

Cost of foraging in the subterranean rodent *Ctenomys talarum*: effect of soil hardness

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Abstract: Subterranean burrows provide inhabitants with shelter, a relatively stable thermal environment, and potentially access to food resources. However, one cost of living in such burrows is the energetically expensive mode of locomotion. Soil hardness and the physiological capabilities of animals are likely important factors that affect the cost of burrow construction, and hence, distribution of burrows. We assessed the effect of soil hardness on the cost of digging by captive individual *Ctenomys talarum* Thomas, 1898 in soft soils. Digging metabolic rate (DMR) was higher in harder soil than in softer soil ($408.30 \pm 51.35 \text{ mL O}_2\text{-h}^{-1}$ vs. $267.59 \pm 20.97 \text{ mL O}_2\text{-h}^{-1}$, respectively). In *C. talarum*, a higher soil hardness augments DMR by increasing, in terms of the cost of burrowing model, the costs of shearing and of pushing the removed soil. Additionally, these costs differ between *C. talarum* and other subterranean species (e.g., *Thomomys bottae* (Eydoux and Gervais, 1836)), depending on soil hardness and digging mode. Thus, the relationship between digging cost and soil hardness appears to be one of the most important factors that affect burrowing efficiency in subterranean rodents.

Résumé : Les terriers souterrains fournissent à leurs occupants le gîte, un environnement thermique relativement stable et un accès potentiel à des ressources alimentaires. Cependant, le mode de locomotion à coût énergétique relativement élevé est l'un des prix du logement dans ces terriers. La dureté du sol et les capacités physiologiques des animaux sont vraisemblablement des facteurs importants qui affectent le coût de construction des terriers et, par conséquent, leur répartition. Nous évaluons l'effet de la dureté du sol sur le coût du creusage chez des individus captifs de *Ctenomys talarum* Thomas, 1898 dans des sols mous. Le taux métabolique durant le creusage (DMR) est plus élevé dans les sols durs que dans les sols plus mous ($408,30 \pm 51,35 \text{ mL O}_2\text{-h}^{-1}$ vs. $267,59 \pm 20,97 \text{ mL O}_2\text{-h}^{-1}$). Dans un modèle du coût du creusage chez *C. talarum*, une dureté accrue du sol augmente DMR en accroissant le coût du détachement de la terre et du déplacement du sol enlevé. De plus, ces coûts ne sont pas les mêmes chez *C. talarum* que chez d'autres animaux hypogés (par ex., chez *Thomomys bottae* (Eydoux et Gervais, 1836)) en fonction de la dureté du sol et du mode de creusage. Ainsi la relation entre le coût du creusage et la dureté du sol semble être l'un des facteurs les plus importants affectant l'efficacité du creusage des terriers chez les rongeurs hypogés.

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Introduction

Decisions about locomotion are part of many fitness-related behaviors, such as foraging, predator avoidance, and physiological characteristics, that include mechanical work and energy budget (Swingland and Greenwood 1983; Djawdan and Garland 1988; Garland et al. 1988; Kenagy and Hoyt 1989; Houston 1992). To balance conflicting demands for food and for safety from predation, feeding animals can vary the amount of time that they devote to harvesting patches, which vary in predation risk and feeding rates, or can use vigilance to trade off food and safety while feeding from a food patch (Brown 1999). For example, in *Octodon degu* (Molina, 1782), the proportion of time devoted to pausing behavior and vigilance across habitats has been discussed as evidence that this species perceives higher predation risk in open areas and that this

flexible movement behavior reflects an adaptive antipredator response (Vásquez et al. 2002)

Regarding mechanical work and energy cost of movements, body size has been proposed as a main factor affecting maximal locomotor performance in mammals. Numerous factors associated with the mechanics, energetics, and storage of elastic energy during locomotion change with body size (Jones and Lindstedt 1993). In this sense, maximal aerobic capacity is allometrically related to body size and is limited by some step in oxygen transport (Jones and Lindstedt 1993). Although larger mammals seem to have more efficient muscles for movement (Alexander 2005), some small mammals, which have carried out highly energetic muscular work in hypoxic environments, have physiological adaptations that improve oxygen transport. Such is the case for subterranean rodents that improve oxygen transport by high hemoglobin–oxygen affinity or by having higher quantities of small red blood cells (Busch 1987)

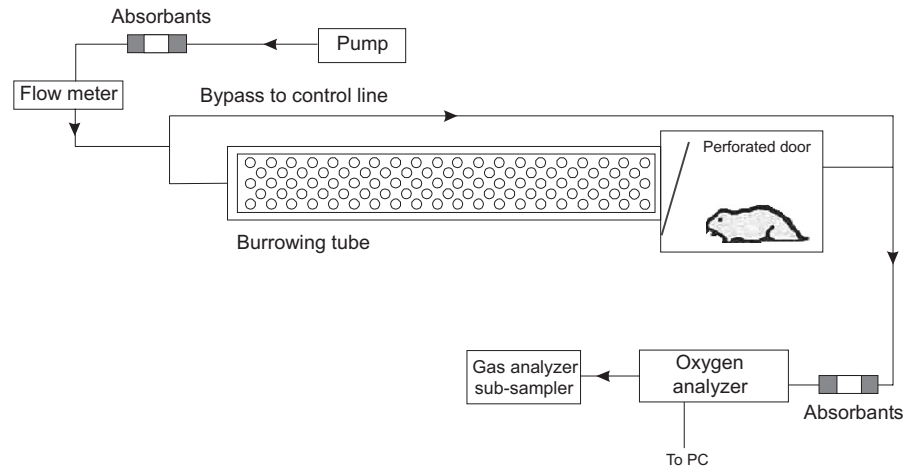
Although movements underground are expensive (Vleck 1979; du Toit et al. 1985; Lovegrove 1989; Luna et al. 2002), subterranean burrows provide shelter, a relatively stable thermal environment, and access to food resources (Nevo 1999). Moreover, cost of movements underground can be augmented also, because primary productivity is usually related to soil type, and hence, poor quality or quantity of food items available underground may force the extension

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Fig. 1. Respirometry system used to measure the oxygen consumption of *Ctenomys talarum* during digging. Absorbants are IQB[®] (CO₂ absorbent) and Silica Gel (water scrubber). Drawn not to scale.



of the burrow in random directions in search of or to gain access to food resources (Buffenstein 2000).

Soil hardness and the physiological capabilities of animals are likely the most important factors affecting the cost of burrow construction. Increases in soil hardness should affect daily energy balance directly by increasing burrowing costs (Vleck 1979), or indirectly by animals consuming poor-quality food items associated with low primary productivity in harder soils (Vleck 1981; Andersen 1982; Perissinotti 2003). Vleck (1979) examined the effect of soil hardness on the cost of digging by Botta's pocket gophers (*Thomomys bottae* (Eyedoux and Gervais, 1836)) and he found that the energy used in burrow construction could be partitioned into energy used to shear soil loose and energy used to push loosened soil out of the tunnel. Thus, digging efficiency can be evaluated by these components.

Talas tuco-tucos (*Ctenomys talarum* Thomas, 1898) occur in coastal grasslands in Argentina (Woods 1984). Along the Atlantic coast, two discrete populations are recognized (Reig et al. 1990); the northern population lives in soft soils (gravely sand, Mar de Cobo locality), whereas the southern population lives in hard soils (sandy loam, Necochea locality). Like Botta's pocket gophers, tuco-tucos construct tunnels parallel to the soil surface (Antinuchi and Busch 1992). However, tuco-tucos forage differently than Botta's pocket gophers in that the former feed mainly on aerial plants, whereas the latter consume roots underground (Comparatore et al. 1995). Thus, tuco-tucos might not be as confined to subterranean life as Botta's pocket gophers (see Luna and Antinuchi 2003), and burrowing decisions of tuco-tucos may be less affected by soil primary productivity than those of Botta's pocket gophers.

The relationship among soil hardness, foraging mode, and plant productivity could determine a particular digging cost for each subterranean species in a given environment. In this study, we examined the effect of soil hardness on digging cost in *C. talarum* individuals living permanently in soft soils. Given the uncompromising underground life of *C. talarum* compared with the life of strictly subterranean rodents, we expected that digging metabolic rate (DMR) would be greater than that observed in strictly subterranean species, such as *T. bottae*, in harder soils.

Materials and methods

Study animals

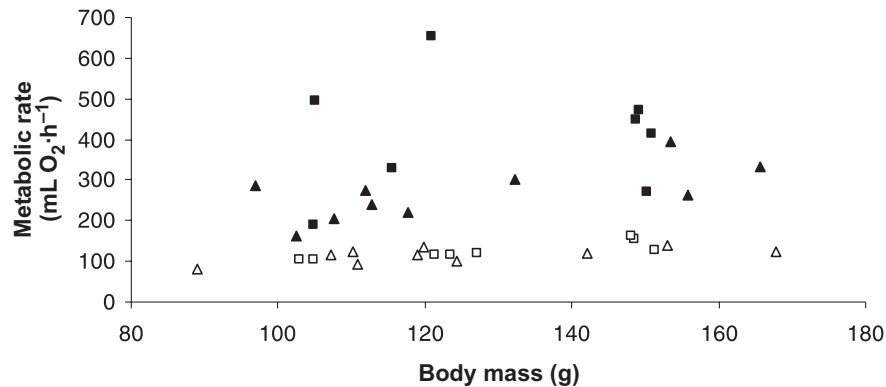
Animals of both sexes (9 males and 9 females) were live-trapped in Mar de Cobo (37°45'S, 57°56'W; Buenos Aires Province, Argentina). They were taken to the laboratory and housed in individual cages (0.30 m × 0.40 m × 0.25 m) with wood shavings as nesting material. The animal room was kept at 24 ± 1 °C and the photoperiod was 12 h light : 12 h dark (lights on at 0700). Animals were fed mixed native grasses, carrots, lettuce, corn, alfalfa, and sunflower seeds ad libitum. Water was not provided because *C. talarum* do not drink free water (Zenuto et al. 2001). The metabolic rate of each individual was measured once in each soil condition to estimate both DMR and resting metabolic rate (RMR).

Soil was collected in both Mar de Cobo (gravely sand) and Necochea (sandy loam; 38°37'S, 58°50'W; Buenos Aires Province, Argentina), near where the animals were known to occur, using a steel tube (0.11 m diameter, ~1.1 m long). We dug down to the mean burrow depth (0.20 m below ground) and then ran the steel tube horizontally to extract 1 m of soil sample. Each cylinder of soil was transposed to a PVC tube of the same diameter and carried to the laboratory. This procedure allowed us to maintain the same properties of the intact soil that was verified in the natural habitat (Antinuchi and Busch 1992; Luna et al. 2002). Soil hardness was estimated as the force that must be exerted to penetrate soil to a given depth, using a penetrometer (Malizia et al. 1991).

Oxygen consumption measurements

Oxygen consumption was measured using a computerized positive-pressure open-flow respirometry system (Sable System, Henderson, Nevada). Digging and resting chambers were equivalent to those described by Luna et al. (2002) and Luna and Antinuchi (2006). In brief, the digging chamber system consisted of a cube-shaped acrylic soil collector attached to an acrylic tube. A perforated tube containing the soil extracted in the field was placed inside the acrylic tube, leaving an air space between the perforated tube and the outer tube to permit airflow through the system (total air

Fig. 2. Metabolic rate during digging and resting related to body mass in *C. talarum* in soft and hard soils. Triangles represent soft soil, squares represent hard soil, solid symbols represent the digging metabolic rate, and open symbols represent the resting metabolic rate.



volume 19.17 L). A metallic perforated door separated the cube-shaped acrylic soil collector and the acrylic tube (Fig. 1). A cylindrical chamber was used to estimate RMR of *C. talarum* (total volume 1.84 L).

Digging chamber received air at 3 L·min⁻¹ from a flow-meter (Cole-Parmer Instrument Company, Vernon Hills, Illinois) and the resting chamber received air at 1 L·min⁻¹ from a mass flow controller (Sierra Instruments, Monterey, California). In both cases, air passed through a CO₂ absorbent (IQB®) and water scrubber (Silica Gel) before and after passing through the chamber. Excurrent air from both chambers was subsampled at 180 ± 10 mL·min⁻¹ and oxygen consumption was obtained from an Oxygen Analyzer FC-1B every 0.5 s by a Datacan V PC program (Sable System, Henderson, Nevada).

To permit a complete mixing of the inlet air, the digging chamber was left for at least 35 min to equilibrate (calculated from Lasiewski et al. 1966). After equilibrium had been reached, we opened the perforated door of the digging chamber and the *C. talarum* usually began burrowing within 10 min of release until it had reached the opposite end of the chamber. Individual digging experiments lasted ~55–65 min. Data were discarded and the trial repeated if the individual stopped digging and remained inactive in the respirometry system. Each individual was measured once in each soil condition to estimate both DMR and RMR. Oxygen consumption values were calculated using eq. 4a of Withers (1977). DMR was estimated for each individual as the mean value of the plateau of oxygen consumption. RMR was measured as the lowest 5 min steady-state values of the last 30 min of a 90 min trial. An equivalent of 19.94 J·(mL O₂)⁻¹ was used to convert oxygen consumption into values of energy consumption (Vleck 1979). Oxygen consumption of soil microfauna was negligible. Baseline of the respirometry system was set at 20.95% oxygen before the beginning of each experimental trial.

To examine the effect of soil hardness on DMR, we used two soil types in the respirometry system: one extracted from Mar de Cobo and the other from Necochea. After each burrowing trial we determined the mass of soil removed by the individual, dried the soil sample at 60 °C to constant mass, and calculated the percent moisture. Average burrowing speed (BS) was estimated as the total length burrowed over the total time expended. In each burrowing trial,

the net cost of transport was calculated as the slope of the DMR/BS regression (Taylor et al. 1970).

Data were evaluated in terms of Vleck's (1979) cost of burrowing model, which divides the cost of constructing a burrow into the costs of shearing and of pushing the soil out of the tunnel. The model is a second-order polynomial equation:

$$E_{\text{seg}}/M_{\text{soil}} = K_s(S) + 0.5K_p(S)^2$$

where E_{seg} is the energy cost of constructing a burrow segment of length S , K_s is the energy cost of shearing 1 g of soil, K_p is the energy cost of pushing 1 g of soil 100 cm, and M_{soil} is the mass of soil excavated per distance burrowed. E_{seg} was estimated from the total oxygen consumption at several different burrow lengths during each experiment. The K_s and K_p constants were determined by fitting the previous equation to the observed values of E_{seg} of individuals for each soil condition.

Statistics

All values are means ± SE. Student's t tests were used to test the null hypotheses that soil hardness and moisture content did not differ between soil types, and that mean body mass did not differ between sexes. ANCOVA was used to test the null hypothesis that there were no differences in DMR or RMR between sexes or soil conditions. Body mass was used as a covariate in the ANCOVA analysis.

Because the same individuals were used to estimate both DMR and RMR, a repeated-measures ANOVA was used to test the null hypothesis that there was no difference in mass-specific DMR and RMR between soil type and sexes. Between-subject factors were soil type and sex, and within-treatment factors were metabolic rates (digging and resting). After metabolic rate analyses were performed, data on BS from both sexes were pooled and a Student's t test was used to test the null hypotheses that there were no differences in this variable between soil conditions. ANCOVA was used to evaluate differences in slope and y intercept of the relationship between DMR and BS for both soil types. The least-squares method was used to estimate the regression coefficients (Zar 1984) of the relationship between DMR and BS, and between $E_{\text{seg}}/M_{\text{soil}}$ and S , in each soil type.

Table 1. Digging metabolic rate (DMR), resting metabolic rate (RMR), and burrowing speed (BS) in *Ctenomys talarum* in soft and hard soils.

Soil type	Body mass* (g)	DMR (mL O ₂ ·h ⁻¹)	RMR (mL O ₂ ·h ⁻¹)	BS (m·h ⁻¹)
Soft	125.7±7.8	267.59±20.97a	114.77±5.76a	4.87±0.75a
Hard	130.7±7.4	408.30±51.35b	125.73±7.57a	3.61±0.46a

Note: Values are means ± SE and the variables with different letters are significantly different between soil types.

*There were significant differences in body mass between sexes in either soil type ($P < 0.001$).

Table 2. Parameters of cost of burrowing model for *C. talarum* (Ct) and *T. bottae* (Tb) in soft and hard soils.

Soil type and species	Body mass (g)	K_s (J·g ⁻¹)	K_p (J·g ⁻¹ ·cm ⁻¹)	M_{soil} (g·cm ⁻¹)	E_{seg} (kJ)	Reference
Soft						
Tb	143	0.335	0.0045	60.8	3.41	Vleck 1979
Ct	126	0.333	0.0055	44.5	2.71	This study
Hard						
Tb	143	0.461	0.0099	67.0	6.43	Vleck 1979
Ct	126	2.718	-0.0117	42.6	9.09	This study

Note: Model parameters are cost of shearing (K_s), cost of pushing (K_p), mass of soil removed (M_{soil}), and energy of constructing a burrow segment (E_{seg}) with a length (S) of 100 cm.

Results

Sandy loam from Necochea (soil hardness = 36.79 ± 2.17 kg·cm⁻², hereinafter soft soil) was harder than gravelly sand from Mar de Cobo (soil hardness = 27.42 ± 1.56 kg·cm⁻², hard soil; Student's t test, $t = -3.52$, $P < 0.001$, $n = 69$). Soil moisture was similar between soil types (3.2% ± 0.2%; Student's t test, $t = -1.30$, $P = 0.21$, $n = 18$). Body mass differed between sexes (BM_{female} = 110.95 ± 3.60 g, BM_{male} = 144.85 ± 5.95 g; Student's t test, $t = -4.87$, $P < 0.001$, $n = 18$).

Digging metabolic rate was higher for *C. talarum* burrowing in hard soil than for those burrowing in soft soil (ANCOVA, $F_{[1,14]} = 6.68$, $P = 0.02$, $n = 18$), and did not differ between sexes for either soil type (ANCOVA, $F_{[1,14]} = 0.64$, $P = 0.44$, $n = 18$; Fig. 2, Table 1). RMR did not differ between soil types or sexes (ANCOVA, $F_{[1,14]} = 0.02$, $P = 0.88$, $n = 18$; Table 1).

Mass-specific DMR and RMR differed in the two soil types (repeated-measures ANOVA, $F_{[1,14]} = 6.93$, $P = 0.02$, $n = 18$). There were no differences between sexes in either mass-specific DMR or RMR (repeated-measures ANOVA, $F_{[1,14]} = 0.02$, $P = 0.88$, $n = 18$). Mass-specific DMR was higher in hard soil (3.18 ± 0.45 mL O₂·g⁻¹·h⁻¹) than in soft soil (2.14 ± 0.13 mL O₂·g⁻¹·h⁻¹; repeated-measures ANOVA, $F_{[1,14]} = 8.46$, $P = 0.01$, $n = 18$). BS did not differ between soil type (Student's t test, $t = 1.07$, $n = 18$, $P = 0.30$; Table 1). Slopes of the regression for DMR and BS did not differ between soil types (ANCOVA, $F_{[1,15]} = 0.09$, $P = 0.77$), while the y intercept did differ between soil types (ANCOVA, $F_{[1,15]} = 17.43$, $P < 0.01$). The regression equation for the relationship between DMR and BS in soft soil was DMR = 16.942BS + 185.15 and in hard soil was DMR = 27.216BS + 310.13.

Data of the parameters of the cost of burrowing model (Vleck 1979), including M_{soil} and E_{seg} , are summarized in Table 2.

Discussion

Adaptations that affect energy balance and foraging strategy should be subject to relatively intense selection. In surface-dwelling rodents (Pyke 1978), the two most important behaviors for understanding foraging energetics are locomotion to and scratch-digging at a foraging site (Morgan and Price 1992). The effect of soil hardness on scratch-digging metabolic rate has been estimated in *Dipodomys deserti* Stephens, 1887. This species employs a lower DMR in softer substrates (Morgan and Price 1992). In the semifossorial rodent *Octodon degus* (Molina, 1782), closely related to *C. talarum*, excavating in hard soils is energetically more expensive than in soft soil when the relationship between mass of soil removed and DMR is considered (Ebensperger and Bozinovic 2000). Thus, not only the effective DMR but also the volume of soil removed may determine the digging efficiency in aboveground or semifossorial species. So, digging cost of those species tend to be higher than those of subterranean species of similar size, which is the case for *C. talarum* or *T. bottae* (Vleck 1979; Ebensperger and Bozinovic 2000; Luna et al. 2002). This study is the first to assess the effect of soil hardness on digging cost by a subterranean taxon other than the family Geomyidae. As expected, the cost of digging for *C. talarum* was greater (by 41%) in harder soil than in softer soil (Table 1). Taylor et al. (1970) defined the net cost of transport as the relationship between net metabolic rate and speed in terrestrial mammal locomotion and they found a linear relationship between these variables. Our results showed a similar relationship, with DMR increasing linearly with BS in both soil types. For an individual of *C. talarum* to increase BS implies an allometric increment in the cost of transport, which was the same in either soft soil or hard soil (i.e., equal regression slope). In this relationship, the y intercept represents the cost of posture and is defined as the metabolic rate at zero speed (Taylor et al. 1970; Schmidt-Nielsen

1972). The cost of posture varied from 1.55 RMR to 2.59 RMR in soft and hard soils, respectively. Because BS was relatively the same when the animals were digging in either soft soil or hard soil and the y intercept was higher in hard soils, but the slope did not differ, the cost of transport observed in hard soil reflects a greater digging cost in this substrate.

In the cost of burrowing model (Vleck 1979), because the costs of shearing and of pushing in soft soil are similar between *T. bottae* and *C. talarum* (Table 2), differences in E_{seg} can be ascribed to differences in body mass. In the larger *T. bottae*, the mass of soil removed per centimetre of tunnel (M_{soil}) is directly related to the burrow radius, hence to body mass (Vleck 1979; Andersen 1982). Even though *C. talarum* constructs tunnels larger than expected for its body mass in soft soils (Luna et al. 2002), a lower M_{soil} could explain the lower segment cost for this species. Low cohesiveness among soil particles in Mar de Cobo (soft soils) probably affects the bulk of soil removed, thus the differences in M_{soil} .

In hard soils, variables other than body mass explain differences between the burrowing model parameters for the two species. Higher E_{seg} for *C. talarum* than for *T. bottae* is due to the cost of shearing (K_s) being 5.8 times higher in *C. talarum* than in *T. bottae* (Table 2), which could be the result of different burrowing efficiency that is related to digging mode. *Ctenomys talarum* breaks the soil with its forelimbs (Vassallo 1998; F. Luna, personal observation), whereas *T. bottae* uses its incisors (Lessa and Thealer 1989; Stein 2000). In harder soils, breaking soil using the chisel-teeth mode could be more energetically efficient than using the scratch-digging mode. Furthermore, differential shearing costs of *C. talarum* compared with that of *T. bottae* in hard soils are not evident in softer soils, where the cost of shearing was similar for both species (Table 2).

The cost of pushing soil outside the tunnel was similar for both species in each soil type and was slightly higher in hard soil. We assume that the absolute value of K_p is similar in both soil types, despite the finding of a negative value in hard soils for *C. talarum*. There are two possible explanations for this negative coefficient. First, *C. talarum* might not push all the excavated soil out of the burrowing tube, which results in an underestimated K_p parameter. Second, $E_{\text{seg}}/M_{\text{soil}}$ data fit a linear model for at least the first excavated distance (see Materials and methods for the equation). The first explanation does not fit our results because *C. talarum* removed all excavated soil and because the data for individuals that closed the tunnel in the respirometry system were discarded and the trial repeated. On the other hand, *C. talarum* spent noticeably more time shearing soil than pushing soil during the hard-soil trial. Consequently, the apparent linearity of the data must be interpreted with caution, since it could be a consequence of K_p being proportionally smaller than K_s (0.43%) and thus statistically undetectable over the distance burrowed.

Hildner and Soulé (2004) proposed another view regarding the relationship between differences in DMR and in burrowing efficiency. They estimated the digging cost of six populations of *T. bottae* that differed in genetic variability and in burrowing efficiency, and observed that individuals from populations with less genetic variability exhibited a higher DMR in the same soil hardness. The population of *C. talarum* in Mar de Cobo is less genetically variable than

other populations (i.e., Necochea; Cutrera et al. 2006). Therefore, if this was a general relationship, then a lower DMR would be expected for individuals from less genetically variable populations compared with those from highly genetically variable populations digging in the same soil type. No such relationship was found when we analyzed the DMRs of *C. talarum* from Mar de Cobo and from Necochea digging in hard soils (F. Luna and C.D. Antinuchi, unpublished data). Similarly, *Spalacopus cyanus* (Molina, 1782) (closely related to *C. talarum*), which exhibits similar efficiencies in digging economy, appears to differ genetically among populations (Bozinovic et al. 2005).

On the other hand, comparisons of the effect of soil hardness on DMR and on the architecture of the tunnel systems among different subterranean rodents are scarce, but some other inter-specific generalizations can be made. First, all subterranean rodents excavate relatively similar tunnel systems (Nevo 1999), with attributes that tend to minimize digging cost (Vleck 1981; Antinuchi and Busch 1992). Thus, soil hardness could explain constraints on the extension of tunnel systems (Reichman et al. 1982) and on the distribution of tunnelling species. Despite the restrictions imposed on daily energy budgets, affecting both physiological parameters and behavior, by the increment in digging costs owing to soil hardness, a balanced budget could be attained by other mechanisms. First, subterranean rodents, including *C. talarum*, do not appear to dig constantly (Gettinger 1984; Busch et al. 1989). Antinuchi et al. (2006) estimated that only a small percentage of the daily energy expenditure of *C. talarum* under laboratory conditions is associated with digging costs (only 4.84%). Similar findings were reported for *T. bottae* (Gettinger 1984) and *Thomomys talpoides* (Richardson, 1828) (Andersen and MacMahon 1981). Both studies suggest that energy expenditure by pocket gophers owing to burrowing is lower (*T. bottae*, 7.93%; *T. talpoides*, 11.05%) than those related to maintenance and thermoregulatory costs.

Second, other activities could decrease foraging costs, hence daily expenditure; these activities include occupancy of empty burrows (Malizia et al. 1995), construction of tunnels with angles no greater than 40° (F. Luna, personal observation), or avoidance of extreme ambient temperatures (see Luna and Antinuchi 2006). Furthermore, Heth (1989) proposed that differences in digging cost for *Nannospalax ehrenbergi* (Nehring, 1898) (even if DMR was not estimated) are of little relevance to the difference in burrow length shown in hard and soft soils. This difference is related to food requirement rather than to digging cost (Heth 1989). Thus, variations in tunnel systems of some strictly subterranean rodents appear to be affected by factors other than soil hardness.

In conclusion, digging produces a high physiological cost, which is exacerbated by hard soils. Differential cost of digging could be related to burrowing behaviors, since specific modes of shearing and pushing soils differ in energy efficiencies in different soil hardness. Notwithstanding the high cost of digging, a balanced daily budget can be attained by other mechanisms that permit survival and reproduction in the subterranean habitat.

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