotheses at an intraspecific level. We compared seven populations of the subterranean rodent *Spalacopus cyanus* or cururo from different geographic localities with contrasting habitat conditions. We measured BMR and digging metabolic rate (DMR) through open flow respirometry. Our results support neither the thermal-stress nor the cost-of-burrowing hypothesis. Cururos from habitats with contrasting climatic and soil conditions exhibited similar BMR and DMR when measured under similar semi-natural conditions. It is possible that *S. cyanus* originated in Andean locations where it adapted to relatively hard soils. Later, when populations moved into coastal areas characterized by softer soils, they may have retained the original adaptation without further phenotypic changes.
© 2005 Elsevier Inc. All rights reserved.

Keywords: Subterranean mammals; Thermal stress; Cost-of-burrowing; Intraspecific energetics; Basal and digging metabolic rates

1. Introduction

The convergent evolution of subterranean forms of life among mammals is a fascinating and puzzling evolutionary phenomenon (Nevo, 1999). A subterranean existence has developed in several mammalian taxonomic orders, including marsupials, rodents, insectivores, and edentates (Nevo, 1999). Subterranean forms include species that live underground and only rarely come to the surface. Interestingly, subterranean mammals often exhibit convergent morphological features that include compact bodies, short tails and necks, microphthalmic eyes, large and powerful forefeet, pectoral girdles and associated muscles (Nevo, 1979, 1999).

Understanding and explaining the selective pressures underlying differences in metabolic rate within and across species has been a major topic among evolutionary physiological ecologists. Rates of metabolism have been linked to different biotic and abiotic factors as evidence of metabolic adaptation to different environments (Bozinovic, 1992; Spicer and Gaston, 1999; McNab, 2002). The abiotic microenvironment faced by subterranean mammals is considered to be relatively stable, humid, hypoxic and hypercapnic, and thermally constant (e.g., Rosenmann, 1959; McNab, 1966; Arieli, 1979; Contreras, 1983; see Nevo, 1999 for a review). Subterranean mammals must cope with the high energy costs of underground activity, including the interplay between digging and foraging (Ebensperger and Bozinovic, 2000). The observation that subterranean mammals show lower than–allometrically expected–basal metabolic rates (BMR) (McNab, 1979;

Contreras, 1983; Contreras and McNab, 1990; Lovegrove, 1986) has been related to an adaptation to decrease these energetic costs. Several competing hypotheses have been suggested to explain how physical microenvironmental conditions and underground life affect energetics of subterranean mammals. Two of these are the thermal-stress and the cost-of-burrowing hypotheses. The thermal-stress hypothesis posits that a lower mass-independent BMR reduces overheating in burrows where convective and evaporative water loss is low (see McNab, 1966, 1979; Contreras, 1983), whereas the cost-of-burrowing hypothesis states that a lower mass-independent BMR may compensate for the extremely high energy expenditure of digging during foraging activity (Vleck, 1979, 1981; but see Lovegrove and Wissell, 1988 for alternative ecological hypotheses such as the aridity-food distribution hypothesis).

Recently and through phylogenetic and conventional allometric analyses, White (2003) examined both hypotheses in approximately 100 species of subterranean and semi-subterranean species. This author concluded that mammalian species from mesic habitats support the thermal-stress hypothesis, but that species from arid habitats support the cost-of-burrowing hypothesis. The contrasting results concerning the effect of underground conditions on the variation of BMR across species is the basis on which we designed the present study to evaluate both hypotheses in an herbivorous subterranean rodent, the cururo (*Spalacopus cyanus*). Typically, studies in evolutionary and ecological physiology emphasize the analyses of species as the units of analysis. Nevertheless little attention has been paid to physiological variability across populations inhabiting different habitats within a region. Thus, because studies at the intraspecific level are critical to understand how differences in metabolic rate evolved and can be affected by environmental factors, we compared the standard and digging energetics of different populations of cururos living under different geographical conditions of soil hardness and environmental temperature.

The thermal-stress hypothesis would be supported by low metabolic rates and high digging rates of cururos in warmer habitats. On the other hand, the cost-of-burrowing hypothesis would be supported by low metabolic rates and high digging rates of cururos in habitats with hard to dig soils. Cururos are good study subjects as the species if found throughout a wide range of environmental conditions. Cururos are found from coastal to high altitude Andean sites, and its latitudinal distribution ranges from 27 to 35°S (Contreras et al., 1987). As expected, habitats occupied by these fossorial rodents range from alpine grasslands in the Andes to savannah in the valleys of central Chile, and to sand dunes and sandy grasslands on the coast (Torres-Mura and Contreras, 1998). In addition, cururos are social subterranean rodents in the family Octodontidae (Reig, 1970; Contreras et al., 1987; Begall and Gallardo, 2000; Urrejola et al., 2005). Cururo colonies maintain and expand an extensive system of tunnels that range from 36 to 720 m[2] (Begall and Gallardo, 2000). Morphology of cururos resembles that of other subterranean rodents, with short tail and ears, small eyes, strong forelimbs and long claws, and long and procumbent incisors (Torres-Mura and Contreras, 1998). Unpublished genetic analyses have revealed that Andean populations are different from the coastal ones, and suggest an Andean origin over a coastal one (J.C. Opazo, pers. comm.).

2. Material and methods

2.1. Study sites and animal husbandry

A total of seven sites from central Chile were sampled between November 2003 and March 2004 (Table 1, Fig. 1), corresponding to high Andean sites, Mediterranean areas in central Chile, and to low altitude areas near the semiarid coast. Andean sites included wetlands ("vegas") dominated by seasonal grasses and small alpine shrubs (Quintanilla, 1980; Cavieres et al., 2000). Habitat of cururos at low altitude sites corresponded to relatively open and semiarid areas of the Mediterranean matorral of central Chile (Gajardo, 1994; Gutiérrez et al., 1993). Mean annual temperatures of all sites

Table 1

Localities and habitat conditions among different studied populations of the subterranean Octodontid rodent *S. cyanus*, *n*=number of individuals studied

Locality and geographic location	*n*	Altitude (m)	Annual temperature[1] (°C)			Soil hardness[2] (kg m^{-2})	Climate
			Max	Mean	Min		
La Parva (33°19′S, 70°17′W)	9	2779.0	12.2	7.5	3.9	578,000±83,000[a]	Andean steppe
Lagunillas (33°36′S, 70°17′W)	5	2250.0	9.5	8.9	7.9	521,000±56,000[a]	Andean steppe
Huenteleuquen (31°33′S, 71°30′W)	4	137.0	21.9	20.6	19.4	649,000±47,000[c]	Semiarid
Los Molles (32°13′S, 71°30′W)	6	39.3	19.2	18.3	17.6	575,000±67,000[a]	Coastal Mediterranean
Ventana (32°46′S, 71°27′W)	6	31.0	18.9	14.4	10.6	576,000±75,000[a]	Coastal Mediterranean
La Serena (29°49′S, 71°16′W)	7	61.0	19.0	14.9	11.3	177,000±70,000[b]	Coastal semiarid
Valparaíso (33°04′S, 71°09′W)	6	213.0	18.9	14.4	10.6	550,000±113,000[a,c]	Central Mediterranean

[1] Source: Ministerio de Obras Públicas, Chile, Agroclimatological data for Latin America and the Caribbean (1985) and di Castri and Hajek (1976).

[2] Similar letters indicate no significant differences after a Tukey post hoc test.
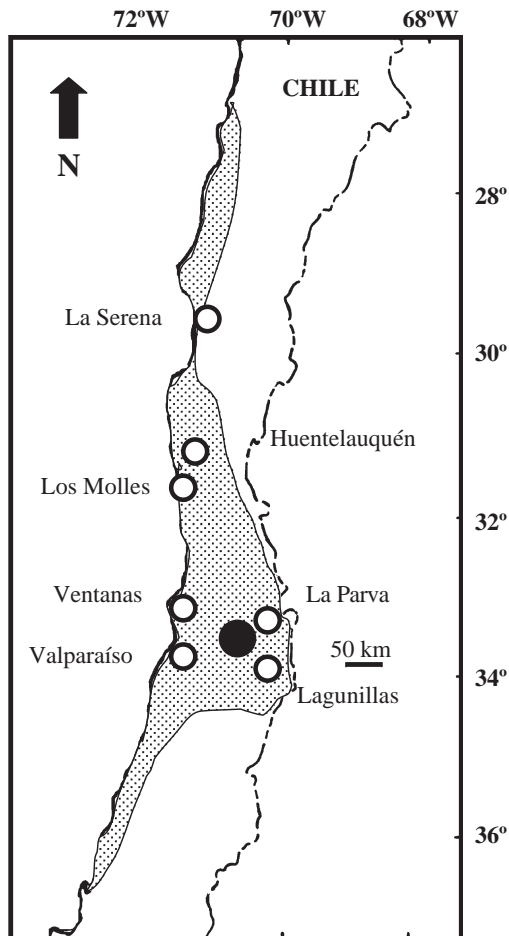
Fig. 1. Geographical distribution of *S. cyanus* (shaded area) and location of study sites (white circles). The city of Santiago (black circle) is also included as a reference. Distribution of *S. cyanus* follows Torres-Mura and Contreras (1998).

were obtained from the Agroclimatological Data for Latin America and the Caribbean (1985), di Castri and Hajek (1976), and Ministerio de Obras Públicas of Chile (see Table 1). Contreras (1983) reported a significant correlation between burrow and ambient temperature, thus air temperature was used as a proxy of habitat as well as microhabitat temperature.

At each site we recorded soil hardness with the use of a Langmann penetrometer (Lacey and Wieczorek, 2003). Soil penetrability, a measure of the force that must be exerted to penetrate soil to a given depth provides an indication of soil hardness. Hardness of soil was recorded at 1-m distances from freshly dug mounds, and encompassing the whole area where cururos were actively digging. At least 30 measurements per locality were obtained (Table 1).

A total of 43 cururos (25 males and 18 females) were caught with the use of padded leg traps. Traps made no damage to the animals, all of which were non-reproductive and looked totally healthy. Cururos were individually maintained in 30×40 cm aquaria provided with a 15-cm layer of loose soil from capture sites, with a photoperiod of LD=12:12 and ambient temperature set at 25 °C. Apples and carrots were provided ad libitum. Animals were kept under these conditions from approximately 10 days before metabolic measurements began.

2.2. Basal metabolic rate

Because our aim was to test for local adaptation, we kept all animals under the same conditions to avoid an acclimatization effect to each habitat condition and time of year. To determine BMR, rodents were fasted for 4 h before placement in 1000-ml steel chambers, at an ambient temperature (T_a) of 30.0 ± 0.5 °C that is within the thermoneutral zone for this species (Contreras, 1983). Although free-living cururos are clearly diurnal (Urrejola et al., 2005), they concentrate their activity during night hours when kept in captivity (Rezende et al., 2003). Thus, BMR was determined once per individual during early mornings according to the following protocol for measurements collected over the last 3-h period of minimum oxygen consumption (VO_2). BMR was measured in a computerized (Datacan V™) open-flow respirometry system (Sable Systems, Henderson, Nevada). The metabolic chamber received dried air at a rate of 800 ml min^{-1} from thermal-mass flow-controllers (Sierra Instruments™, Monterey, California), which ensured adequate mixing in the chamber. Air passed through CO_2-absorbent granules of Baralyme™ and Drierite™ before and after passing through the chamber and was monitored every 5 s by an Applied Electrochemistry O_2-analyzer, model S-3A/I (Ametek™, Pittsburgh, Pennsylvania). Oxygen consumption values were calculated using Eq. (4a) of Withers (1977: p. 122). We converted ml O_2 to J assuming 20.1 J ml^{-1} O_2.

2.3. Digging metabolic rate

To record digging metabolic rate (DMR), we constructed a set up modified from Vleck (1979) and Lovegrove (1989). Soil was collected from the Mediterranean habitats in central Chile and was maintained constant for all populations. The mean percentage of water content of soil was negligible.

Sixty centimeters of humid and sterilized soil was compacted to reach similar soil hardness ($120,022.5 \pm 281.2$ kg m^{-2}, $n=5$) into burrowing tubes (95 cm length and 7 cm diameter, volume=3.6 l) with a long iron (1.3 m) pole and then dried at 70 °C for 1 week. Burrowing tubes ($n=5$) were made of clear acrylic. After soil was dried, the test digging tube was placed inside another (equally transparent) tube that corresponded to the metabolic chamber measuring 106 cm length and 10 cm diameter with a volume of 8.3 l. Differences in diameter between tubes allowed a normal air flow through the metabolic chamber. To further ensure such normal air flow, 2 mm holes were drilled along the burrowing tube every 3 cm (Luna et al., 2002).

At the beginning of each measurement, single cururos were restricted to the end of the tube containing no soil by means of keeping the burrowing tube in a vertical position which prevented any digging. Once the system was stabilized and animals were quiet (ca. 1.5 h), the metabolic chamber was set horizontally and the experiment started. Experiments began near 19:00 to 20:00 h and ended ca. 08:00 h; during all this time, animals were left undisturbed with the lights off. Ambient temperature during measurements was 27 ± 1.0 °C. Instantaneous correction was performed on the data using the Sable system software (Bartholomew et al., 1981).

We videotaped all experiments with a Sony CCD-TR330 video camera placed in front of the burrowing tube and connected to a VCR in closed circuit. Videos allowed us to match episodes of digging activity with records of oxygen consumption. Digging distance and the amount of soil excavated from the burrowing tube were recorded at the end of each experiment. Soil was bolted to one end of the metabolic chamber and weighted. Oxygen consumption was measured as described for BMR records, but using a flow rate of 1000 ml min^{-1}. DMR was estimated when each cururo reached a steady state of VO_2 during burrowing. Each individual was measured only once.

2.4. Variables and statistics

Energetic cost of burrowing for each cururo was computed as the average of metabolic expenditure (per whole animal) recorded during episodes of digging. We also computed digging rate in J h^{-1} g-soil^{-1} as: (digging metabolic rate)×(soil removed)$^{-1}$ (Table 3). We examined the influence of habitat physical characteristics of each locality (mean ambient temperature and soil hardness), on BMR, DMR and digging rate with the use of ANCOVA, and with body mass (m_b) as a covariate. The post hoc Tukey test was used for multiple comparisons. Scaling relationships were computed between BMR, DMR and m_b through linear regressions and correlations from individual cururos. For comparative purposes, we also used the standard equation of BMR=$4.20m_b^{0.663}$ (ml O$_2$ h^{-1}), m_b in grams, for burrowing mammals (McNab, 1988). Reduction in statistical power of tests and unbalanced number of males and females across populations prevented us from entering gender as an independent predictor to our models, thus male and female subjects were pooled. Data fulfilled the assumptions of the tests. Results are reported as mean±1 standard deviation. All statistical analyses were performed using STATISTICA 6.0 (Statsoft: Statistica, 2001).

3. Results

Soil hardness as measured from soil compactability varied significantly across localities (Table 1, $F_{6,331}$=168.41, $P<0.0001$). The softer soil conditions were measured in the coastal site of La Serena, whereas the hardest conditions occurred in lowland and semiarid Huentelauquén. All other sites exhibited similar soil hardnesses (Table 1). As expected, previously available data indicated that ambient temperature was generally lower in Andean as compared with lowland coastal habitats (Table 1).

Body mass of cururos differed significantly among localities (Table 2, one-way ANOVA, $F_{6,36}$=9.221, $P<0.0001$) where animals inhabiting the Andes are larger than their counterparts from low altitude. Contrarily, neither basal metabolic rate (BMR) (Table 2, ANCOVA, $F_{6,35}$=1.139, $P=0.360$), or DMR (Table 2, ANCOVA, $F_{6,35}$=1.495, $P=0.209$) varied significantly among populations when m_b is controlled for. Power of all tests was higher than 99% (Zar, 1996).

Basal metabolic rate of all cururos was $73.7\pm11.3\%$ (N=43) of the expected values for standard burrowing root-eater mammals (McNab, 1988), and ranged from 53.2% to 83.9%. However, cururos from Andean habitats exhibited higher mass-independent BMRs than cururos from lowland habitats (82.7 ± 1.77 versus $68.3\pm12.3\%$), although the difference was not significant (Mann–Whitney U-test, Z=1.549, $P=0.121$). Neither BMR or DMR was correlated with altitude, but mass was correlated with altitude and BMR, and DMR were correlated with mass (Table 4).

After entering m_b as a covariate, both the distance burrowed and the amount of soil removed were significantly lower in Andean individuals from Lagunillas (Table 3, ANCOVA, $F_{6,35}$=2.923, P=0.02 for distance burrowed; and

Table 2

Energetic variables measured in the different populations of the subterranean Octodontid rodent *S. cyanus*

Locality	Body mass[1] (g)	BMR (kJ h^{-1})	%[2]	DMR (kJ h^{-1})	DMR/BMR
La Parva	121.5 ± 19.5^b	1.707 ± 0.366	83.9	3.656 ± 1.481	2.1
Lagunillas	105.1 ± 15.9^b	1.504 ± 0.253	81.4	4.538 ± 0.765	3.0
Huentelauquén	72.4 ± 10.9^a	0.767 ± 0.134	53.2	5.331 ± 3.297	6.9
Los Molles	93.0 ± 18.7^a	1.206 ± 0.484	70.8	6.033 ± 3.034	5.0
Ventana	86.1 ± 10.4^a	1.340 ± 0.216	82.7	2.784 ± 0.664	2.1
La Serena	70.6 ± 13.4^a	0.912 ± 0.299	64.2	4.375 ± 1.236	4.8
Valparaíso	89.9 ± 8.7^a	1.174 ± 0.141	70.4	3.253 ± 0.608	2.8

Sample sizes are provided in Table 1. Basal metabolic rate=BMR, digging metabolic rate=DMR.

[1] Similar letters indicate no significant differences after a Tukey post hoc test.

[2] Percentage of expected BMR based on McNab (1988) for burrowing root-eaters mammals-i.e., BMR=$4.20m_b^{0.663}$ (ml O$_2$ h^{-1}).

Table 3
Distance, energetic rate during digging and soil removed by *S. cyanus* during measurements of cost of digging

Population	Distance burrowed (cm)	Soil removed (kg)	Digging rate[1] (J h^{-1} g-soil^{-1})
La Parva	13.67±9.77[a]	0.65±0.47[a]	21.29±18.41
Lagunillas	6.80±3.42[b]	0.28±0.20[b]	48.78±27.84
Huentelauquén	22.80±18.85[a]	1.12±0.93[a]	8.40±6.28
Los Molles	27.08±14.91[a]	1.12±0.77[a]	16.92±22.60
Ventana	32.17±12.48[a]	1.63±0.55[a]	3.49±0.84
La Serena	27.71±6.94[a]	1.37±0.36[a]	3.98±0.68
Valparaíso	24.83±16.04[a]	1.01±0.73[a]	22.39±38.04

Sample sizes are provided in Table 1. Similar letters indicate non-significant differences after a Tukey post hoc test.

[1] DMR (soil removed)$^{-1}$.

$F_{6,35}$=3.371, P=0.009 for soil removed). Nevertheless, the energetic cost of removing 1 g of soil did not vary across populations (Table 3, ANCOVA, $F_{6,35}$=2.03, P=0.09).

A significant scaling relationship was found between BMR, DMR and m_b (Fig. 2). The allometric equations calculated for individual cururos were:

$$\text{BMR } (\text{kJ h}^{-1}) = 0.01 \ m_b^{1.13\pm0.14}$$

$$r^2 = 0.599, F_{1,41} = 61.419, P \leq 0.0001 \qquad (1)$$

$$\text{DMR } (\text{kJ h}^{-1}) = 0.23 \ m_b^{0.74\pm0.18}$$

$$r^2 = 0.276, F_{1,41} = 15.614, P = 0.0003 \qquad (2)$$

After performing an ANCOVA, a test of parallelism of regression lines revealed that both slopes were undistinguishable ($F_{2,14}$=1.681, P=0.09) while intercepts did differ. In addition, the ratio DMR/BMR was not constant and varied among populations from 2.1 to 6.9, with a mean of 3.81±1.8 (Table 2). When we used the residuals of BMR and DMR to remove the influence of m_b, we detected no statistical correlation between these variables (r=0.03, P=0.862).

4. Discussion

The thermal-stress hypothesis states that a lower mass-independent BMR will reduce the risk of overheating when digging in underground burrow microhabitats (McNab, 1966, 1979; Contreras, 1983). If so, subterranean animals should reduce their metabolic rates and increase their digging rate when in warmer habitats. Alternatively, the cost-of-burrowing hypothesis posits that subterranean mammals exhibit a lower mass-independent BMR to compensate for the extremely high energy demands during digging activity (Vleck, 1979, 1981). This hypothesis predicts low metabolic rates and high digging rates in animals inhabiting hard soils. A recent comparison across species revealed conflicting results between these two variables. BMRs of large (>77 g) fossorial (i.e., truly subterranean) mammals from mesic and arid habitats are not different from BMR of their semi-subterranean (i.e., less adapted to digging) counterparts despite expected differences in their foraging costs, a result consistent with the thermal-stress hypothesis (White, 2003). On the other hand, however, small (<77 g) fossorial mammals from arid habitats were found to have lower BMRs than their similarly sized but semi-subterranean counterparts, a result consistent with the cost-of-burrowing hypothesis (White, 2003). These results led White (2003) to conclude that both hypotheses are not mutually exclusive. Note, however, that small mammals from arid habitats also may decrease BMR to cope with a limited supply of food resources (Du Toit et al., 1985; Lovegrove and Wissell, 1988)).

In this paper we tested the thermal-stress and the cost-of-burrowing hypotheses at an intraspecific level. We compared seven populations of the subterranean rodent *S. cynaus* from different geographic localities with contrasting habitat conditions. We did not examine thermal conductance across populations (McNab, 1966, 1979), but our results do not support the thermal-stress, or the cost-of-burrowing hypothesis. Cururos from habitats with contrasting climatic and soil conditions exhibited similar BMR, DMR, and digging rates when measured under similar semi-natural situations.

As pointed our by Spicer and Gaston (1999), one key question in studies of physiological diversity is how well do between-species patterns in physiological diversity predict patterns across populations? Apparently, the energetics of fossorial species observed at interspecific level does not resemble the energetic patterns at intraspecific level. Future studies should establish not only the generality of our results, but also the mechanistic basis that could account for these patterns at and between different hierarchical-physiological levels.

Low metabolic rates of subterranean small mammals have also been linked to an adaptation to the low pO_2 of underground environments (Nevo, 1999 and references therein), which if correct would lead to a lower basal rate at
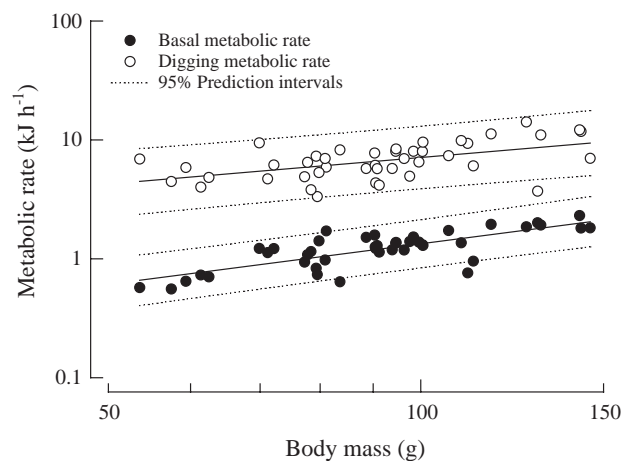

Fig. 2. Double logarithmic relationships between body mass, basal and digging metabolic rate in the subterranean rodent *S. cyanus* from different habitats. Each point represents one individual.

Table 4
Correlation among residuals of basal metabolic rate (BMR), digging metabolic rate (DMR) and body mass with abiotic variables from different habitats of *S. cyanus* (see Table 1)

	Mean ambient temperature (°C)	Soil hardness (kg m^{-2})	Altitude (m)
Residuals of BMR	$r=0.213$; $P=0.169$	$r=0.01$; $P=0.962$	$r=0.07$; $P=0.634$
Residuals of DMR	$r=0.01$; $P=0.928$	$r=0.02$; $P=0.889$	$r=0.06$; $P=0.697$
Body mass (g)	$r=-0.36$; $P=0.01$	$r=0.35$; $P=0.02$	$r=-0.69$; $P=0.001$

Residuals were obtained from the regressions of Fig. 1.

high altitude. Our data did not support this possibility, which agrees with Contreras (1983) who demonstrated that cururos from high- and low-altitude do not differ in their VO₂ values under varying conditions of pO_2. Nevertheless, the use of species of the genus *Ctenomys* might be more appropriate to test this hypothesis further as subterranean ctenomyids include Andean species living above 3500 m of altitude.

We concur with White (2003) in that the thermal-stress hypothesis neglects thermoregulatory adjustments through behavior. Certainly, ground-dwelling small mammals display daily and seasonal patterns of activity time (e.g., Chappell and Bartholomew, 1981a,b; Kenagy et al., 2002). Cururos indeed adjust their surface activity according to diurnal and seasonal changes in environmental temperature under field conditions (Rezende et al., 2003; Urrejola et al., 2005). Animals decrease their surface activity (digging, foraging, and look up) during the warmest time of day (from midday to early afternoon) in summer, but do not do so during wintertime (Rezende et al., 2003). Thus, cururos might cope with thermal constraints inside burrows through shifting their activity according to changes in environmental temperature. Indeed, field animals typically interrupt their underground digging to remain looking up their burrow entrances, a behavior that may have some thermoregulatory value. Other subterranean rodents seem to daily adjust activity to avoid extreme thermal conditions (Benedix, 1994).

Bacigalupe et al. (2002) studied morphological and functional variations in the digging apparatus of coastal and Andean populations of *S. cyanus* inhabiting contrasting conditions of soil hardness. These authors found minimal morphological differentiation between populations in 10 cranial and dental variables. Contrary to expectations, however, animals from habitats with soft soils exhibited larger incisor resistance than cururos from habitats with hard soils. Cururos use their incisors to dig (Reig, 1970, our unpublished data), which resembles the behavior of closely related *Octodon degus* (Ebensperger and Bozinovic, 2000) and *Ctenomys* species when burrowing in hard soils (Giannoni et al., 1996; Vassallo, 1998). These morphological analyses coupled to our energetics data suggest that soil hardness did not represent an important selective factor for subterranean cururos (Bacigalupe et al., 2002), at least at the intraspecific level.

These results contradict the long standing hypothesis and data showing that burrowing is energetically expensive (Ebensperger and Bozinovic, 2000), and that digging cost is a major force influencing anatomy, physiology, and behavior of burrowing organisms so as to minimize these costs. On average, individual cururos increase their energy expenditure 3.8 (range=2.1 to 6.9) times their resting level when digging. This ratio seems low when compared to values of other fossorial rodents tested under dry soil conditions, including *Cryptomys damarensis* (ratio=4.5, Lovegrove, 1989), *Heterocephalus glaber* (ratio=4.3; Lovegrove, 1989), and especially if compared with the semi-subterranean but, phylogenetically more related, *O. degus* (ratio=4.8, Ebensperger and Bozinovic, 2000). Future studies might be needed to assess if digging rate varies with hypoxic or hypercapnic conditions, attributes assumed to characterize the burrows of most subterranean mammals. We predict digging costs of cururos under natural conditions should be high, particularly in areas with more rainfalls such as Andean areas. In general, the DMR to BMR ratios computed for animals digging in damp soil are higher compared with animals burrowing in dry soils (i.e., *Cryptomys*, *Heterocephalus*, *Octodon*; Ebensperger and Bozinovic, 2000). Only *Ctenomys talarum* exhibits particularly low costs when digging in damp soils as measured from DMR/BMR ratios (ratio=2.85, Luna et al., 2002).

No correlation was detected between residuals of BMR, DMR and mean ambient temperature, soil hardness and altitude (Table 4). Nevertheless, body mass was significantly correlated with habitat variables (Table 4). Indeed, large-sized cururos inhabit low temperatures, harder soils and high altitudes. These correlations suggest a size-selection process on body mass but not on mass-independent metabolism. Specifically, Fig. 3 described a negative correlation between body mass, mean annual
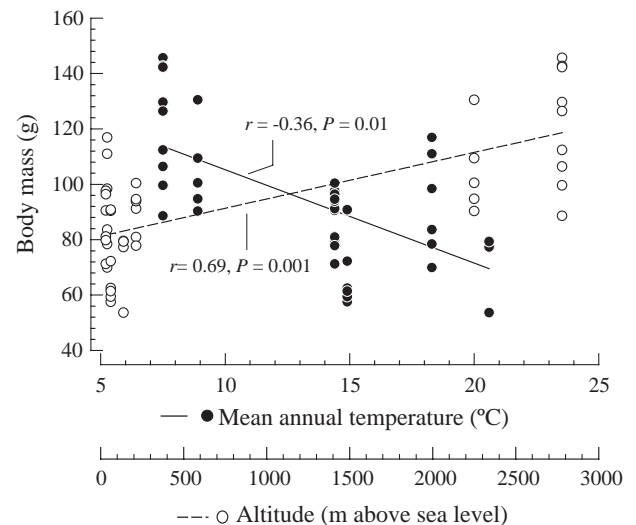

Fig. 3. Correlations between mean annual temperature, altitude and body mass in the subterranean rodent *S. cyanus* from different habitats (see Table 4 for statistical details). Each point represents one individual.

temperature and altitude at each locality. For example, a significant correlation between body mass and temperature may be due to the direct effects of selection on body mass (Table 4). Our results suggest that the thermal environment affects body mass to a higher degree than mass-independent metabolic rate, supporting geographic or climatic rules such as the Bergmann's rule (see Spicer and Gaston, 1999 for a review). It is possible that *S. cyanus* originated in Andean locations where it adapted to relatively low temperatures and hard soils. Later, when populations moved into coastal areas characterized by sandy (softer) soils and higher temperatures, they may have retained the original adaptation without further mass-independent metabolic rate. Evolutionary changes in body mass could have important effects on the selective pressures acting on metabolic rates, and this factor should be taken into account in future studies dealing with the evolution of metabolic rates.

Recently, Hildner and Soulé (2004) reported that differences in DMR among six populations and three subspecies of pocket gophers (*Thomomys bottae*) are linked to differences in genetic variability—i.e., pocket gophers from genetically less variable populations exhibit higher DMR values than pocket gophers from populations with high genetic variability. If these results are general, we predict that the energetically similar populations of *S. cyanus* reported in our study should exhibit relatively similar population genetic variability, a prediction not upheld by current genetic analyses of cururo populations (J.C. Opazo, pers. com.).

Acknowledgements

References

Agroclimatological data for Latin America and the Caribbean, 1985. Food and Agriculture Organization of the United Nations. FAO Plant Production and Protection Series. Number 24.

Arieli, R., 1979. The atmospheric environment of the fossorial mole rat (*Spalax ehrenbergi*), effects of season, soil texture, rain, temperature and activity. Comp. Biochem. Physiol., A 63, 569–575.

Bacigalupe, L.D., Iriarte-Díaz, J., Bozinovic, F., 2002. Functional morphology and geographic variation in the digging apparatus of cururos (*Spalacopus cyanus*: Octodontidae). J. Mamm. 83, 145–152.

Bartholomew, G.A., Vleck, D., Vleck, C.M., 1981. Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in sphingid and saturniid moths. J. Exp. Biol. 90, 7–32.

Begall, S., Gallardo, M.H., 2000. *Spalacopus cyanus* (Rodentia: Octodontidae): an extremist in tunnel constructing and food storing among subterranean mammals. J. Zool. (London) 251, 53–60.

Benedix, J.H., 1994. A predictable pattern of daily activity by the pocket gopher *Geomys bursarius*. Anim. Behav. 48, 501–509.

Bozinovic, F., 1992. Scaling basal and maximum metabolic rate in rodents and the aerobic capacity model for the evolution of endothermy. Physiol. Zool. 65, 921–932.

Cavieres, L.A., Peñalosa, A., Arroyo, M.K., 2000. Altitudinal vegetation belts in the high Andes of central Chile (33°S). Rev. Chil. Hist. Nat. 73, 331–344.

Chappell, M.A., Bartholomew, G.A., 1981a. Standard operative temperatures and thermal energetics of the antelope ground squirrel *Ammospermophilus leucurus*. Physiol. Zool. 54, 81–93.

Chappell, M.A., Bartholomew, G.A., 1981b. Activity and thermoregulation of the antelope ground squirrel *Ammospermophilus leucurus* in winter and summer. Physiol. Zool. 54, 215–223.

Contreras, L.C., 1983. Physiological ecology of fossorial mammals: a comparative study. PhD thesis, University of Florida, Gainesville.

Contreras, L.C., McNab, B.K., 1990. Thermoregulation and energetics in subterranean mammals. In: Nevo, E., Reig, O.A. (Eds.), Evolution of Subterranean Mammals at the Organismal and Molecular Levels. Wiley-Liss, New York, pp. 231–250.

Contreras, L.C., Torres-Mura, J.C., Yánez, J.L., 1987. Biogeography of Octodontid rodents: an eco-evolutionary hypothesis. Fieldiana, Zool 39, 401–411.

di Castri, F., Hajek, E., 1976. Bioclimatología de Chile. Pontificia Universidad Católica de Chile, Santiago, Chile.

Du Toit, J.T., Jarvis, J.U.M., Louw, G.N., 1985. Nutrition and burrowing energetics of the Cape mole-rat *Georychus capensis*. Oecologia 66, 81–87.

Ebensperger, L.A., Bozinovic, F., 2000. Energetics and burrowing behaviour in the semifossorial degu *Octodon degus* (Rodentia: Octodontidae). J. Zool. (London) 252, 179–186.

Gajardo, R., 1994. La Vegetación Natural de Chile: Clasificación y Distribución Geográfica. Editorial Universitaria, Santiago. 165 pp.

Giannoni, S.M., Borghi, C.E., Roig, V.G., 1996. The burrowing behavior of *Ctenomys eremophilus* (Rodentia, Ctenomyidae) in relation with substrate hardness. Mastozool. Neotrop. 3, 161–170.

Gutiérrez, J.R., Meserve, P.L., Jaksic, F.M., Contreras, L.C., Herrera, S., Vásquez, H., 1993. Structure and dynamics of vegetation in a Chilean arid thornscrub community. Acta Oecol. 14, 271–285.

Hildner, K.K., Soulé, M.E., 2004. Relationships between the energetic cost of burrowing and genetic variability among populations of the pocket gopher, *T. bottae*: does physiological fitness correlate with genetic variability? J. Exp. Biol. 207, 2221–2227.

Kenagy, G.J., Nespolo, R.F., Vásquez, R.A., Bozinovic, F., 2002. Daily and seasonal limits of time and temperature to activity of degus. Rev. Chil. Hist. Nat. 75, 567–581.

Lacey, E.A., Wieczorek, J.R., 2003. Ecology of sociality in rodents: a Ctenomyid perspective. J. Mammal. 84, 1198–1211.

Lovegrove, B.G., 1986. The metabolism of social subterranean rodents: adaptation to aridity. Oecologia 69, 551–555.

Lovegrove, B.G., 1989. The cost of burrowing by the social mole rats (Bathyergidae) *Cryptomys damarensis* and *Heterocephalus glaber*: the role of soil moisture. Physiol. Zool. 62, 449–469.

Lovegrove, B.G., Wissell, C., 1988. Sociality in mole rats: metabolic scaling and the role of risk sensitivity. Oecologia 74, 600–606.

Luna, F., Antinuchi, C.D., Busch, C., 2002. Digging energetics in the South American rodent *Ctenomys talarum* (Rodentia Ctenomyidae). Can. J. Zool. 80, 2144–2149.

McNab, B.K., 1966. The metabolism of fossorial rodents: a study of convergence. Ecology 47, 370–380.

McNab, B.K., 1979. The influence of body size on the energetics and distribution of fossorial and burrowing mammals. Ecology 60, 1010–1021.

McNab, B.K., 1988. Complications inherent in scaling the basal rate of metabolism in mammals. Q. Rev. Biol. 63, 25–54.

McNab, B.K., 2002. The Physiological Ecology of Vertebrates. A View from Energetics. Comstock Publishing Associates, Ithaca.

Nevo, E., 1979. Adaptive convergence and divergence of subterranean mammals. Ann. Rev. Ecolog. Syst. 10, 269–308.

Nevo, E., 1999. Mosaic Evolution of Subterranean Mammals: Regression, Progression and Global Convergence. Oxford University Press, Oxford, UK.

Quintanilla, V., 1980. Observaciones fitogeográficas en la alta cordillera de Santiago. Rev. Geogr. Chile 24, 1–14.

Reig, O.A., 1970. Ecological notes on the fossorial octodont rodent *Spalacopus cyanus* (Molina). J. Mammal. 51, 592–601.

Rezende, E.L., Cortés, A., Bacigalupe, L.D., Nespolo, R.F., Bozinovic, F., 2003. Ambient temperature limits above-ground activity of the subterranean rodent *Spalacopus cyanus*. J. Arid Environ. 55, 63–74.

Rosenmann, M.A., 1959. Ctenomys fulvus Philippi; su hábitat. Invest. Zool. Chil. 5, 217–220.

Spicer, J.I., Gaston, K.J., 1999. Physiological Diversity and its Ecological Implications. Blackwell Science, Blackwell.

Statistica, 2001. STATISTICA (Quick Reference) for the Windows Operating System. StatSoft, Inc., Tulsa, Oklahoma.

Torres-Mura, J.C., Contreras, L.C., 1998. *Spalacopus cyanus*. Mamm. Species 594, 1–5.

Urrejola, D., Lacey, E.A., Wieczorek, J.R., Ebensperger, L.A., 2005. Daily activity patterns of free-living cururos (*Spalacopus cyanus*). J. Mammal. 86.

Vassallo, A.I., 1998. Functional morphology, comparative behaviour, and adaptation in two sympatric subterranean rodent genus *Ctenomys* (Caviomorpha: Octodontidae). J. Zool. (London) 244, 415–427.

Vleck, D., 1979. The energy cost of burrowing by the pocket gopher, *Thomomys bottae*. Physiol. Zool. 52, 122–136.

Vleck, D., 1981. Burrow structure and foraging costs in the fossorial rodent, *Thomomys bottae*. Oecologia 49, 391–396.

White, C.R., 2003. The influence of foraging mode and arid adaptation on the basal metabolic rates of burrowing mammals. Physiol. Biochem. Zool. 76, 122–134.

Withers, P.C., 1977. Measurements of VO_2, VCO_2, and evaporative water loss with a flow through mask. J. Appl. Physiol. 42, 120–123.

Zar, J.H., 1996. Biostatistical Analysis, Third edition. Prentice Hall, Upper Saddle River, NJ.