ORIGINAL ARTICLE

Effect of tunnel inclination on digging energetics in the tuco-tuco, *Ctenomys talarum* (Rodentia: Ctenomyidae)

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Abstract Burrows play an important role for many species, providing them with shelter and access to food resources. For subterranean rodents, living underground imposes constraints on morphology and physiology. The convergence in burrow architecture among subterranean rodents has been related to the energy demands imposed by the cost of constructing an entire system. The low frequency of tunnels with downward angles steeper than 40° appears to be a common feature in burrow design. In the subterranean habitat, movements through the soil are expensive and gravity can exert important restrictions on digging energetics when individuals push out the soil removed in steeper digging angles. The aim of this study was to determine the effect of digging angle on digging energetics in *Ctenomys talarum*. The mass of the removed soil and burrowing speed were similar while digging metabolic rate and net cost of transport were higher in individuals digging in tunnels with angles >40° than in those digging tunnels with angles <40°. The cost of constructing a burrow in the horizontal plane differed by 20% from others in which the natural representation of tunnels >40° was considered. Even given that tunnels >40° represented only 6% of the total

burrow length, burrow architecture appears to be constrained by the high energetic cost of constructing in steeper angles.

Introduction

Because selection shapes morphological and physiological specializations of organisms, movements should be energetically efficient in those circumstances and/or environments where a particular species frequently occurs. For animals that move up or down an incline, their movements must be adjusted to consider the effect of gravity and the slope of the inclined plane on body weight (Reichman and Aitchison 1981). Thus, movements in inclined angles will be common if the energy expended or gained results in an improvement of fitness. Taylor et al. (1972) showed that running uphill involves a relative increase in energy cost rather than running on a plane. In animals that run down an incline, the energy cost is smaller than when they run up or horizontally because they recover most of the mechanical energy stored as potential energy when they moved uphill (Taylor et al. 1972; Armstrong et al. 1983).

In most subterranean species, a different picture is shown. They move underground to gain access to underground plant parts for food by excavating burrow systems that they dig themselves. The construction of these systems, composed by a main tunnel connected to lateral branches that reach the soil surface (Antinuchi and Busch 1992; Busch et al. 2000), is an energetically demanding process (Vleck 1979; Du Toit et al. 1985; Lovegrove 1989; Luna et al. 2002; Antinuchi et al. in press). Moreover, unlike surface-dwelling animals, subterranean rodents must lift the excavated soil

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uphill, incurring an additional cost of movement. This high energetic cost might have constrained the design of burrow systems, producing convergence in most subterranean species (see Nevo 1999; Busch et al. 2000).

Although it has been proposed in *Thomomys bottae* that the vertical force component used for lifting soil against gravity is a small part of their total moving cost (Seabloom et al. 2000), in this species, as well as in *Ctenomys mendocinus* and *Geomys bursarius*, lateral branches almost never reach angles steeper than 40° upward of the main tunnel (Rosi et al. 1996; Andersen 1982, 1988), which suggests that digging in angles of 40° would be a ceiling either to morphological capabilities or to maintain a balanced energy budget. Tunnels with steeper angles have been observed in burrows of many subterranean species (popholes). Popholes are short tunnels (~0.10 m) rising vertically from the main tunnel to the surface, but are not used to lift soil through them.

Members of the genus *Ctenomys* live in burrow systems (Reig et al. 1990), they are distributed widely in South America (Woods 1984). Among various *Ctenomys* species, the architecture of tunnel systems appears to be similar (Rosi et al. 1996; Antinuchi and Busch 1992; Pearson 1959; Altuna 1983). *Ctenomys talarum* lives in coastal grasslands (Buenos Aires Province, Argentina). As for others species of the genus, tunnel systems show a linear pattern with no differences in total burrow length between sexes (Antinuchi and Busch 1992). Unlike other subterranean rodents (i.e., *T. bottae*, Vleck 1979), *C. talarum* feed mainly on aerial plant parts near the burrow openings (Comparatore et al. 1995). Even that foraging on the surface, for *C. talarum*, appears to be less costly than subterranean foraging (Luna unpublished data), this species must have access to new food patches through the construction of new tunnel systems (Luna et al. 2002).

Vleck (1981) proposed that the cost of burrowing should increase with burrow depth, but the way in which a tunnel angle affects the energetic cost of burrowing and, hence, the energetic budget of constructing an entire burrow system have never been evaluated. Therefore, estimations of these parameters as a function of burrow incline angles in *C. talarum* could indicate how environmental factors and digging energetic cost determine the convergence of burrow architecture in subterranean rodents. The aim of this study was to evaluate the effect of down-slope digging angle on the cost of constructing an entire burrow in *C. talarum*.

Materials and methods

Study animals

Animals of both sexes (24 individuals) were live-trapped in Mar de Cobo (37°45′S, 57°56′W, Buenos Aires Province,

Argentina). 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. To standardize the ambient regime, the animal room was kept at 25±1°C, and the photoperiod was 12:12 h light/dark (lights turned on at 7.00 A.M.). Animals were fed mixed grasses, carrots, lettuce, corn, alfalfa, and sunflower seeds ad lib. Water was not provided because *C. talarum* does not drink free water. Soil samples were collected in Mar de Cobo using a steel tube to extract soil below ground. This procedure maintained the physical properties of the extracted soil in which *C. talarum* lives (moisture: 3.3± 1.4%, hardness: 27.8±9.5 kg·cm^{-2}, for further information see Luna et al. 2002).

Oxygen consumption measurements

Oxygen consumption was measured using a computerized positive pressure open-flow respirometry system (Sable System, Henderson, NV, USA). Resting metabolic rate (RMR) and digging metabolic rate (DMR) were measured in the same individual in different trials. The digging chamber consisted of a cube-shaped acrylic soil collector (0.2 m length, 0.2 m height, 0.2 m width) attached to an acrylic tube (1.1 m length, 0.11 m diameter). A perforated tube (1 m length, 0.1 m diameter, 6 mm hole diameter, Fig. 1; for details, see Luna et al. 2002) 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. Between the soil collector and the outer acrylic tube, we attached a metallic perforated door that separated both areas once we connected the whole system. The metallic door permits free airflow through the entire system. A cylindrical chamber was used to estimate metabolic rate during resting of the *C. talarum*. The digging chamber (total volume 19.1 l) and the resting chamber (1.8 l) were comparable to those described in Luna et al. (2002).

Digging and resting chambers received dry and CO_2-free air at 3,000 ml min^{-1} from a flowmeter (Cole-Parmer Instrument, Vernon Hills, IL, USA) and at 1,500 ml min^{-1} from a mass flow controller (Sierra Instruments, Monterey, CA, USA). Air passed through a CO_2-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).

To allow a complete mixing of the inlet air, once the system was completely connected and closed, the digging chamber was left for 30 min to achieve equilibration (calculated from Lasiewski et al. 1966). After the equilibration period, we opened the perforated door, switching a

Fig. 1 Respirometry system used to measure the oxygen consumption of *C. talarum* during digging. Absorbants: IQB® (CO$_2$-absorbent) and Silica Gel (water scrubber). Not to scale
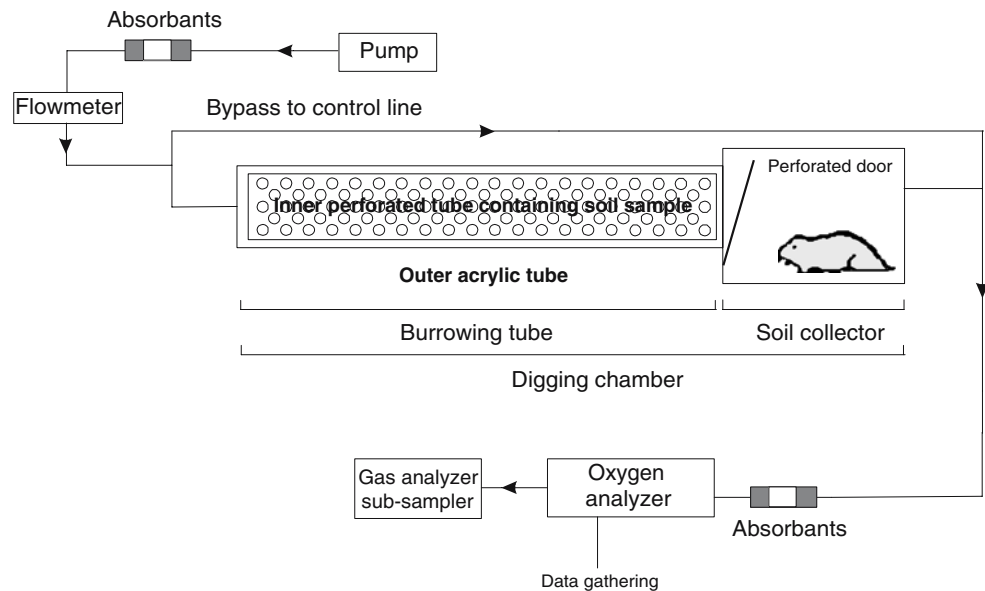
magnetic lock without opening the system, and the animals usually began to burrow within the following 10 min and continued until they reached the opposite end of the chamber. Data were discarded when animals stopped digging and remained inactive (for at least 5 min) in the digging chamber. Individual digging experiments lasted ~55–65 min. Rates of oxygen consumption were calculated by equation 4a of Withers (1977).

$$\dot{V}_{O_2} = \dot{V}(F_{IO_2} - F_{EO_2}/1 - F_{IO_2}) \tag{1}$$

where $\dot{V}$ is the flow rate through the system, F_{IO_2} is the incurrent oxygen concentration (0.2095), and F_{EO_2} is the oxygen concentration in the excurrent air. DMR was estimated as the maximum of oxygen consumption. RMR was estimated as the lowest 5-min steady state in the last 30 min of a 90-min trial. An equivalent of 20.1 J ml^{-1} O$_2$ was used to convert oxygen consumption to energy values (Schmidt-Nielsen 1990). Oxygen consumption of soil microfauna was negligible. Thus, we set the baseline of the respirometry system to 20.95% of oxygen before the beginning of each experiment.

Effect of digging angle

To estimate the effect of digging angle on metabolic rate, the metabolic chamber was placed in three fixed angles (0, −25, and −50° with respect to the horizontal plane). An estimation of a threshold angle (test a range of angles) was not performed because, based on previous studies (see "Introduction"), we assumed that this angle is 37°. Because no differences in DMR between sexes were reported (Luna et al. 2002), these data were pooled. Burrowing speed (BS) was estimated as the quotient between total lengths burrowed and the time elapsed during a digging trial. The net cost of transport

(NCOT) was calculated as (DMR−RMR)/BS (Taylor et al. 1970; Seymour et al. 1998). Cost of burrowing was calculated according to Vleck (1979).

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

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 values were determined by fitting the previous equation to the observed values of E_{seg} of individuals for each condition.

Burrow construction cost

To estimate the mean cost to construct an entire burrow system, in terms of cost of the burrowing model (Vleck 1979), we analyzed the data of 15 (seven males and eight females) excavated burrows mapped by Antinuchi and Busch (1992). We assumed these animals deposited all excavated soil on the surface because the proportion of backfilling tunnels is low (Malizia et al. 2000). For each burrow, we estimated the main tunnel segment length between laterals, the depth of each segment, and the length of lateral tunnels. Then, we classified arbitrarily all segments as horizontal (<40° and popholes, the later are classified as horizontal because they are not used to lift soil) or inclined (>40°). Once all segments were classified, we estimated the mean cost destined to construct an entire burrow system considering or not tunnel slopes. Finally, we compared statistically both energetic budgets.

Statistics

All data are expressed as mean±SE. Normality and homoscedasticity of variables were verified with Kolmogorov–Smirnov goodness of fit and Levene's tests, respectively (Zar 1984). We used the Mann–Whitney test only when assumptions of the parametric tests failed. Because the same individual was used to test DMR and RMR, a repeated-measured analysis of covariance (ANCOVA) was used to test the null hypothesis of no differences in DMR and RMR among horizontal (0°) and fixed descendent angles (−25 or −50°). Before the analysis, parallelisms between variables were verified with Wilks' Lambda test. The between-subject factor was digging angle, and within-treatment factors were DMR and RMR. Body weight was used as covariate when ANCOVA was performed. ANOVA was used to test the null hypothesis of no differences in BS or NCOT among digging angles. ANCOVA was used to test differences in slope and y-intercept of the relationship between DMR and BS among angle treatments.

Mann–Whitney was used to test the null hypothesis of no differences in M_{soil} between digging angles. We used the equation proposed by Vleck (1979) to estimate the coefficients that describe the relationship between oxygen consumption and burrow distance in *C. talarum*. Bootstrap analysis was used to estimate the SE of parameters of the model with PopTools (Hood 2001). Student *t* test was used to test the null hypothesis of no differences in total cost of constructing an entire burrow estimated with the natural representation of tunnels >40°.

Results

No statistical differences in body weight of the individuals used in the treatments were detected (Kolmogorov–Smirnov goodness of fit, $P>0.05$, Levene, $P=0.09$, df=22, $t=1.08$, $P=0.29$, Table 1). Differences in MR between resting and digging among slope conditions were observed (Wilks, $P=0.18$, Levene, $P>0.05$, repeated measures ANCOVA, df=2, $F=4.32$, $P=0.02$). We did not detect differences in RMR of individuals used to evaluate DMR among slope conditions

(Scheffé, all comparisons, $P>0.05$). DMR was not different between slopes of 0 and −25° (Scheffé, $P>0.05$). DMR in a slope of −50° was higher than those observed in 0 and −25° (Scheffé, −50 vs −0°, $P<0.01$; −50 vs −25°, $P<0.01$, Fig. 2). BS was not different between slopes of 0, −25, and −50° (Kolmogorov–Smirnov goodness of fit, $P>0.05$, Levene, $P=0.13$, ANOVA, df=2, $F=1.85$, $P=0.18$, Table 1). Slopes of regression of the relationship between DMR and BS were not different between digging angles (Wilks, $P=0.17$, Levene, $P>0.05$, ANCOVA, df=1, $F=3.60$, $P=0.07$), while y-intercept did differ (df=1, $F=7.49$, $P=0.01$). In the relationship between DMR and BS, the y-intercept can be defined as the cost of posture (Taylor et al. 1970). In this relationship, the metabolic rate value of the y-intercept is greater than RMR. Schmidt-Nielsen (1972) suggests that this difference is related to posture associated with the cost of activity in small mammals. As expected, the costs of posture differ 2.12 and 3.16 times RMR, at 0 and −50°, respectively. NCOT was different between slopes of −50 and 0 or −25° (ANOVA, df=2, $F=4.90$, $P=0.02$, Tukey, −50 vs −0°, $P=0.03$, −50 vs −25°, $P<0.04$, Table 1), but no differences were observed between 0 and −25° (Tukey, $P>0.05$).

To estimate coefficients of cost of the burrowing model (Vleck 1979), and because no differences in DMR between digging angles of 0 and −25° were observed, we classified arbitrarily DMR data into two categories, <40° (0 and −25°) and >40° (−50°, see above). M_{soil} was not different between slopes of 0 and −50° (45.13 ± 3.28 g cm^{-1}, Mann–Whitney, $Z=0.10$, $P=0.92$). Coefficients of Eq. 2 in angles <40° were $K_s = 0.333 \pm 0.007$ J g^{-1} and $K_p = 0.0055 \pm 0.0001$ J g^{-1} cm^{-1}, in angles >40° were $K_s = 0.494 \pm 0.009$ J g^{-1} and $K_p = 0.0057 \pm 0.0001$ J g^{-1} cm^{-1} (K_s and K_p obtained in both digging angles did not overlap their 95% confidence interval after Bootstrap analysis, see "Materials and methods" for details). These coefficients were used in the calculation of the cost of constructing a burrow segment. The cost of constructing a burrow in the horizontal plane differed from another in which the natural representation of tunnels >40° was considered (df=23, $t=-3.99$, $P<0.01$, Table 2).

Table 1 Body weight, digging metabolic rate, resting metabolic rate, burrowing speed, and net cost of transport of *C. talarum* in different digging angles

Angle	BW (g)	DMR (ml O$_2$ h^{-1})	RMR (ml O$_2$ h^{-1})	BS (m h^{-1})	NCOT (J m^{-1})
0 to −25°	126.18±4.96[a]	251.92±15.97[a1]	114.44±4.81[a2]	4.78±0.47[a]	681.07±122.87[a]
−50°	137.68±11.62[a]	354.71±36.46[b1]	131.11±11.65[a2]	3.32±0.31[a]	1475.33±227.85[b]

Data are expressed as mean±SE. Small letters refer to differences among angle treatment. Small numbers refer to differences between digging and resting conditions.
BW body weight, *DMR* digging metabolic rate, *RMR* resting metabolic rate, *BS* burrowing speed, *NCOT* net cost of transport

Fig. 2 Digging metabolic rate (*DMR*) of *C. talarum* related to body weight in two downslope angles. *Triangles*, DMR in 0 and −25°. *Squares*, DMR in −50°
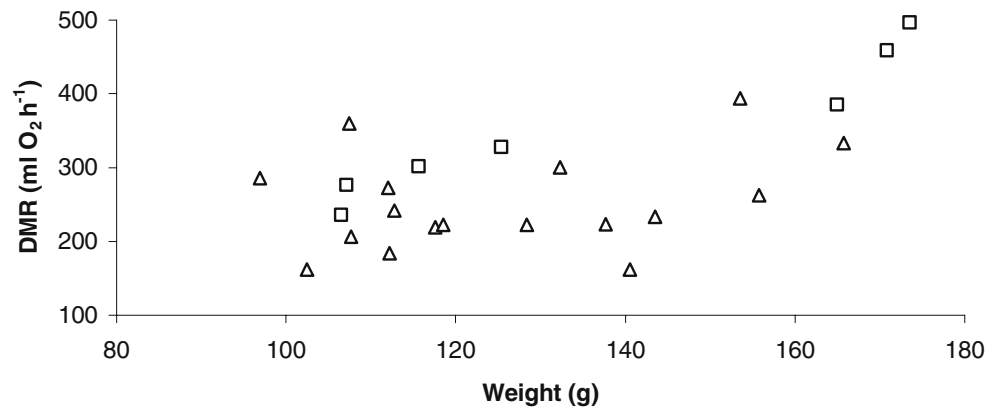
Discussion

Subterranean rodents live in a structurally simple environment (Nevo 1999). It consists of several foraging tunnels connected to a single deep, central tunnel (Busch et al. 2000). Given the substantial energetic cost of foraging in the subterranean habitat (Vleck 1981), it is expected that selection favors the location of burrows and/or structures that minimize the energetic cost of constructing it. In this way, White (2005) reported a positive allometric relationship between body weight and burrow cross-section area for burrowing animals, not only in mammals but also in other members of the phylum Chordata (classes Osteichthyes, Amphibia, and Reptilia) and in the phylum Arthropoda (classes Arachnida, Insecta, and Malacostraca). For burrowing mammals, extrinsic factors such as humidity, porosity, and water-holding capacity of the soil, as well as food availability, have been proposed as determinants of a burrow's location and design because these factors are related to soil hardness and, hence, to digging cost (Busch et al. 2000; Luna and Antinuchi 2006). Sumbera et al. (2003) observed in *Heliophobius argenteocinereus* that

burrow architecture changed from linear to reticulate design in the dry season when soil is hard to dig and, concordantly, Williams and Cameron (1990) found in *Geomys attwateri* that mean burrow depths also change between seasons.

Particularly, in subterranean rodents, burrow parameters such as number of branches, tunnel length, diameter, depth, and the way in which underground obstacles are avoided have been analyzed to assess the relationship between energy cost and benefits of foraging underground (Heth 1989; Vleck 1981; Andersen 1982; Kimchi and Terkel 2003). Regarding the effect of digging angle, in *C. talarum*, the mass of removed soil, as well as the BS, were not different between segments of tunnels constructed with different angles. Consequently, the NCOT and, specifically, the cost of posture were higher when digging tunnels with angles >40° than when digging those with angles <40°. In agreement, the cost of constructing a burrow in the horizontal plane differed by 20% from another in which the natural representation of tunnels >40° was considered. Despite the low representation (nearly 6%) of tunnels with angles >40° in excavated burrows, they represent an increment of, at least, 20% of the cost of constructing an entire system (Table 2).

Vleck (1981) proposed that, for *T. bottae*, digging laterals at the steepest angle possible is a compromise between the reduction of pushing efficiency, when soil is falling back into the system, and the possibility of constructing a short tunnel, lowering energetic cost. Moreover, Taylor et al. (1970) stated that in surface-dwelling species, body weight affects NCOT, and Reichman and Aitchison (1981) demonstrated that, as an animal's mass increases, the maximum ascendant angle slope at which they will move decreases.

On the other hand Seabloom et al. (2000) analyzed geometry of *T. bottae* burrows in different hillslope angles and concluded that individuals did not adjust tunnels' geometry to minimize the digging cost at different hillslopes. However, despite the fact that the conclusion of Seabloom et al. (2000) appears to contrast with our results, they also found that *T. bottae* orient their lateral branches

Table 2 Cost of constructing a burrow segment in *C. talarum*, estimated in terms of cost of burrowing model (Vleck 1979), on excavated tunnel systems mapped by Antinuchi and Busch (1992)

Angle	Cost of construction[a] (KJ m^{-1})			
	Segments<40°	Popholes	Segments>40°	Total
0°	3.16 (88.62)	1.63 (5.64)	1.31 (5.74)	6.10[1]
−50°			1.81 (5.74)	7.32[2]

Angle of 0° represent the cost of constructing a tunnel system with all tunnels horizontal, −50° represent the cost taking the natural representation of tunnels >40°. In parenthesis are the percentages of the total burrow length. Parameters used for 0° are K_s=333 J Kg^{-1} and K_p=550 J Kg^{-1} m^{-1}, and for −50° are K_s=494 J Kg^{-1} and K_p=570 J Kg^{-1} m^{-1}. Small numbers refers to differences among angle treatment.

[a] Mean total burrow length=15.01 m of 15 (seven females and eight males) burrow systems of *C. talarum*

downslope, giving a net sediment flux down the hillslope (see Gabet 2000), and that laterals do not exceed angles of 40°. Also, in agreement with our results, Kimchi and Terkel (2003) found that *Spalax ehrenbergi* dig horizontal or inclined tunnels depending on the size of the obstacle to bypass. So, when individuals dig in angles greater than 40°, energetic restrictions on daily budget affecting digging efficiency might determine direct effects on movements' patterns and, hence, burrow geometry.

Finally, burrow architecture could be modeled, among others factors, by energetic restrictions imposed by digging angle. As observed, the increment in the cost of constructing a burrow system due to the increment in digging angle (Table 2) might be restrictive in maintaining a balanced daily energy budget. Despite nonphysical factors, as the capacity of burrowing mammals to explore the surrounding area to gather food has been proposed as a determinant of fractal burrow architecture (Le Comber et al. 2002; Romañach and Le Comber 2004), direct effects of gravity appear to contribute to determine the convergence among burrow systems designs in phylogenetically unrelated subterranean rodents.

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