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Mole rats (*Spalax ehrenbergi*) select bypass burrowing strategies in accordance with obstacle size

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Abstract Mole rats inhabit extensive individual tunnel systems. Since the energetic cost of burrowing far exceeds that of surface locomotion, excellent orientation ability is crucial. Here we examined whether mole rats can bypass an obstacle (ditch) intersecting an existing tunnel in order to rejoin the two tunnel sections. The mole rats dug two bypass types, depending on the size of the obstacle confronting them: a bypass around the small ditches, parallel and close to the ditch walls; or a bypass beneath the floor of the large ditches. These results demonstrate that the mole rat has the ability to avoid obstacles by digging accurate and energy-conserving bypass tunnels. In order to utilize such a capacity, the mole rat must possess both the means to evaluate the size of the obstacle as well as the ability to perceive its exact position relative to the original tunnel that it will rejoin. Possible mechanisms of orientation that could explain such ability are briefly discussed.

Introduction

The blind mole rat is a solitary, subterranean rodent that digs and inhabits its own individual extensive and winding tunnel system, which it never leaves unless forced to. Burrowing incurs high energetic costs (Vleck 1979, 1981) and involves contending with a hypoxic and hypercapnic atmosphere (Arieli 1990). Thus, there is strong evolutionary advantage for the mole rat, like other subterranean mammals, to possess a highly developed directional orientation sense in order to avoid unnecessary digging.

Due to inherent difficulties in observing and studying subterranean mammals both in the laboratory and the field, information about spatial orientation ability of subterranean animals is limited. High homing ability has

been found both in *Thomomys* (Howard and Childs 1959) and in *Scapanus* (Giger 1973). The European mole can deviate from its set course in order to avoid local obstacles and then resume its previous direction. High spatial learning and memory ability has been found in the blind mole rat (Kimchi and Terkel 2001). Further, when parts of the burrow systems of the African mole rat are damaged, the animals reconnect them by new tunnels parallel to the original destroyed section (Eloff 1951). The ability to reconstruct destroyed tunnels efficiently has also been suggested from incidental observations in the pocket gopher (Reichman and Smith 1990), golden mole (MacDonald 1985), naked mole rat (Brett 1991) and African mole rat (Jarvis and Sale 1971).

This study examined under controlled field conditions the blind mole rat's ability to detour various sized obstacles (ditches) blocking its tunnel and reconnect the two tunnel sections with minimum energy cost.

Methods

Animals and study site

The experiment was conducted on the blind mole rat (*Spalax ehrenbergi*) at sites around the Tel-Aviv area, Israel, in uncultivated open fields consisting mostly of grasses and geophytes. It was carried out over 1998–2000 during the rainy season (October to April) when the mole rats are highly active.

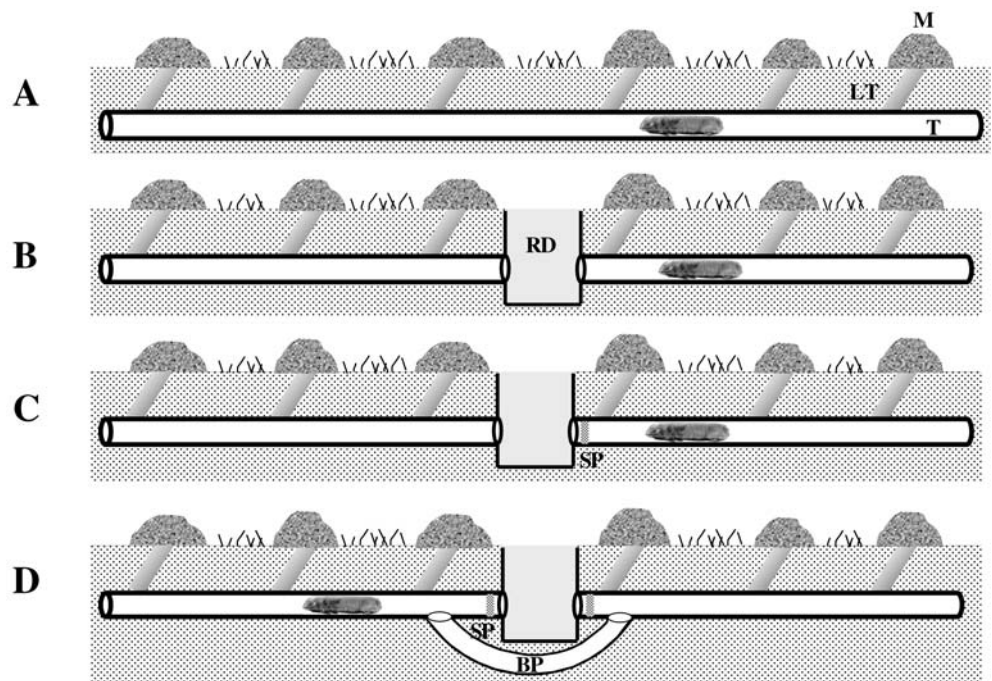
Procedure

Above-ground signs of mole rat activity can be seen in the appearance of new mounds of excavated soil. We located active mole rat territories that had a continuous straight line of at least six mounds (Fig. 1A). We then created one obstacle in each territory by opening up a section of a tunnel and digging a rectangular ditch across it, with at least three mounds on each side. All ditches were dug to a depth of 15–20 cm below that of the mole rat's tunnel (Fig. 1B). The ditches were divided into two categories according to size: (1) small ditches in five different sizes and (2) large ditches in four different sizes.

The second part of the procedure was based on the reliable and consistent natural behavior of the mole rat. Since normally its tunnel system has no surface exits, it tends to block any exposed part of the tunnel with a soil plug (Fig. 1C). One day after

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Fig. 1 Schematic drawing of the stages in obstacle detour by the mole rat: **A** an active mole rat territory with a straight line of mounds, **B** a rectangular ditch dug to intersect the tunnel, **C** soil plug placed by mole rat to block one side of exposed tunnel openings, **D** exposed bypass dug by mole rat to reconnect the two sections of the tunnel, after blocking both tunnel openings. *T* straight line tunnel, *M* mound, *LT*= lateral tunnel, *RD* rectangular ditch, *SP* soil plug, *BP*= bypass tunnel



positioning the ditches, we examined whether the mole rats had indeed sealed both tunnel openings (positioned at the two opposite side walls of the ditch). Soil blocking both openings indicated that the animal had dug a bypass to reconnect the two sections and could again pass freely along the entire tunnel. If both sides were not sealed we continued to examine the ditch daily for 5 days. Whenever soil blocks were observed on both sides of the ditch we used a hoe to expose the bypass tunnel that had reconnected the two sides of the original tunnel (Fig. 1D).

The bypass tunnels were measured (see below), photographed and later drawn to scale on graph paper. Each mole rat was tested only once.

Parameters measured

The following data were collected: total length of bypass tunnel, distance of bypass tunnel from ditch, depth of original tunnel, depth of bypass tunnel, and bypass pattern. To determine the energetic efficiency of burrowing the bypass tunnel, we calculated an additional parameter that we termed “bypass burrowing efficiency”, which was the ratio between the length of the bypass dug by the mole rat and the shortest theoretical bypass length expressed as a percentage. The latter length took into account that any bypass tunnel must be at least 10 cm from the ditch boundary in order to prevent it collapsing into the ditch.

Energy cost estimation

The mole rats dug two different types of bypasses: (1) burrowing around the ditch borders (side bypass) or (2) burrowing under the ditch floor (beneath bypass).

To estimate actual energy cost of burrowing the bypass tunnel, as well as theoretical energy cost had the mole rats used the alternative possible strategy (beneath bypass in the large ditches or side bypass in the small ditches), we used the formula provided by Vleck (1979, 1981).

Statistical analysis

The length of bypass actually dug was compared with the theoretical shortest possible bypass, using a paired *t*-test for each of the ditch sizes followed by a combined probabilities test (χ^2 test)

for all independent *t*-tests in each size category. This comparison was done separately for the two categories of ditch size. The burrowing efficiencies of bypass tunnels (Table 1) for small ditches (side bypasses) were compared with those for large ditches (beneath bypasses) using the Mann-Whitney *U* test (Table 1). Finally, the actual energetic cost of digging the specific type of bypass tunnel was compared with the theoretical cost if the mole rat had used the alternative type of bypass tunnel (Wilcoxon’s signed ranks test for each of the ditch sizes and then combined probabilities test in each size category). This comparison was done separately for the two categories of ditches.

Results

It was found that 72% (36/50) of the mole rats burrowed a bypass tunnel and reconnected the two sections of the original tunnel when encountering a small rectangular ditch, compared with 67% (23/34) when encountering a large rectangular ditch. Even mole rats that did not reconnect their tunnel segments did block one of the openings, for all ditches.

Mole rats that rejoined the two parts of the disconnected tunnel burrowed the bypass using one of the two strategies, according to the size of the obstacle. For small ditches all mole rats dug their bypass around the ditches, at a distance of 15–30 cm from the ditch edges and at the depth of the original tunnel. For large ditches, all the mole rats dug the bypass 10–15 cm beneath the ditch bottom.

Regarding the large ditches, no significant difference was found between the length of the actually burrowed bypass and the theoretically shortest possible beneath bypass (Table 1, $\chi^2_8=15$, $P=0.6$). However, for the small ditches the length of the burrowed bypass was significantly longer than the theoretically shortest possible side bypass (Table 1, $\chi^2_{10}=55$, $P<0.01$). Despite the above, no

Table 1 Length of actually dug bypass compared with the theoretical shortest possible length for different size ditches. Bypass burrowing efficiency parameter was calculated by dividing

the length of the actual bypass tunnel dug by each mole rat by the shortest theoretical length of bypass

Type of obstacle	Ditch size (cm)	N	Type of ypass	Length of bypass (cm)		Bypass burrowing efficiency (%)
				Shortest theoretical bypass	Actual dug bypass (mean±SE)	
Small ditch	60×20	7	Side ^a	120	194±19	135±15
	60×50	13	Side	150	186±14	124±13
	90×40	6	Side	170	230±13	135±9
	150×20	5	Side	210	225±17	107±11
	120×60	5	Side	220	250±15	114±12
Large ditch	300×20	7	Beneath ^b	90	97±10	108±8.0
	400×20	5	Beneath	90	105±5	116±5.8
	300×40	6	Beneath	110	120±11	109±4.5
	300×50	5	Beneath	120	125±15	104±6.5

^a Side bypass: bypass tunnel burrowed parallel to the ditch walls at the same depth as the original tunnel system ^b Beneath bypass: bypass tunnel burrowed beneath the ditch floor

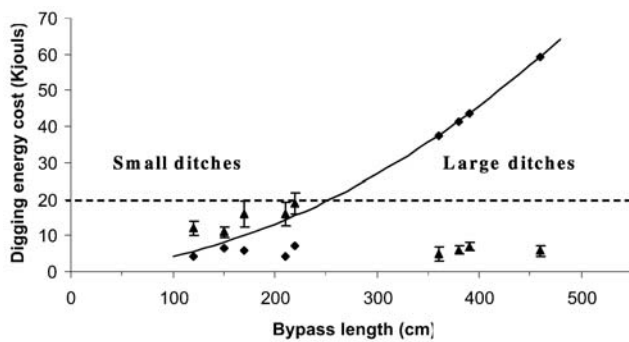


Fig. 2 Actual and theoretical energy cost of two bypass burrowing strategies in different size ditches. ▲ Actual energy cost (mean±SE) of bypass burrowing for small (side bypass) and large (beneath bypass) ditches. ◆ Theoretical energy cost of the alternative strategy of bypass burrowing for small (beneath bypass) and large (side bypass) ditches. Regression *curved line* represents minimum energy cost of side bypass burrowing for different ditch boundary lengths; based on Vleck (1979, 1981). *Dashed line* represents maximum ditch boundary length for which mole rat used side bypass; and maximum distance between two mounds observed in the field (Heth 1989; Zuri and Terkel 1996)

significant difference was found between burrowing efficiencies of bypasses for small and large size ditches (Table 1, $U_{5,4}=4$, $P=0.14$).

Calculation of energy cost of burrowing the side bypass (in small ditches) revealed that mole rats expended 11–19 kJ (depending on ditch size); whereas burrowing a beneath bypass (in large ditches), required an expenditure on average of only 5–7 kJ (Fig. 2). When the actual energy cost expended in digging the specific type of bypass tunnel was compared with the theoretical energy cost of using the alternative type of bypass (Fig. 2), it was found that for small ditches, actual energy expended to dig the side bypass was significantly greater than for the alternative strategy (a beneath bypass) ($\chi^2_{10}=22$, $P<0.05$). Conversely, actual energy cost expended to dig a beneath bypass under large ditches was significantly lower than for the alternative strategy ($\chi^2_8=61$, $P<0.001$).

Discussion

The subterranean niche offers shelter from the surface environment, escape from surface predators and access to underground food resources. These advantages are gained at the expense of the high energetic cost of burrowing (Vleck 1979). Adaptations that affect the energy balance when burrowing are subject to intense selection in fossorial mammals. In the natural habitat of subterranean mammals, sections of tunnel system are occasionally prone to collapse due to external mechanical forces (e.g. rain, animals), thus blocking the tunnel or exposing part to the surface.

In this study we examined the ability of mole rats to construct a detour around different sized ditches in order to rejoin the original tunnel. We found that they used two different bypass strategies depending on the size of ditch encountered. They burrowed a bypass around ditches of up to 150 cm length, and a bypass beneath large (over 300 cm length) ditches. None of the animals encountering a large ditch attempted to dig a bypass around it, and none of the animals encountering a small ditch attempted to dig a bypass beneath it.

Theoretical calculation of bypass length and energy cost of burrowing a bypass using each of the two above strategies, revealed that a bypass burrowed beneath the ditch floor is the shortest and most energy saving for both large and small ditches.

Field studies of the tunnel structure of mole rats have revealed that tunnel depth remains constant if climate (i.e. rainfall) and microclimate (i.e. soil type) factors do not change significantly. In the rainy season (the time of this study) mole rats always burrow their tunnels 15–20 cm below the surface (Heth 1989, 1991; Zuri and Terkel 1996). Several primary factors influence optimal tunnel depth for the mole rat: cost of burrowing increases with burrow depth, primarily due to correlation between depth and lateral length (working against gravity) (Vleck 1981). Therefore, mole rat burrows should theoretically be as close to the surface as possible. Further, as the mole rat randomly searches for underground geophytes (Heth et al. 1989), its tunnel depth must also correspond to the

geophyte's depth. Consequently, depth of the foraging burrows probably represents a compromise between energetic costs and the depth of its subterranean food. Indeed, a field study has shown that the depth of roots and bulbs eaten by the mole rat in Israel (Galil 1960) correlates well with its tunnel depth (Heth 1991). Any significant change in tunnel depth would therefore expose the mole rat to conditions unfavorable to survival. Thus it is highly reasonable to assume that for all ditch sizes the mole rat would prefer not to increase burrowing depth unless essential.

The mole rat's solution to this conflict when it is faced with small ditches, requiring only slightly more energy to burrow a bypass around than beneath, is to maintain burrow depth and use a side bypass. However, when faced with large ditches, requiring much greater (6–10-fold) energy expenditure to burrow a side bypass than to burrow beneath it (Fig. 2) it will shift its strategy, dig a beneath bypass and then return to optimum burrowing depth.

According to Vleck (1981) a segment length ranging from 0.6 to 2.4 m corresponds to the minimum energy cost per meter burrowed by the pocket gopher. This range was found to be highly correlated with the distance between two mounds actually dug by the mole rat (Heth 1989; Zuri and Terkel 1996). In the present study it was also shown that if the detour length is less than 250 cm the mole rat remains at the optimum tunnel depth and uses a side bypass to detour a ditch. However, when the theoretical detour segment length greatly exceeds that requiring minimum energy expenditure, it will alter the burrowing strategy that otherwise enables it to remain within the optimum segment length range (Fig. 2).

The behavior described here demonstrates that the mole rat possesses highly efficient spatial orientation ability, enabling it to avoid obstacles by digging short, accurate bypass tunnels. To succeed in this, it must be able both to evaluate the size of the obstacle and to perceive its own exact position relative to the original tunnel that it wishes to rejoin.

We suggest two mechanisms of orientation that might explain such ability. Mole rats produce seismic signals for intraspecific communication, by tapping their head on the tunnel roof, to which other mole rats respond both behaviorally and neurologically (Heth et al. 1987; Rado et al. 1987, 1998). Such seismic vibrations might also be used for orientation. The mole rat might detect differences in reverberation according to the different type and size of the medium encountered (soil, rock or air). Thus, it is quite possible that they were able to sense the dimensions of the ditch from the differently reverberating signals, and consequently selected the best strategy to detour round it (Kimchi and Terkel 2002).

Further, to reach the disconnected far tunnel section and accurately rejoin the two damaged sections the mole rat may also possess a mental map of its tunnel system mainly based on a memorized set of landmarks (Gallistel 1990). Such a map enables high flexibility, so that if one path leading to a goal is blocked another can be easily found and followed, or if one prominent landmark is destroyed an alternative landmark can be used (O'Keefe and Nadel 1978).

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