



# Detours by the blind mole-rat follow assessment of location and physical properties of underground obstacles

TALI KIMCHI & JOSEPH TERKEL

Department of Zoology, George S. Wise Faculty of Life Sciences, Tel-Aviv University

(Received 3 July 2002; initial acceptance 28 August 2002;  
final acceptance 19 February 2003; MS. number: 7388R)

Orientation by an animal inhabiting an underground environment must be extremely efficient if it is to contend effectively with the high energetic costs of excavating soil for a tunnel system. We examined, in the field, the ability of a fossorial rodent, the blind mole-rat, *Spalax ehrenbergi*, to detour different types of obstacles blocking its tunnel and rejoin the disconnected tunnel section. To create obstacles, we dug ditches, which we either left open or filled with stone or wood. Most (77%) mole-rats reconnected the two parts of their tunnel and accurately returned to their original path by digging a parallel bypass tunnel around the obstacle at a distance of 10–20 cm from the open ditch boundaries or 3–8 cm from the filled ditch boundaries. When the ditch was placed asymmetrically across the tunnel, the mole-rats detoured around the shorter side. These findings demonstrate that mole-rats seem to be able to assess the nature of an obstacle ahead and their own distance from the obstacle boundaries, as well as the relative location of the far section of disconnected tunnel. We suggest that mole-rats mainly use reverberating self-produced seismic vibrations as a mechanism to determine the size, nature and location of the obstacle, as well as internal self-generated references to determine their location relative to the disconnected tunnel section.

© 2003 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Spatial orientation is among the most fundamental of the cognitive processes that animals require for survival. Without the ability to orient accurately, animals would have difficulty in finding food and water sources, in returning to their nest or home, and in locating potential mates. Almost all studies of spatial orientation to date have concerned animals that live above ground (reviewed by Able 1980; Schöne 1984; Thinus-Blanc 1996; Wehner et al. 1996; Healy 1998; Golledge 1999). Only limited work has been done on subterranean mammals, owing to the inherent difficulties of observing and studying them, both in the laboratory and in the field (Burda et al. 1990a).

The blind mole-rat, *Spalax ehrenbergi*, is a fossorial rodent that digs and inhabits its own individual, extensive and winding underground tunnel system (Heth 1989; Zuri & Terkel 1996). Like other subterranean mammals that construct burrow systems, it requires a highly developed and efficient directional orientation sense if it is to survive in its harsh underground environment (Hildebrand 1985). The mole-rat must contend with the high energy demand of excavating soil, which may reach as much as 360–3400 times more than the

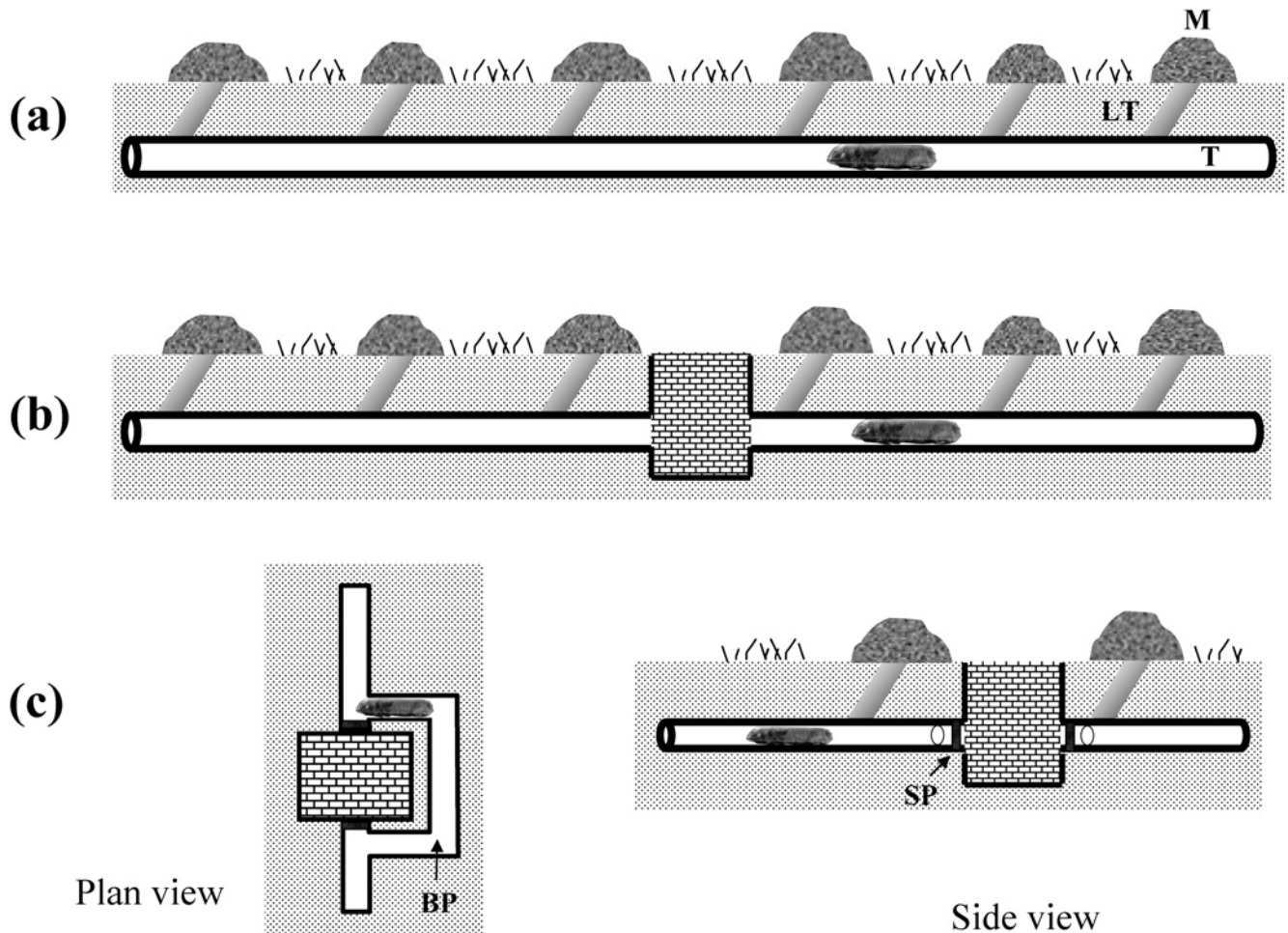
energy required when moving the same distance above ground (Vleck 1979, 1981), as well as the hypoxic and hypercapnic atmosphere within a sealed tunnel system (Arieli 1990).

In a series of laboratory experiments, we showed that the mole-rat possesses the ability to orient towards a goal in a complex tunnel system, and that it uses at least three mechanisms of orientation: (1) motor sequence orientation (Watson 1907) in which the animal learns and memorizes a specific route (sequence of turns) leading to the goal (Kimchi & Terkel 2001a); (2) path integration (Gallistel 1990), based on gathering and integrating self-generated cues to update its position relative to the departure and goal point (Kimchi & Terkel 2002b); and (3) the earth's magnetic field (Kimchi & Terkel 2001b).

In addition to finding the shortest path to a goal, efficient orientation below ground also requires the ability to avoid or detour any obstacle blocking the animal's path. In a field study (Kimchi & Terkel 2003), we reported on the ability of mole-rats to detect the presence of different-sized ditches that we had dug to block their tunnel path, to estimate the ditch size, and to burrow a highly efficient bypass to detour the obstacle and rejoin the disconnected tunnel section.

In the present study we investigated whether the mole-rat can distinguish between obstacles of different

Correspondence: T. Kimchi, Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv, 69978, Israel (email: kimhita@post.tau.ac.il).



**Figure 1.** Schematic drawing of the stages of the experiment on obstacle detouring by the mole-rat. (a) An active mole-rat territory with a straight line of mounds; (b) a rectangular ditch filled with stone bricks dug to intersect the tunnel; (c) exposed bypass dug by mole-rat to reconnect the two sections of the tunnel, after it had blocked both tunnel openings with soil as seen from the side and above. T=straight-line tunnel; M=mound; LT=lateral tunnel; SP=soil plug; BP=bypass tunnel.

densities: an empty (open) ditch, or a ditch filled with wood or stone. Then, by digging asymmetrical open ditches, we examined the ability of the mole-rat to estimate the relative position of an obstacle blocking its tunnel and to identify the shortest side along which to dig its bypass. Finally, by varying the obstacle's spatial arrangement relative to the mole-rat's disconnected tunnel, we examined whether it can assess the direction and distance of the separated, far tunnel section, relative to its present position.

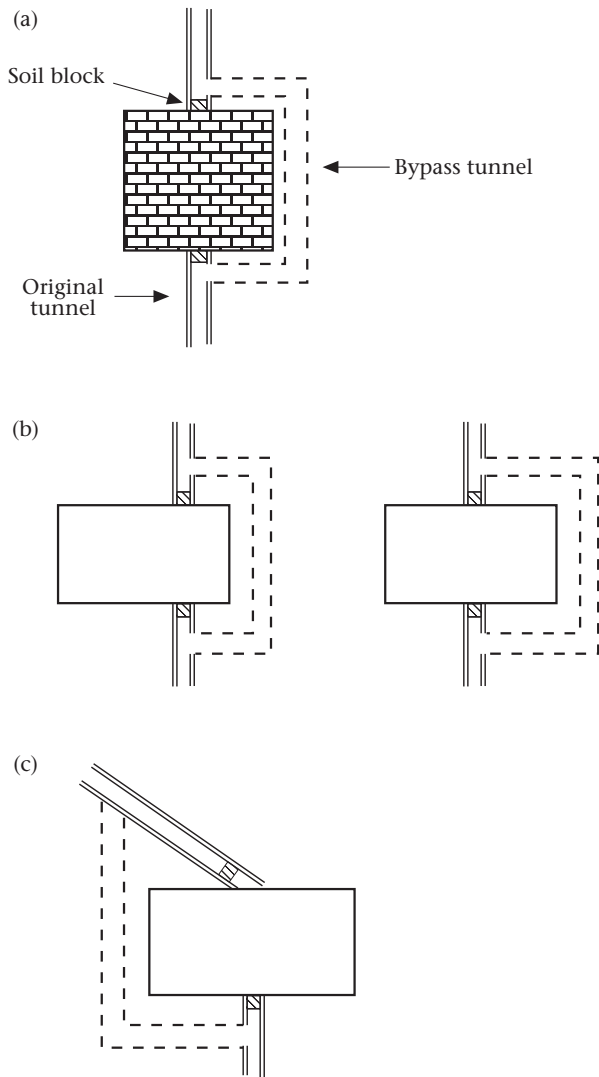
## METHODS

### Study Animals and Study Site

We studied blind mole-rats belonging to the chromosomal species  $2N=58$  (Nevo 1991), at three sites around the Tel-Aviv area, Israel. The sites were uncultivated open fields with dominant vegetation of grasses and geophytes. The study was carried out over 3 years (1998–2001) during the rainy season (October to April) when the mole-rats are highly active, in contrast to the dry season.

### Procedure

In the field, mole-rat activity can be identified by the appearance of new mounds of excavated soil, either in a straight line or scattered over the field. We chose active mole-rat territories that had a continuous straight line of at least six fresh mounds (the freshest mound has the moistest soil; Fig. 1a). We then created an obstacle by digging a rectangular ditch across a tunnel so that at least three mounds could be observed from each side of it (Fig. 1b). The ditches were dug symmetrically or asymmetrically with respect to the tunnel at a depth of 15–20 cm below that of the mole-rat's tunnel (i.e. if tunnel depth was 20 cm beneath the surface, ditch depth was set 35–40 cm beneath the surface; Fig. 1b). The ditches were divided into four categories: (1) two sizes of symmetrical ditches filled with stone bricks ( $60 \times 50$  and  $140 \times 40$  cm; Fig. 2a); (2) two sizes of symmetrical ditches filled with wooden planks ( $60 \times 20$  and  $60 \times 50$  cm); (3) an open ditch ( $80 \times 40$  cm) placed asymmetrically so that the mole-rat's tunnel axis was placed 15 cm from one side of the ditch and 65 cm from the other (asymmetrical



**Figure 2.** Different strategies of bypass burrowing for different types of obstacles. (a) Wood and stone obstacles. (b) Asymmetrical open ditch type I and symmetrical ditch. (c) Asymmetrical open ditch type II.

ditch type I, Fig. 2b) and burrowing a bypass around the shorter side would require significantly less energy; and (4) an open ditch (80 × 40 cm) placed symmetrically relative to the tunnel axis to be used (for comparison with the asymmetrical ditch).

To determine whether the mole-rat can also assess the direction and distance of the disconnected tunnel section ahead, relative to its present position in its tunnel system, we chose a curved tunnel as identified by the location of the mounds above ground. An open symmetrical ditch (150 × 40 cm) was placed across the inflection of the tunnel curve (asymmetrical ditch type II, Fig. 2c). In all cases, the oblique far tunnel segment contained fewer mounds and was shorter than the straight tunnel segment on the near side of the ditch (Fig. 2c).

The second part of the procedure was based on the reliable and consistent natural behaviour of the mole-rat to block immediately with a soil plug any part of its

tunnel that becomes exposed to air. Twenty-four hours after positioning the obstacles, we returned to examine whether the mole-rats had sealed the tunnel openings at each end of the ditch. In the open ditches soil blocking could be seen easily from above. If both sides were not sealed we continued to examine the ditch daily for 5 days. Soil blocks at both tunnel openings indicated that the mole-rat had dug a bypass to reconnect the two sections of the tunnel and could again pass freely along the entire tunnel. After 5 days, if both openings had still not been blocked, the mole-rat was considered not to have burrowed a bypass.

Soil blocks adjacent to solid obstacles could be observed only after we had removed the materials with which we had sealed the tunnel openings. Thus, for solid obstacles we examined whether the mole-rats had sealed the tunnel openings only 5 days after positioning the obstacles. In all territories where soil blocks were observed on both sides of the obstacle we used a hoe to expose the bypass tunnel (Fig. 1c). These tunnels were then measured (see below), photographed and later drawn to scale on graph paper. Each mole-rat was tested only once.

## Parameters

We collected the following data from the exposed bypass tunnels: total length of bypass tunnel; distance of bypass tunnel from the ditch boundary; depth of original tunnel; depth of bypass tunnel. To examine the efficiency of burrowing the bypass tunnel, we derived a 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. In the open ditch type obstacles, the shortest theoretical bypass length took into account that any bypass tunnel must be at least 10 cm from the ditch boundary to ensure that it would not collapse into the ditch.

## Statistical Analysis

We compared the length of the bypass that was actually dug to the theoretical shortest possible bypass that could have been dug, using a paired *t* test for each of the ditch sizes, followed by a combined probabilities test ( $\chi^2$  test) for all independent *t* tests in each obstacle type. This comparison was done separately for the three obstacle types (ditch, stone and wood). A Mann-Whitney *U* test was used to compare the burrowing efficiencies of bypass tunnels between the obstacle types: (1) symmetric versus asymmetric (Types I and II) open ditches; (2) wood versus stone obstacles; (3) open ditches (symmetric and asymmetric) versus solid (stone and wood) obstacles.

## RESULTS

We found that 80% (8/10) of the mole-rats burrowed a bypass tunnel to reconnect the two sections of the original tunnel when encountering a stone obstacle, 82% (9/11) when encountering a wooden obstacle, and 72%

**Table 1.** Bypass burrowing strategies relative to size, physical properties and position of the obstacle

Type of obstacle	Percentage of dug bypasses (N)	Obstacle side preference	Distance from obstacle boundary (cm)
Symmetrical stone obstacle	80 (8)	Equally from both sides	3–8
Symmetrical wooden obstacle	82 (9)	Equally from both sides	3–8
Symmetrical ditch	72 (13)	Equally from both sides	10–20
Asymmetrical ditch, type I	71 (5)	Shorter side	10–20
Asymmetrical ditch, type II	71 (5)	Shorter side	10–20

Different groups of mole-rats were tested for each of the five types of obstacle (see Fig. 2). Each mole-rat was tested only once.

**Table 2.** Length of bypass dug ( $\bar{X} \pm SE$ ) compared to the theoretical shortest possible length for five types of obstacle

Type of obstacle	Size of ditch (cm)	N	Shortest theoretical bypass (cm)	Length of bypass (cm)	Bypass burrowing efficiency ( $\bar{X} \pm SE$ )
Stone obstacle	60×50	5	110	116±14	105±5
	140×40	3	180	191±4	106±3
Wooden obstacle	60×20	5	80	87±7	108±8
	60×50	4	110	115±5	105±4
Symmetrical ditch	80×40	10	150	186±14	124±13
Asymmetrical ditch, type I	80×40	5	110	134±13	122±14
Asymmetrical ditch, type II	150×40	5	160	192±15	120±11

In asymmetrical ditch type I, the ditch was dug across a straight tunnel section so that one side of the ditch was closer to the tunnel axis (Fig. 2b). The shortest theoretical bypass was calculated as a bypass from the side to which the tunnel axis was closest. In asymmetrical ditch type II the ditch was dug across a curved tunnel section (Fig. 2c). The shortest theoretical bypass was calculated as a bypass in the direction of the tunnel's internal curve. Bypass burrowing efficiency was calculated as the ratio between the length of the bypass and the shortest theoretical bypass length.

(23/32) when encountering either a symmetrical or an asymmetrical open ditch (Table 1).

Bypass tunnels around solid obstacles were dug closer to the obstacle than those dug around open ditches. The mole-rats dug their bypass around the solid stone or wooden obstacle boundaries at the depth of the original tunnel, keeping it parallel and close to the obstacle (3–8 cm, Fig. 2a), while around the open ditches the tunnels were dug at the same depth but at 10–20 cm from the boundaries (Fig. 2b), regardless of ditch size (Table 1).

When digging a bypass around a symmetrical open ditch, the mole-rats showed no significant laterality preference ( $\chi^2_1=0.39$ ,  $P=0.53$ ), whereas for ditches placed asymmetrically they always (10/10) burrowed around the shorter side of the ditch (Table 1, Fig. 2b, c).

It was apparent under all conditions that the mole-rat constantly evaluated its distance from the obstacle edge while burrowing, sensing when it had reached the corner of the rectangular obstacle, altering its burrowing direction according to the angle of the obstacle corner and continuing to burrow parallel to the obstacle's next side. This was repeated at each corner until the final turn, which reconnected the bypass burrow with the disconnected far section of the original tunnel (Fig. 2).

In the asymmetrical ditch type II (Fig. 2c) in every case the mole-rats retreated to the straight (main) part of their tunnel system as soon as we began to dig the ditch; thus they always approached the obstacle from the straight (near) tunnel section, and not from the shorter oblique (far) tunnel section (Fig. 2c). In all cases when the mole-rats reached the second corner of the obstacle they continued to burrow straight until they rejoined the original oblique tunnel, rather than turning to continue burrowing parallel to the third ditch wall, as occurred when the tunnel was straight (Fig. 2b, c).

The length of the bypass around the open ditch obstacle was significantly longer than the theoretically shortest possible side bypass ( $\chi^2_6=85$ ,  $P<0.01$ ; Table 2); whereas around stone and wooden obstacles no significant difference was found between the length of the bypass and the theoretically shortest possible bypass length ( $\chi^2_4=50$ ,  $P=0.6$ ,  $\chi^2_4=45$ ,  $P=0.7$ , respectively; Table 2). The measure of bypass burrowing efficiency for the solid obstacles was significantly greater than for the open ditches ( $U=295$ ,  $N_1=20$ ,  $N_2=17$ ,  $P<0.05$ ; Table 2), but no significant differences were found in bypass burrowing efficiency between the open symmetrical and asymmetrical ditches, or between the stone and wooden obstacles

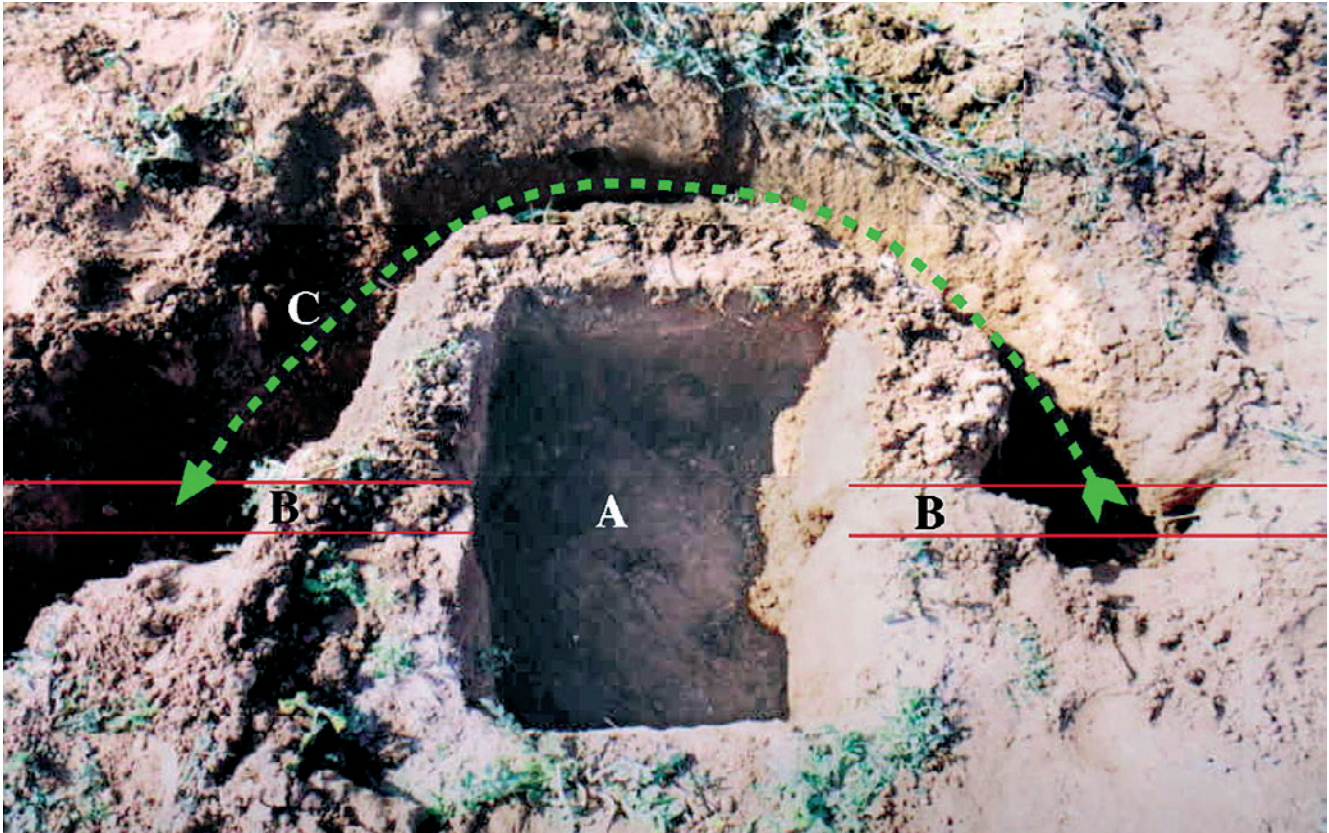


Figure 3. Actual bypass dug around a small ditch: A: Small ditch; B: location of the original tunnel; C: bypass tunnel around the ditch.

( $U=120$ ,  $N_1=N_2=10$ ,  $P=0.2$ ,  $U=50$ ,  $N_1=9$ ,  $N_2=8$ ,  $P=0.1$ , respectively; Table 2).

## DISCUSSION

Our results show that the mole-rat can efficiently detour obstacles blocking its tunnels by using various bypass burrowing strategies to find and rejoin its disconnected tunnel segment. Different bypass burrowing strategies were used depending on the physical properties of the obstacle encountered (Table 1): a side bypass, 10–20 cm from the obstacle boundaries, for symmetrical (Figs 2a, 3) and asymmetrical open ditches (Fig. 2b, c), or a side bypass 3–8 cm from the obstacle boundaries, for wooden or stone obstacles (Fig. 2a).

The choice of bypass burrowing strategy reflects a balance between energy conservation and safety. When the ditch is a solid obstacle, with no risk of the tunnel collapsing, digging can be close to the obstacle boundary, thereby conserving energy; with an open ditch the bypass must be far enough from its boundary to prevent its collapse into the ditch, thereby exposing the animal to the surface (Fig. 3).

The dimensions of the blocking obstacle also affect the bypass strategy. Kimchi & Terkel (2003) found that mole-rats dig a bypass around small ditches and under large ones (over 300 cm long). In the present study, all obstacles were significantly shorter than 300 cm, and in

all cases the mole-rats burrowed around rather than under the obstacle.

We also examined whether the mole-rat can estimate and compare the relative dimensions of both right and left arms of an obstacle placed asymmetrically with respect to its tunnel. The mole-rats in our study distinguished between the two arms and burrowed their bypass along the shorter side, while showing no preference for a particular side in symmetrically placed ditches (Fig. 2b, Table 1). The mole-rat can thus accurately estimate the shorter side before beginning to dig the bypass.

To complete a detour tunnel the mole-rat must also estimate the location of the disconnected distal tunnel section and rejoin it accurately, thereby gaining a twofold profit. First, tunnel burrowing involves a high energy cost (Vleck 1979, 1981); thus, when the disconnected tunnel portion is significantly longer than the required bypass, it is more profitable to rejoin the tunnel than to abandon it. Second, the mole-rat's tunnel system contains valuable food resources in the storage chambers and a sleeping or reproductive nest, as well as routes to feeding sites and vital escape paths. The adaptive advantages of constructing a bypass to rejoin these resources are therefore clear (Table 2).

When we dug a ditch across the inflection of a curved tunnel (asymmetrical ditch type II), all the mole-rats selected the shortest side (positively correlated with the least angle of curvature of the tunnel; Fig. 2c), suggesting

an awareness of the spatial arrangement of their tunnel system and their own relative location.

### Mechanism of Orientation

Mammals living above ground use vision (Schöne 1984), hearing (e.g. bats: Busnel & Fish 1980; shrews: Gould et al. 1971; Forsman & Malmquist 1988) and touch (Carvell & Simons 1990) to estimate obstacle dimensions, location and nature.

In contrast, subterranean mammals such as the mole-rat are functionally blind, precluding use of vision, and possess poor auditory sensitivity to airborne sounds, limited to low-frequency sounds (Heffner & Heffner 1992), which are strongly attenuated by the soil. Finally, although mole-rats apparently have a well-developed tactile sense (Klauer et al. 1997; Kimchi & Terkel 2000), this sensory channel could not explain their detection and avoidance of obstacles in this study, since their bodies never touched the obstacle while bypass burrowing.

We suggest that the mole-rat uses seismic vibrations to detect and estimate obstacle characteristics. Mole-rats produce vibratory low-frequency seismic signals for communication by striking the head against the tunnel roof, to which other mole-rats respond both behaviourally and neurologically (Heth et al. 1987; Rado et al. 1987, 1998). This head drumming may also serve as an echolocation mechanism, with the mole-rat using vibrations reverberating from the obstacle to determine its size, shape and nature. In a preliminary field study we found that mole-rats frequently produced low-frequency seismic signals while burrowing a bypass. Spectral analysis revealed that these seismic waves can be used to detect buried objects with a vertical resolution of 10–30 cm (Kimchi & Terkel 2002a).

The second stage of successfully detouring an obstacle relates to goal orientation to the disconnected far tunnel section. This requires an orientation mechanism enabling precise assessment of both direction and distance of the goal relative to the animal's current position.

One possible mechanism is a mental map based on a memorized set of landmarks (Gallistel 1990; Bennett 1996). This enables the animal to be flexible, so that if one path leading to a goal is blocked another can be easily found and followed, or if one landmark is destroyed (e.g. by a storm) an alternative can be used (O'Keefe & Nadel 1978).

Below ground, subterranean mammals such as the mole-rat may use nonvisual cues, such as tactile references and self-motion cues, to organize their environment as a set of interlinked places. Starting from a familiar reference point, the animal may change its location and continuously update its position through self-motion cues. It thus constructs a map system by associating nonvisual stable references from the environment with self-generated position information (Etienne et al. 1999). Such a system allows it to plan and execute a suitable direct path (shortcut) to a goal through the principle of vector addition (Etienne et al. 1998).

Studies of two subterranean mammals, the African mole-rat, *Cryptomys bigalkei* (Eloff 1951) and the

European mole, *Talpa europea* (Quilliam 1966), found that after part of their tunnel system was destroyed they dug a new tunnel to reconnect the two sections. Similarly, laboratory rats, *Rattus norvegicus*, tested for their ability to reach a hidden goal by burrowing a tunnel in sand dug a direct path back to the departure site after a previously learned winding path connecting departure and goal sites was blocked (Zanforlin & Poli 1970). Since visual cues were unavailable, these burrowing species probably used internal cues (derived from the vestibular and somatosensory system) in a path integration process.

Use of path integration has been demonstrated in several surface-dwelling rodents tested in conditions resembling those found underground. Path integration based on purely internal cues enables animals to keep track of their position relative to their departure site, and subsequently return home by a direct path at the end of a foraging excursion (Mittelstaedt & Mittelstaedt 1980; Etienne et al. 1986, 1996; Benhamou 1997). A similar ability has been found in the blind mole-rat (Kimchi & Terkel 2002b).

One limitation of path integration in the absence of external references is that of rapid drifting (Etienne et al. 1988); however, if combined with stable external references its reliability is greatly enhanced (Benhamou et al. 1990). Subterranean mammals may use the earth's magnetic field as the primary directional reference to measure their rotation and thus compensate for the accumulation of errors in the path integration. Evidence for this is found in laboratory experiments in which the Zambian mole-rat, *Cryptomys anselli* (Burda et al. 1990b) and the blind mole-rat (Kimchi & Terkel 2001b) used the earth's magnetic field to determine the location of their sleeping nest. Blind mole-rats also used the geomagnetic field as a directional reference to find the path to a goal in a multiple labyrinth (Kimchi & Terkel 2001b). Other nonvisual landmarks such as directional, seismic and olfactory cues may provide additional long-term stable directional references (Kimchi & Terkel 2002a).

### Acknowledgments

We deeply appreciate the help of Dr A. Terkel and Ms N. Paz in preparing and editing the manuscript and Professor D. Wool for statistical advice. This study was supported by the Adams Super Center for Brain Studies, TAU. We also thank the two anonymous referees for their most helpful suggestions and comments on the manuscript.

### References

- Able, K. P. 1980. Mechanisms of orientation, navigation, and homing. In: *Animal Migration, Orientation, and Navigation* (Ed. by S. A. Gauthreaux), pp. 283–373. New York: Academic Press.
- Arieli, R. 1990. Adaptation of the mammalian gas transport system to subterranean life. In: *Evolution of Subterranean Mammals at the Organismal and Molecular Levels: Progress in Clinical and Biological Research* (Ed. by E. Nevo, O. A. Reig & R. Alan), pp. 251–268. New York: A. Liss.

- Benhamou, S. 1997. Path integration by swimming rats. *Animal Behaviour*, **54**, 321–327.
- Benhamou, S., Save, J.-P. & Bovet, P. 1990. Spatial memory in large-scale movements: efficiency and limitation of the egocentric coding process. *Journal of Theoretical Biology*, **145**, 1–12.
- Bennett, A. T. D. 1996. Do animals have a cognitive map? *Journal of Experimental Biology*, **199**, 219–224.
- Burda, H., Bruns, V. & Muller, M. 1990a. Sensory adaptations in subterranean mammals. In: *Evolution of Subterranean Mammals at the Organismal and Molecular Levels: Progress in Clinical and Biological Research* (Ed. by E. Nevo, O. A. Reig & R. Alan), pp. 269–293. New York: A. Liss.
- Burda, H., Marhold, S., Westenberger, T., Wiltshko, R. & Wiltshko, W. 1990b. Evidence for magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus* (Bathyergidae). *Experientia*, **46**, 528–530.
- Busnel, R. G. & Fish, J. F. (Eds) 1980. *Animal Sonar Systems*. New York: Plenum.
- Carvell, G. E. & Simons, D. J. 1990. Biometric analyses of vibrissal tactile discrimination in the rat. *Journal of Neuroscience*, **10**, 2638–2648.
- Eloff, G. 1951. Orientation in the mole-rat *Cryptomys*. *British Journal of Psychology*, **42**, 134–145.
- Etienne, A. S., Maurer, R., Saucy, F. & Teroni, E. 1986. Short-distance homing in the golden hamster after a passive journey. *Animal Behaviour*, **34**, 696–715.
- Etienne, A. S., Maurer, R. & Saucy, F. 1988. Limitations in assessment of path dependent information. *Behaviour*, **106**, 81–111.
- Etienne, A. S., Maurer, R. & Seguinot, V. 1996. Path integration in mammals and its interaction with visual landmarks. *Journal of Experimental Biology*, **199**, 201–209.
- Etienne, A. S., Maurer, R., Berlie, J., Reverdin, B., Rowe, T., Georgakopoulos, J. & Seguinot, V. 1998. Navigation through vector addition. *Nature*, **396**, 161–164.
- Etienne, A. S., Maurer, R., Georgakopoulos, J. & Griffin, A. 1999. Dead reckoning (path integration), landmarks, and representation of space in a comparative perspective. In: *Wayfinding Behavior: Cognitive Mapping and other Spatial Process* (Ed. by R. G. Golledge), pp. 197–228. Baltimore: Johns Hopkins University Press.
- Forsman, K. A. & Malmquist, M. G. 1988. Evidence for echolocation in the common shrew, *Sorex araneus*. *Journal of Zoology*, **216**, 655–662.
- Gallistel, C. R. 1990. *The Organization of Learning*. Cambridge, Massachusetts: Bradford Books/MIT Press.
- Golledge, R. G. (Ed.) 1999. *Wayfinding Behavior: Cognitive Mapping and other Spatial Process*. Baltimore: Johns Hopkins University Press.
- Gould, E., Negus, N. C. & Novick, A. 1971. Evidence for echolocation in shrews. *Journal of Experimental Zoology*, **156**, 19–38.
- Healy, S. 1998. *Spatial Representation in Animals*. Oxford: Oxford University Press.
- Heffner, R. S. & Heffner, H. E. 1992. Hearing and sound localization in blind mole rats (*Spalax ehrenbergi*). *Hearing Research*, **62**, 206–216.
- Heth, G. 1989. Burrow patterns of the mole rat *Spalax ehrenbergi* in two soil types (terra-rossa and rendzina) in Mount Carmel, Israel. *Journal of Zoology*, **217**, 39–56.
- Heth, G., Frankenburg, E. & Nevo, E. 1987. Vibrational communication in subterranean mole rats (*Spalax ehrenbergi*). *Behavioral Ecology and Sociobiology*, **21**, 31–33.
- Hildebrand, M. 1985. Digging of quadrupeds. In: *Functional Vertebrate Morphology* (Ed. by M. Hildebrand, D. M. Bramble, K. F. Liem & D. B. Wake), pp. 89–110. Cambridge, Massachusetts: Belknap Press.
- Kimchi, T. & Terkel, J. 2000. Importance of touch for the blind mole rat (*Spalax ehrenbergi*) in learning a complex maze. *Israel Journal of Zoology*, **46**, 165 (Abstract).
- Kimchi, T. & Terkel, J. 2001a. Spatial learning and memory in the blind mole rat (*Spalax ehrenbergi*) in comparison with the laboratory rat and Levant vole. *Animal Behaviour*, **61**, 171–180.
- Kimchi, T. & Terkel, J. 2001b. Magnetic compass orientation in the blind mole rat *Spalax ehrenbergi*. *Journal of Experimental Biology*, **204**, 751–758.
- Kimchi, T. & Terkel, J. 2002a. Seeing and not seeing. *Current Opinion in Neurobiology*, **12**, 728–734.
- Kimchi, T. & Terkel, J. 2002b. Mole rats (*Spalax ehrenbergi*) use path integration mechanism for spatial orientation. *Israel Journal of Zoology*, **48**, 172 (Abstract).
- Kimchi, T. & Terkel, J. 2003. Mole rats (*Spalax ehrenbergi*) select bypass burrowing strategies in accordance with obstacle size. *Naturwissenschaften*, **90**, 36–39.
- Klauar, G., Burda, H. & Nevo, E. 1997. Adaptive differentiations of the skin of the head in a subterranean rodent, *Spalax ehrenbergi*. *Journal of Morphology*, **233**, 53–66.
- Mittelstaedt, H. & Mittelstaedt, M. L. 1980. Homing by path integration in a mammal. *Naturwissenschaften*, **67**, 566–567.
- Nevo, E. 1991. Evolution theory and process of active speciation and adaptive radiation in subterranean mole rats, *Spalax ehrenbergi* superspecies in Israel. *Evolution Biology*, **25**, 1–125.
- O'Keefe, J. & Nadel, L. 1978. *The Hippocampus as a Cognitive Map*. London: Oxford University Press.
- Quilliam, T. A. 1966. The mole's sensory apparatus. *Journal of Zoology*, **149**, 76–88.
- Rado, R., Levi, N., Hauser, H., Witcher, J., Adler, N. I., Wollberg, Z. & Terkel, J. 1987. Seismic signalling as a means of communication in a subterranean mammal. *Animal Behaviour*, **35**, 1249–1251.
- Rado, R., Terkel, J. & Wollberg, Z. 1998. Seismic communication signals in the blind mole rat (*Spalax ehrenbergi*): electrophysiological and behavioral evidence for their processing by the auditory system. *Journal of Comparative Physiology*, **183**, 503–511.
- Schöne, H. 1984. *Spatial Orientation: The Spatial Control of Behavior in Animals and Man*. Princeton, New Jersey: Princeton University Press.
- Thinus-Blanc, C. 1996. *Animal Spatial Cognition. Behavioral and Neural Approaches*. Singapore: World Scientific.
- Vleck, D. 1979. The energy cost of burrowing by the pocket gopher *Thomomys bottae*. *Physiological Zoology*, **52**, 391–396.
- Vleck, D. 1981. Burrow structure and foraging cost in the fossorial rodent *Thomomys bottae*. *Oecologia*, **49**, 391–396.
- Watson, J. B. 1907. Kinesthetic and organic sensations: their role in the reaction of the white rat in the maze. *Psychology Review Monograph*, **8**, 1–100.
- Wehner, R., Michel, B. & Antonsen, P. 1996. Visual navigation in insects: coupling of egocentric and geocentric information. *Journal of Experimental Biology*, **199**, 129–140.
- Zanforlin, M. & Poli, G. 1970. The burrowing rat: a new technique to study place learning and orientation. *Licenziate le bozze il*, **16**, 653–670.
- Zuri, I. & Terkel, J. 1996. Locomotor patterns, territory, and tunnel utilization in the mole rat *Spalax ehrenbergi*. *Journal of Zoology*, **240**, 123–140.