

# Digging energetics in the South American rodent *Ctenomys talarum* (Rodentia, Ctenomyidae)

Facundo Luna, C. Daniel Antinuchi, and Cristina Busch

**Abstract:** *Ctenomys* is the most speciose among subterranean rodents. There are few studies on energetics of *Ctenomys*, and none of them have focused on the energetics of digging. The present study aims to quantify the energetic cost of burrowing in *Ctenomys talarum* in natural soil conditions and to compare the energetics data with those reported for other subterranean rodents. Digging metabolic rate (DMR) in gravelly sand for *C. talarum* was  $337.4 \pm 65.9$  mL O<sub>2</sub>·h<sup>-1</sup> (mean  $\pm$  SD). No differences in DMR were detected between sexes. Moreover, DMR was 295.9% of resting metabolic rate. In terms of a cost of burrowing model, the mass of soil removed per distance burrowed ( $M_{\text{soil}}$ ) in gravelly sand was  $44.5 \pm 6.7$  g·cm<sup>-1</sup>. Coefficients of the equation that related the energy cost of constructing a burrow segment of length  $S$  and  $M_{\text{soil}}(E_{\text{seg}}/M_{\text{soil}})$  were  $K_s = 0.33 \pm 0.32$  J·g<sup>-1</sup>, which is the energy cost of shearing 1 g of soil, and  $K_p = 0.0055 \pm 0.0042$  J·g<sup>-1</sup>·cm<sup>-1</sup>, which is the energy cost of pushing 1 g of soil 100 cm. Regarding the cost of burrowing model, our data showed that *C. talarum* has the lowest DMR in gravelly sand among unrelated subterranean rodents analyzed. Moreover, despite *C. talarum* feeding aboveground, the foraging economics was similar that of to other rodents.

**Résumé :** Parmi les rongeurs souterrains, *Ctenomys* est le genre qui compte le plus d'espèces. Il existe peu de travaux sur les bilans énergétiques de *Ctenomys* et aucun de ces travaux ne concerne les coûts énergétiques reliés au creusement. Nous avons tenté de quantifier les coûts énergétiques du creusement chez *Ctenomys talarum* dans le sol, en nature, et de comparer ces données aux résultats obtenus chez d'autres rongeurs fouisseurs. Le taux de métabolisme de *C. talarum* pendant le creusement (DMR) dans du sable graveleux a été estimé à  $337,4 \pm 65,9$  mL O<sub>2</sub>·h<sup>-1</sup> (moyenne  $\pm$  écart type). Nous n'avons pas détecté de différences entre le métabolisme des mâles et celui des femelles. De plus, le métabolisme DMR équivaut à 295,9 % du taux de métabolisme au repos. D'après le modèle du coût du creusement, la masse de sable graveleux excavée par unité de distance ( $M_{\text{soil}}$ ) est de  $44,5 \pm 6,7$  g·cm<sup>-1</sup>. Les coefficients de l'équation qui relie le coût de la construction d'un segment de terrier de longueur  $S$  et  $M_{\text{soil}}(E_{\text{seg}}/M_{\text{soil}})$  sont  $K_s = 0,33 \pm 0,32$  J·g<sup>-1</sup>, qui représente le coût de l'excavation de 1 g de sol, et  $K_p = 0,0055 \pm 0,0042$  J·g<sup>-1</sup>·cm<sup>-1</sup>, qui est l'énergie nécessaire pour pousser 1 g de sol sur une distance de 100 cm. D'après la comparaison avec le modèle, nos données indiquent que *C. talarum* a le métabolisme DMR le plus bas en sol graveleux de tous les rongeurs fouisseurs non apparentés analysés. En outre, en dépit de son alimentation hors terre, les coûts énergétiques reliés à la quête de nourriture chez *C. talarum* sont semblables à ceux qui prévalent chez les autres rongeurs.

[Traduit par la Rédaction]

## Introduction

Many mammals evolved to live in a subterranean habitat. For these mammals, burrows play an important role in their interactions with the environment. Only a small group of herbivorous mammals live permanently in burrows (Nevo 1999), building extensive and elaborate tunnel systems, which provide shelter and access to food.

The architecture of burrows is convergent among phylogenetically unrelated subterranean rodents. Burrow systems consist of foraging tunnels connected laterally to a main tunnel, which includes a single nest, blind tunnels, and areas for hoarding food (Pearson 1959; Vleck 1981; Andersen 1982;

Altuna 1983, 1992; Antinuchi and Busch 1992; Rosi et al. 1996; Lacey et al. 1997).

The energetic costs associated with living underground are assumed to be high, since foraging and other subterranean activities imply tunnel extension. Soil type affects tunnel extension and therefore the architecture of the burrow system (Heth 1989; Antinuchi and Busch 1992). Subterranean rodents can modify burrow extension according to soil type as a way to reduce energy costs. On the other hand, physical properties of the underground environment play an important role in burrow design. Thus, minimum burrow length appears to be related to the surface area necessary to allow sufficient oxygen diffusion to the tunnel system (Kennerly 1964), whereas maximum burrow length appears to be correlated with both primary productivity and resource availability (Jarvis and Sale 1971; Reichman et al. 1982; Heth 1989). Since primary productivity is related to soil type, poor quality or quantity of food items available underground may force the extension of the burrow in random directions in order for a rodent to find food, increasing its energy expenditure (Buffenstein 2000).

Vleck (1979) partitioned the energetic cost of constructing a segment of a tunnel into the energy used to shear soil from

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the face of the tunnel ( $K_s$ ) and the energy used to push loosened soil back out of the tunnel system ( $K_p$ ). Based on his previous work, Vleck (1981) proposed a model that estimates the length of the tunnel segment between two ascending lateral tunnels that minimizes the cost of foraging ( $S_{\min}$ ). This model includes soil type, depth and length of the ascending laterals, burrow diameter, and other tunnel system characteristics.

Reichman et al. (1982) suggested that *Thomomys bottae* extends its burrow length by the addition of basic building units, related to  $S_{\min}$  in terms of Vleck's model (1981), consisting of equal branch length and equal distances between branching points along the burrow. Therefore, differences in total burrow length between individuals (Heth 1989; Rosi et al. 1996) can be seen as a difference in the number of basic building units that determine the main tunnel length. Such differences were related to food requirements (Heth 1989). In hard soils, an increase in search activities due to low food availability plus an increment in digging energy expenditure could also affect the total burrow length.

As stated above, the model that represents the cost of burrowing in subterranean rodents assumes that individuals must extend the tunnel system to locate food underground. Nonetheless, the validity of such a model is restricted only to species that gather food underground (Vleck 1979).

Digging metabolism has been described in geomyids (Vleck 1979), bathyergids (Du Toit et al. 1985; Lovegrove 1989), and a semifossorial octodontid (Ebensperger and Bozinovic 2000). Although *Ctenomys* is the most speciose among subterranean rodents (Reig et al. 1990), few studies have been conducted to obtain data on their energetics (McNab 1979; Busch 1989; Contreras and McNab 1990), and none of them have focused on the energetic cost of digging.

*Ctenomys* occurs broadly in South America and is distributed throughout Argentina, south of Brazil, and in areas of Chile, Peru, Bolivia, Paraguay, and Uruguay (Woods 1984). *Ctenomys* inhabits a sealed burrow system parallel to the soil surface. Furthermore, at a microspatial scale, members of this genus occur in porous and well-drained soils (Contreras 1973). *Ctenomys talarum* lives in coastal grasslands (Comparatore et al. 1991; Antinuchi and Busch 1992). In contrast with other subterranean rodents, *C. talarum* forages aboveground venturing away from its tunnels for brief periods to gather vegetation (Busch et al. 2000).

Since *C. talarum* differs in foraging habits with respect to other subterranean rodents (Comparatore et al. 1995; del Valle et al. 2001), but needs to access a new plant patch through a new tunnel system, the burrowing energetics of this species is required to complete a general picture of the digging energetics of subterranean rodents. The present study aims to quantify the energetic cost of burrowing in natural soil conditions in *C. talarum* and to compare the energetic data with those of other subterranean rodents. In general, high digging resting metabolic rate ratios are expected when low basal metabolic rate and limited food resource are observed (Vleck 1979; Du Toit et al. 1985; Lovegrove 1989). Since *C. talarum* shows low resting metabolic rate (RMR) (with respect to that expected by Kleiber's equation (Busch 1989)) and feeds mainly aboveground (Comparatore et al. 1995; del Valle et al. 2001), lower digging to resting metabolic rate ratios and lower energy parameters in terms of a

cost of burrowing model (Vleck 1979) than those observed for other subterranean rodents are expected.

## Materials and methods

### Study animals

Animals of both sexes (seven males and seven females) were livetrapped in Mar de Cobo (37°45'S, 57°56'W), Buenos Aires Province, Argentina, from November 2000 to March 2001. Captured animals were carried to the laboratory and housed individually in cages (0.30 × 0.40 × 0.25 m). Wood shavings were provided as nesting material. The animal room was kept at 24 ± 1°C (mean ± SD) and the photoperiod was 12 h light : 12 h dark (lights turned on at 7:00). Animals were fed with mixed grasses, carrots, lettuce, corn, alfalfa, and sunflower seeds ad libitum. Water was not provided, since *C. talarum* does not drink free water.

Soil samples were collected in Mar de Cobo using a steel tube extractor at 0.20 m below ground (1 m long and 0.11 m diameter). This procedure maintain physical property of the extracted soil where *C. talarum* inhabit (Antinuchi and Busch 1992).

### Oxygen-consumption measurements

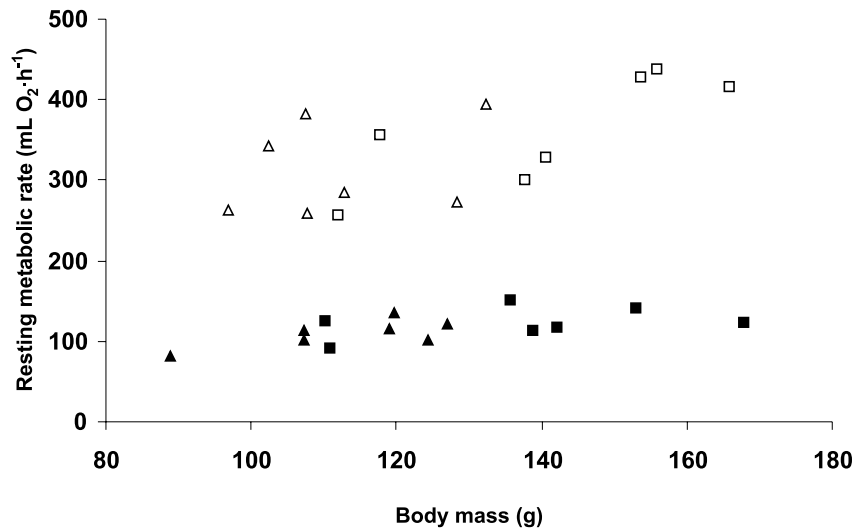
Oxygen consumption was measured using a computerized positive pressure open-flow respirometry system (Sable System, Henderson, Nev.). The chamber system consisted of a soil collector acrylic box (40.5 L) attached to a double acrylic tube (13.6 L). The inner sieved tube contained burrowing soil. The cylindrical air space between the sieved inner and outer tubes (0.01 m) was left to permit airflow through the system. The chamber system received dry and CO<sub>2</sub>-free air at 4000 mL·min<sup>-1</sup> from a mass flow controller (Sierra Instruments, Monterey, Calif.). Air passed through CO<sub>2</sub> absorbent (IQB<sup>®</sup>) and a water scrubber (Silica Gel) before and after passing through the chamber. Excurrent air from the metabolic chamber was subsampled at 180 ± 10 mL·min<sup>-1</sup> (mean ± SD) and oxygen consumption was obtained from an electrochemical oxygen analyzer (FC-1B) every 5 s set by a Datacan V PC program (Sable System).

Each soil sample was transferred to the sieved tube (1 m long and 0.11 m in diameter), which was placed inside an outer acrylic tube (1.20 m long and 0.12 m in diameter). The acrylic tube was attached to the end of the soil collector. Animals usually began to burrow within 10 min and continued until they reached the opposite end of the chamber. Data were discarded when animals stopped digging and remained inactive in the respirometry system for several minutes.

Oxygen consumption values were measured using eq. 4a of Withers (1977, p. 122). RMR was measured as the 5-min lowest steady-state values of a 90-min trial. Mean digging metabolic rate (DMR) and total digging metabolic rate (TDMR) were estimated for each individual as an integral of the relationship between oxygen consumption and time (hours) or burrow length (metres), respectively, from the beginning to the end of each soil sample trial.

Data were expressed as the mass-specific rate of oxygen consumption (millilitres O<sub>2</sub> per gram per hour). An equivalent of 20.1 J·mL O<sub>2</sub><sup>-1</sup> was used to convert oxygen consumption to energy values (Schmidt-Nielsen 1990). To compare

**Fig. 1.** Relationship between digging and resting metabolic rate and body mass of individuals of *Ctenomys talarum*. ■, males; ▲, females; open symbols, digging metabolic rate; solid symbols, resting metabolic rate.



digging metabolic rate in terms of Vleck's model (1979), 19.94 J·mL O<sub>2</sub><sup>-1</sup> was used.

Oxygen consumption of soil microfauna was negligible. Thus, we set the baseline of the respirometry system at 20.95% oxygen before the beginning of each experiment. For measurements of resting and digging metabolic rates, the respirometry system was kept at 25 ± 1°C, which is the thermoneutral zone of *C. talarum* (Busch 1989).

After each burrowing trial, the volume of removed soil was estimated. Removed soil samples were dried at 60°C to constant mass, and percent moisture, granulometry, and density were estimated. Average burrowing speed was estimated as the quotient between total length burrowed and total time expended.

Cost of burrowing was calculated according to Vleck (1979):

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

where  $E_{\text{seg}}$  is the energy cost of constructing a burrow segment of length  $S$ ,  $M_{\text{soil}}$  is the mass of soil excavated per distance burrowed,  $K_s$  is the energy cost of shearing 1 g of soil, and  $K_p$  is the energy cost of pushing 1 g of soil 100 cm.

### Statistics

Resting and digging metabolic rates and mean and total burrowing energy expenditure are expressed as mean ± SD. ANCOVA was used to test the null hypothesis of no differences in individual oxygen consumption between resting or digging metabolic rate between sexes. Body mass was used as a covariate when ANCOVA was performed. Repeated-measures ANCOVA was used to test the null hypothesis of no differences in individual oxygen consumption between resting and digging metabolic rate.

ANCOVA was used to test the null hypothesis of no differences in either individual oxygen consumption or energy expenditure between total digging metabolic rate or total digging energy expenditure between sexes. Student's  $t$  test was used to test the null hypothesis of no differences in body weight between sexes and to test the null hypothesis of no differences in mean energy expenditure during burrow-

ing, rate of soil removal of excavated soil, and burrowing speed between sexes.

The least squares method was used to estimate the regression coefficients (Zar 1984) according to a cost of burrowing model (Vleck 1979). Bootstrap analysis was used to estimate the standard deviation of parameters of the model with PopTools (Hood 2001).

### Results

The percentage of sand in the soil was always above 90%, including medium (<0.5 to >0.25 mm, 42.4 ± 2.6%) and fine sand (<0.25 to >0.125 mm, 49.5 ± 1.0%), like primary fractions present in the granulometric analysis (gravelly sand, U.S. Department of Agriculture). The low percentage of the clay-loam fraction (<62 mm, 0.06 ± 0.03%) determines soil with low water-carrying capacity. Soil moisture was 3.3 ± 1.4%, soil hardness was 27.8 ± 9.5 kg·cm<sup>-2</sup>, and density was 1.6 ± 0.1 g·cm<sup>-3</sup>. In the same area, Antinuchi and Busch (1992) established that total plant biomass was 592 ± 231 g. Aerial plant biomass was 287 ± 202 g, corresponding to a dense plant cover (F. Luna, personal observation).

No differences were detected in RMR (116.8 ± 18.7 mL O<sub>2</sub> h<sup>-1</sup>; ANCOVA,  $F_{[1]} = 0.15$ ,  $P = 0.91$ ,  $n = 14$ ) and DMR (337.4 ± 65.9 mL O<sub>2</sub>·h<sup>-1</sup>; ANCOVA,  $F_{[1]} = 0.24$ ,  $P = 0.63$ ,  $n = 14$ ) between sexes. DMR was 295.9% of RMR (repeated measures MANCOVA,  $F_{[1]} = 144.3$ ,  $P < 0.01$ ,  $n = 28$ ) (Fig. 1). No differences were detected in TDMR per metre of burrowing soil between sexes (3.2 ± 1.0 L O<sub>2</sub>·m<sup>-1</sup>; ANCOVA,  $F_{[1]} = 0.60$ ,  $P = 0.46$ ,  $n = 14$ ). Statistical differences in body mass ( $M$ ) were detected between sexes ( $M_{\text{male}} = 140.4 ± 19.9$  g,  $M_{\text{female}} = 112.6 ± 13.2$  g; Student's  $t$  test,  $t = -3.09$ ,  $P < 0.01$ ,  $n = 28$ ).

*Ctenomys talarum* spent 54.0 ± 8.6 J·g<sup>-1</sup>·h<sup>-1</sup> digging in damp gravelly sand. No statistical differences were detected in this variable between sexes (Student's  $t$  test,  $t = 1.06$ ,  $P = 0.31$ ,  $n = 14$ ). No differences were found in total digging energy expenditure per metre of burrowing soil between sexes (64.5 ± 20.3 kJ·m<sup>-1</sup>; ANCOVA,  $F_{[1]} = 0.60$ ,  $P = 0.46$ ,  $n = 14$ ) (Table 1).

**Table 1.** Digging energy expenditure per hour (DEE) and total digging energy expenditure per metre of excavated soil (TDEE) in *Ctenomys talarum*.

|        | Mass (g)   | DEE (kJ·h <sup>-1</sup> ) | TDEE (kJ·m <sup>-1</sup> ) |
|--------|------------|---------------------------|----------------------------|
| Female | 112.6±13.2 | 6.3±1.2                   | 68.7±23.2                  |
| Male   | 140.4±19.9 | 7.2±1.4                   | 60.2±17.5                  |
| Total  |            | 6.8±1.3                   | 64.5±20.3                  |

**Note:** Values are given at the mean ± SD.

Rate of soil removal was  $269.2 \pm 176.2$  g·min<sup>-1</sup>. No differences between sexes were found in both soil mass removed per minute of burrowing trial (Student's *t* test,  $t = -0.06$ ,  $P = 0.95$ ,  $n = 14$ ) and mean burrowing speed ( $4.7 \pm 2.1$  m·h<sup>-1</sup>; Student's *t* test,  $t = -0.11$ ,  $P = 0.91$ ,  $n = 14$ ).

In terms of the cost of burrowing model,  $M_{\text{soil}}$  for gravelly sand in damp conditions was  $44.5 \pm 6.7$  g·cm<sup>-1</sup>. The coefficients of equations that related  $E_{\text{seg}}/M_{\text{soil}}$  to burrowed distance ( $R^2 = 0.593$ ,  $P < 0.05$ ) for each individual were  $K_s = 0.33 \pm 0.32$  J·g<sup>-1</sup> and  $K_p = 0.0055 \pm 0.0042$  J·g<sup>-1</sup>·cm<sup>-1</sup> (Table 2).

## Discussion

Subterranean rodents expend considerable time and energy digging, and these expenditures are reflected in the morphological adaptations exhibited by these animals (Nevo 1999; Stein 2000). Foraging involves extensive burrowing, and the energetic costs associated with underground life are assumed to be high, especially in species that rarely emerge aboveground. Depending on soil type, this may result in energy expenditures more than 300 times higher than those required to move the same distance across the soil surface (Vleck 1979). However, subterranean habitats are beneficial in buffering environmental instability and protecting against predators (Nevo 1999). These benefits are gained at the expense of the high energy cost involved in constructing and extending the burrow.

Available data suggest that subterranean rodents that dig in damp, compacted sand show a DMR that is twice the RMR. According to expectations, when *C. talarum* digged in damp gravelly sand, DMR was 2.85 times RMR. Nevertheless, DMR/RMR in *C. talarum* was low when compared with other phylogenetically unrelated subterranean rodents (Table 3). In a previous study, Busch (1989) reported that *C. talarum*'s RMR was lower than the expected by Kleiber's equation. Our data confirm Busch's (1989) findings, and low DMR/RMR ratios should be related to low costs of digging, since RMR was the expected for subterranean rodents.

During digging, *C. talarum* expended energy at 53% that of the closely related semifossorial rodent *Octodon degus* (Ebensperger and Bozinovic 2000). The energy cost of soil removal by *C. talarum* was several times lower and the rate of soil removal of *C. talarum* was 7.1 times higher than observed in *O. degus* in damp soils (Ebensperger and Bozinovic 2000). Despite the fact that *O. degus* and *C. talarum* use a similar mode to break the soil, subterranean dependence establishes restrictions on the daily energetic budget, and as a consequence, subterranean species are more efficient in terms of energy expenditure and soil removed per unit of time than semifossorial species.

In *C. talarum*, the energy cost of constructing a segment of tunnel was lower than observed in other strictly subterranean rodents. However, despite their different digging mode, different unrelated subterranean species (Lessa and Thealer 1989; Vassallo 1998; Stein 2000) showed similar  $K_s$  and  $K_p$  (Table 2). In damp gravelly sand, *C. talarum* breaks the soil mostly with forelimbs in a scratch-digging mode (Vassallo 1998; this study), whereas *T. bottae*, *Thomomys talpoides*, *Heterocephalus glaber*, *Cryptomys damarensis*, and *Georychus capensis* are chisel-tooth diggers (Lessa and Thealer 1989; Stein 2000). On the other hand, *C. talarum*, *H. glaber*, *C. damarensis*, and *G. capensis* remove loosened soil moving backwards, kicking the soil, whereas *Thomomys* species turn 180° and push the loosened dirt (Stein 2000). Therefore, different digging behaviors in gravelly sand soils show similar efficiencies. Thus, assuming that soils inhabited by *C. talarum* are more friable than those inhabited by other subterranean rodents, the low cost of digging in *C. talarum* could be related to low soil cohesiveness.

In *C. talarum*, a lower commitment to subterranean life than *T. bottae* should be expected, since the former species feeds mainly aboveground. Consequently, low digging efficiency with respect to other subterranean rodents could be possible. However, both species showed similar  $K_s$  and  $K_p$ . Thus, despite the fact that *C. talarum* feeds mainly aboveground, it needs to reach new food patches through extending its burrow system. Once a new patch is found, individuals venture out from the burrow to gather food.

In addition, the burrow segment length that maximizes the foraging efficiency and minimizes the digging cost ( $S_{\text{min}}$ ) was estimated from Vleck's (1981) model. Despite the fact that the estimation of  $S_{\text{min}}$  was different from that reported for natural burrows of *C. talarum* (0.9 m; Antinuchi and Busch 1992), the former was similar to the  $S_{\text{min}}$  estimated for *T. bottae* (1.33 m; Vleck 1981). It is likely that the difference could be explained, since burrow structures of *C. talarum* do not meet the model assumptions. Popholes are common in *C. talarum* burrows but, in contrast with *T. bottae* burrows (Vleck 1981), no lateral tunnels were found in the gallery systems of *C. talarum* (Antinuchi and Busch 1992). In the same way, the low cohesiveness of soil inhabited by *C. talarum* could explain the smaller segment of burrow and the related energy cost required to pack the excavated soil of the new tunnel.

Besides the effect of soil properties on cost of burrowing, differences in body size have been proposed to influence the cost of burrowing (Vleck 1981; Andersen 1982), since increments in body size will produce increments in burrow diameter. Therefore, in species showing sexual dimorphism, differences in burrow attributes and burrowing cost between sexes should be expected.

Although *C. talarum* shows sexual dimorphism in body size (Zenuto et al. 1999), no differences in DMR between sexes were detected. Furthermore, no difference in the rate of soil removal between sexes was observed. This agrees with the fact that no differences in either burrow diameter or burrow length have been reported between sexes (Antinuchi and Busch 1992; Zenuto et al. 1999).

McNab (1966) hypothesized that similar burrow characteristics between sexes can be explained, since males dig burrows according to their adult body size and females dig

**Table 2.** Cost of burrowing parameters (Vleck 1979) for subterranean rodents (except *O. degus*) in damp sand.

| Species                           | $K_s$<br>(J·g <sup>-1</sup> ) | $K_p$<br>(J·g <sup>-1</sup> ·cm <sup>-1</sup> ) | $M_{soil}$<br>(g·cm <sup>-1</sup> ) | Soil density<br>(g·cm <sup>-3</sup> ) | Reference                          |
|-----------------------------------|-------------------------------|---|-------------------------------------|---------------------------------------|------------------------------------|
| <i>Cryptomys damarensis</i>       | 0.28                          | 0.0036  | 42.8                                | 1.7                                   | Lovegrove 1989                     |
| <i>Thomomys bottae</i>            | 0.34                          | 0.0045  | 62.9                                | 1.6                                   | Vleck 1979                         |
| <i>Thomomys talpoides</i>         | 0.67                          | 0.0065  | ?                                   | ?                                     | Vleck and Kenagy in Lovegrove 1989 |
| <i>Ctenomys talarum</i>           | 0.33                          | 0.0055  | 44.5                                | 1.6                                   | This study                         |
| <i>Octodon degus</i> <sup>a</sup> | 24.1                          |   |                                     | ?                                     | Ebensperger and Bozinovic 2000     |

<sup>a</sup>Semifossorial rodent.

**Table 3.** Body mass, resting metabolic rate (RMR), digging metabolic rate (DMR), and ratio of digging to resting metabolic rate (DMR/RMR) of subterranean rodents (except *O. degus*) in damp soil.

| Family and species                | Body mass (g) | RMR<br>(mL O <sub>2</sub> ·g <sup>-1</sup> ·h <sup>-1</sup> ) | DMR<br>(mL O <sub>2</sub> ·g <sup>-1</sup> ·h <sup>-1</sup> ) | DMR/RMR                  | Type of soil  | Reference                          |
|-----------------------------------|---------------|---|---|--------------------------|---------------|------------------------------------|
| <b>Bathyergidae</b>               |               |   |   |                          |               |                                    |
| <i>Heterocephalus glaber</i>      | 32            | 0.64  | 3.36  | 5.25                     | Damp sand     | Lovegrove 1989                     |
| <i>Cryptomys damarensis</i>       | 152           | 0.57  | 2.58–2.86 <sup>a</sup>  | 4.52–5.02 <sup>a</sup>   | Dry–damp sand | Lovegrove 1989                     |
| <i>Georchus capensis</i>          | 197           | 1.13 (0.59) <sup>b</sup>                                      | 3.41  | 3.01 (5.80) <sup>b</sup> | Loose sand    | Du Toit et al. 1985                |
| <b>Geomyidae</b>                  |               |   |   |                          |               |                                    |
| <i>Thomomys bottae</i>            | 143           | 0.84  | 4.10  | 4.80                     | Damp sand     | Vleck 1979                         |
| <i>Thomomys talpoides</i>         | 75            | 1.65  | 4.08  | 2.47                     | ?             | Vleck and Kenagy in Lovegrove 1989 |
| <b>Ctenomyidae</b>                |               |   |   |                          |               |                                    |
| <i>Ctenomys talarum</i>           | 126           | 0.95  | 2.69  | 2.85                     | Damp sand     | This study                         |
| <b>Octodontidae</b>               |               |   |   |                          |               |                                    |
| <i>Octodon degus</i> <sup>c</sup> | 203           | 1.24  | 6.68  | 5.40                     | Damp soil     | Ebensperger and Bozinovic 2000     |

<sup>a</sup>No statistical difference between dry and damp sand.

<sup>b</sup>Value in parentheses is RMR estimated in Lovegrove (1987).

<sup>c</sup>Semifossorial rodent.

burrows according to body size at pregnancy. However, the same burrow diameter for both sexes can be explained when females construct a large tunnel diameter to permit males access to their burrows during reproductive periods. As was reported under laboratory conditions, males of *C. talarum* visit the female's burrow for courtship and copulation (Zenuto et al. 2001).

To conclude, regarding the cost of burrowing model parameters (Vleck 1979), our data show that *C. talarum* had a low DMR in gravelly sand, owing to soil cohesiveness and not to high digging efficiency. Moreover, despite food habit differences of *C. talarum* with respect to unrelated subterranean rodents, the cost of foraging remains energetically comparable, since burrows are used to locate nearby food patches. Field studies are needed to assess the relationship among burrow traits, age structure, reproductive status, feeding ecology, seasonality, and burrowing metabolism in *C. talarum*.

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