

DAILY MOVEMENTS AND MAXIMUM SPEED IN *CTENOMYS TALARUM* (RODENTIA: CTENOMYIDAE) IN ARTIFICIAL ENCLOSURES

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Ctenomys talarum is a solitary subterranean rodent that maintains exclusive territories by constant movement through a sealed tunnel system. In this study we evaluate the distance traveled in an artificial burrow and maximum natural locomotor speed reached in a 24-h period. Distance moved per day was $179.99 \text{ m} \pm 69.62 \text{ SD}$, and ratio of distance moved to total burrow length was 12.4:1. Maximum locomotor speed was $0.75 \text{ m/s} \pm 0.01 \text{ SD}$. No relationships were found between either distance moved or speed and photoperiod or ambient temperature, and between body mass and distance moved or locomotor speed. Distance moved by *C. talarum* is related to maintenance of burrow and territorial defense, and locomotor speed, probably, responds to aboveground predation.

Key words: *Ctenomys*, daily movements, maximum speed, subterranean rodent

Many aspects of behavior in free-living animals are linked to size of areas that they inhabit and their movements within these areas (Swingland and Greenwood 1983). In subterranean rodents, use of an area is not only restricted by biological constraints but also by environmental factors, which may limit the extent of the burrow system (Zuri and Terkel 1996).

Subterranean herbivorous rodents of the genus *Ctenomys* (tuco-tucos) occur widely in South America. They are distributed throughout Argentina, southern Brazil, and some areas of Chile, Paraguay, Bolivia, Uruguay, and Peru (Woods 1984). *Ctenomys* live in a permanently sealed burrow system parallel to the soil surface (Antinuchi and Busch 1992; Rosi et al. 1996), from which they forage on aerial parts of plants. The burrow system, both in solitary species (Altuna 1983; Antinuchi and Busch 1992; Pearson 1959; Rosi et al. 1996) and in the unique social species (Lacey et al. 1997), consists of feeding tunnels that connect a

main tunnel with the soil surface. The main tunnel includes a single nest and blind tunnels. Architecture of *Ctenomys talarum* burrows is convergent with those of other phylogenetically unrelated subterranean rodents such as *Thomomys bottae* (Vleck 1981) and *Geomys bursarius* (Andersen 1982). Vleck (1979) hypothesized that convergence in burrow architecture could be related to optimization of the energy budget for digging.

Captive *C. talarum* individuals show arrhythmic patterns of locomotor activity under seminatural conditions (Luna et al. 2000). *C. talarum* is an aggressive species that maintains an exclusive territory (Busch et al. 1989). Its apparent arrhythmicity has been attributed to the constant need for territorial defense against conspecifics and predators, which requires continuous traveling throughout the burrow system (Luna et al. 2000).

In this study we evaluate distance traveled in an artificial burrow system and maximum locomotor speeds reached in a 24-h

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period by *C. talarum* under seminatural and controlled photoperiod and under different ambient temperature conditions. We hypothesize that distance moved and speed of movement, like the pattern of activity, are independent of environmental conditions.

MATERIALS AND METHODS

Ctenomys talarum is a small rodent (mean body mass, 120 g for females and 160 g for males) associated with different types of friable soils (Busch et al. 2000). It is found along the coast of Buenos Aires Province, Argentina, possibly extending into Santa Fe Province (Redford and Eisenberg 1992). Twenty-four adult *C. talarum* (12 males and 12 females) were collected using plastic live traps, similar to those described by Zenuto et al. (2002), from a sandy dune belt at Mar de Cobo, Buenos Aires Province, Argentina (37°45'S, 57°56'W; Pampeana biogeographic province—Cabrera and Willink 1973), during July and November 1998.

Individuals were taken to the laboratory and housed individually in artificial burrow systems similar to those described by Zenuto et al. (2001), with 12L:12D seminatural photoperiod and 21 ± 2°C temperature. Ambient relative humidity ranged from 50% to 70%. These systems were built with white polyvinyl chloride (PVC) tubes (3 m long, 0.1 m in diameter), connecting a resource cage and a nest box. Animals were fed mixed grasses, sweet potatoes, lettuce, sunflower seeds, corn, carrots, and alfalfa ad lib. *C. talarum* does not drink water; therefore, no free water was provided.

Total distance moved per day and maximum natural locomotor speed—defined as the speed that an individual can reach when unhindered—were determined in another artificial burrow system. This system comprised 3.5 m of tunnel—built with black PVC tubes (0.09 m in diameter)—connected to an open resource cage and a sealed nest box, with a structural complexity similar to that described for natural burrows (Antinuchi and Busch 1992; Zenuto et al. 2001). Movements and speed were recorded with 10 contact microswitches (Audioled, Mar del Plata, Buenos Aires, Argentina) fixed, about every 0.35 m, on the floor of the artificial burrow system. Microswitches were arranged so that weight of animals closed electrical contacts. For recording individual activity, microswitches

were connected to the parallel printer port of a personal computer by a shielded cable (Antinuchi et al. 1999). Each individual was held for 24 h in the artificial system, during which their activity was recorded. With the position and gap between microswitches in the artificial burrow system known, total movement in a day was estimated as the sum of all sectors that *C. talarum* traveled, and speed as the minimal time observed to cross 2 consecutive microswitches. The artificial burrow system was placed in an animal room with controlled photoperiod and temperature.

Locomotor parameters were measured under 2 experimental conditions. In the 1st treatment, ambient temperature was 21 ± 2°C and photoperiod either 12L:12D (seminatural, defined as natural photoperiod regimen in laboratory conditions) or 0L:24D (controlled). In the 2nd treatment, photoperiod was 12L:12D (controlled), and ambient temperature was either 10 ± 1°C or 35 ± 1°C. Each individual was used only once in all experimental conditions.

One-way analysis of variance (ANOVA) was used to test effects of temperature and photoperiod on distance moved per day and on locomotor speed of tuco-tucos under experimental conditions. Linear regression analysis and ANOVA were used to test for relationships between body mass and both distance moved per day and maximum natural locomotor speed. Results are presented as mean ± SD.

RESULTS

Ctenomys talarum in artificial burrows moved 177.99 m/day ± 69.62. We observed no differences in total distance moved between individuals tested in seminatural (12L:12D) and controlled photoperiods (0L:24D; ANOVA; *d.f.* = 1, *F* = 1.89, *n* = 12, *P* = 0.20; Table 1), or between individuals tested at 10 and 35°C (ANOVA; *d.f.* = 1, *F* < 0.01, *n* = 12, *P* = 0.94; Table 1). Total distance moved divided by total burrow length for this species was 12.4:1.

Maximum speed attained by *C. talarum* in artificial burrows was 0.75 m/s ± 0.01, and no differences were observed among individuals tested in the 2 photoperiods (ANOVA; *d.f.* = 1, *F* = 2.08, *n* = 12, *P* =

TABLE 1.—Effect of varying photoperiod and ambient temperature on total distance moved and maximum locomotor speed of *Ctenomys talarum* in an artificial burrow system. Sample size was 6 for each group. There were no significant differences in either distance or speed ($P > 0.05$) when photoperiod or ambient temperature (T_a) was varied. Photoperiod of 12L:12D is seminatural.

Experimental condition		Distance moved (m/day)		Maximum locomotor speed (m/s)	
Photo-period	T_a (°C)	\bar{X}	<i>SD</i>	\bar{X}	<i>SD</i>
12L:12D	21 ± 2	163.18	39.18	0.75	0.01
0L:24D	21 ± 2	131.25	41.14	0.76	0.02
12L:12D	10	206.94	77.57	0.75	0.01
12L:12D	35	210.59	88.79	0.74	0.01

0.18) or ambient temperatures (ANOVA; $d.f. = 1, F = 0.27, n = 12, P = 0.60$; Table 1).

No relationship between body size and total distance moved per day or between body size and maximum locomotor speed was found (total distance moved per day; ANOVA; $d.f. = 1, F = 1.42, n = 24, P = 0.25, r^2 = 0.01$; maximum speed; ANOVA; $d.f. = 1, F = 1.21, P = 0.29, r^2 = 0.01$).

DISCUSSION

Distance moved per day in *C. talarum* is notably shorter than distances moved in natural burrows by other fossorial rodents (*T. bottae*, 574 m/day—Gettinger 1984; *Nannospalax ehrenbergi*, 462 m/day—Zuri and Terkel 1996).

Phylogenetically unrelated subterranean rodent species have similar burrow-system designs (Begall and Gallardo 2000; Nevo 1999). However, local differences in soil attributes and natural history and physiology of different burrowing species contribute to intra- and interspecific differences in diameter and depth of tunnels and total burrow lengths (Andersen 1982; Best 1973; Heth 1989). For example, natural burrows of *C. talarum* (14 m—Antinuchi and Busch 1992) are considerably shorter than natural

burrow lengths of 48 m that have been reported for *T. bottae* (Reichman et al. 1982) and 29 m for *N. ehrenbergi* (Zuri and Terkel 1996). Yet total distances moved by these species relative to lengths of their burrow systems remain similar. If one assumes that total distance moved per day by *C. talarum* in the artificial burrows was similar to distance moved in a natural burrow of similar length, the ratio of total distance moved to total burrow length for this species is about 13:1, within the range of ratios for the other fossorial species (12:1 and 16:1, respectively, for *T. bottae* and *N. ehrenbergi*).

Movement of other fossorial mammals within their burrow systems is associated with feeding (Bennett 1992), maintenance of burrow systems, or territorial defense (Zenuto et al. 2001) and are constrained by soil characteristics that determine plant cover as well as burrow-system size (Comparatore et al. 1991). Even though diet and availability of food are very different among subterranean species, these similar ratios might reflect a compromise between energy cost of travel through burrows and the times needed to travel to detect or avoid predators, to repel competitors, to maintain the tunnels, and to feed.

Luna et al. (2000) report that neither photoperiod nor temperature was an effective zeitgeber for entrainment of activity in *C. talarum*. They suggest that the arrhythmic activity they observed was related to a need for constant burrow defense, which likely was independent of environmental influences and, therefore, not directly responsive to photoperiod or temperature. Our results are consistent with this reasoning. Total distances moved should also relate to size of burrow system and locomotor speed and not to ambient conditions of temperature or photoperiod.

Maximum speeds in *C. talarum* are not dramatically different from those reported for *C. fulvus* (1 m/s—Hickman 1985) but are greater than those of other fossorial species (*Tachyoryctes splendens*, 0.12 m/s—

Hickman 1983; *T. bottae*, 0.25 m/s—Vleck 1979). Subterranean rodents show general body modifications that enhance digging and excavation of burrows (Stein 2000). Such modifications to limb structure contribute to relatively lower running speeds than those expected for surface-dwelling rodents of the same body mass as *C. talarum* (Garland 1983). Locomotor speed affects total distance traveled in a given period of time, contributing to greater total distances moved per day in surface-dwelling species (Kenagy and Hoyt 1989; Thompson 1985).

Because larger species typically run faster than smaller ones (Farley et al. 1993; Garland 1983; Taylor et al. 1970), one might hypothesize relationships between body size and total distance moved per day and between body size and maximum locomotor speed. No such relationships could be demonstrated in our study. Kenagy and Hoyt (1989) suggest that by running rather than walking around their home ranges, *Spermophilus saturatus* saves both time and energy. In herbivorous subterranean rodents, home range is restricted to the relatively smaller, immediate area of the burrow system, where food resources are generally predictable. It seems likely that the slower speeds at which *C. talarum* moves through burrow systems would have only negligible effects on daily energy expenditures.

Adaptations for subterranean existence evolved several times during the Miocene, Pliocene, and Pleistocene, following episodes of cooling and aridization (Nevo 1999). Despite the assumption that the subterranean niche imposes similar selective pressures on all its mammalian inhabitants, regional variation in climate, soils, and vegetation may be important in generating adaptive differences among species (Busch et al. 2000). Therefore, differences in the degree of commitment to subterranean life can be observed. Whereas African and Asian species are active almost exclusively underground, North and South American species use the surface to forage on aerial

parts of plants near the burrow openings (Comparatore et al. 1995; Gettinger 1984).

Usually, it has been assumed that subterranean rodents are protected from intensive predation (Nevo 1979, 1995; Reig et al. 1990). However, Busch et al. (2000) proposed a dichotomy regarding the degree of predation on different lineages of subterranean rodents that depends on their commitment to fossoriality. In African and Asian species, which spend much less time aboveground, predation pressures within the burrow appear to be important (Busch et al. 2000), whereas in North and South American species, aboveground predation appears to be more important. African and Asian species like *T. splendens* move more slowly (Hickman 1983) than do geomyid and ctenomyid species (*T. bottae*—Vleck 1979; *C. fulvus*—Hickman 1985; *C. talarum*, this study) and are preyed upon underground, mostly by snakes (Busch et al. 2000). Although data on predation within the burrow system of *C. talarum* are scarce, snakes such as *Bothrops alternatus* (yará) have been captured in their burrows. When snakes were found within burrows, the tunnel that connects with other parts of the tunnel system was found plugged, probably as a defense mechanism (C. D. Antinuchi, in litt.). Maximum speed of these snakes, which move with concertina locomotion inside the burrow, is low (<0.5 m/s—M. Meneghel, in litt.), and the observed speed of individuals of *C. talarum* should easily allow them to evade snakes within burrows. In contrast, predation upon *C. talarum* aboveground is high (Vassallo et al. 1994), and predators such as raptors, faster than snakes, would exert strong selection pressure for greater locomotor speeds in this species.

Trends that are observed in locomotor performance of fossorial rodents probably result through an interplay of selection pressures. Greater subterranean specialization requires morphological adaptations that improve digging, at the expense of speed and distances traveled. Lesser commitments

to subterranean life, associated with above-ground food habits and increasing predation pressures, tend to favor morphologies more suited for traveling performance, at the expense of exaggerated morphological adaptations for digging.

RESUMEN

Ctenomys talarum es un roedor subterráneo que mantiene territorios exclusivos mediante movimientos dentro del sistema de túneles. En este estudio evaluamos la distancia recorrida en un sistema de cuevas artificial y la velocidad natural máxima alcanzada en 24 h. La distancia recorrida diaria fue de $179.99 \text{ m} \pm 69.62 \text{ DE}$ y la relación entre distancia recorrida y largo total de los túneles fue de 12.4:1. La velocidad máxima fue de $0.75 \text{ m/s} \pm 0.01 \text{ DE}$. No se observó relación entre la distancia recorrida o la velocidad y el fotoperíodo o la temperatura ambiental, así como entre la masa corporal y la distancia recorrida o la velocidad. La distancia recorrida por *C. talarum* esta relacionada con el mantenimiento de los sistemas de galerías y la defensa territorial y la velocidad, probablemente en respuesta a presiones de predación en superficie.

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