University of South Bohemia in České Budějovice
Faculty of Science

Mgr. Thesis

Exploratory and spatial learning abilities in two African mole-rats with different social system.

Bc. Vladimír Mazoch
Supervisor: Mgr. Radim Šumbera, PhD.

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Annotation:
The goal of this study was to examine differences in the exploratory activity, spatial learning and memory between two strictly subterranean rodents with different social systems, solitary silvery mole-rat (*Heliophobius argenteocinereus*) and social giant mole-rat (*Fukomys mechowii*) in a maze resembling natural burrows. Although the giant mole-rats showed better performance in most of the parameters of the test, this could not be easily explained by superior learning abilities of social species. The differences found could be more attributed to different motivation in both species. The solitary mole-rat was remarkably more cautious and moved with lower velocity, spent more time in the maze, made more errors and traveled a longer path before reaching the reward box.

Prohlašuji, že svoji diplomovou práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury (I have worked out this thesis myself only with help of cited literature).

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své diplomové, a to v nezkrácené podobě – v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou - elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách.

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1. Introduction

1.1. Subterranean mammals

More than 300 mammal species, including at least 250 rodents, inhabit subterranean ecotope (Burda 2003; Nevo 1999). This unique dark environment is typical by relatively stable temperature and humidity. On the other hand, due to the high energy cost of movement (Vleck 1979), low food supply and expected high concentration of CO_2 and low O_2 (Burda et al. 2007) subterranean existence could be very harsh and demanding.

1.2. African mole-rats (Bathyergidae, Rodentia)

African mole-rats are an Old world family of hystricognathous rodents endemic to sub-Saharan Africa. All bathyergids are herbivorous, strictly subterranean rodents. They feed on geophytes - plants with subterranean storage organs as bulbs, roots and tubers, which are often patchily distributed. All bathyergids inhabit extensive systems of self-constructed burrows with most tunnels located in the depth of geophytes (Bennett & Faulkes 2000; Jarvis 2003).

Among mammals they are famous because of the remarkable variability in social systems. There is a gradient from strictly solitary genera (*Georychus*, *Bathyergus* and *Heliophobius*), through social (*Fukomys* and *Cryptomys*) and minimally two eusocial mole-rats (*Heterocephalus glaber* and *Fukomys damarensis*) (Jarvis & Bennett 1991).

1.3. Spatial cognition

Cognitive processes such as perception, learning and memory play an important role in foraging, mate choice and many other behaviors (Shettleworth 2001). Spatial orientation is defined as a self-controlled maintenance or change of body position relative to environmental space (Jander 1975). Navigation is the process of determining and maintaining a course or trajectory (Gallistel 1989) with the aim of finding a spatial goal by use of stimuli that have no predictable relationship to the goal (Dusenbery 1992).

1.4. Spatial orientation in subterranean mammals

Efficient spatial orientation in all animals is necessary for vital activities like finding food sources, mates and shelters. It is strongly emphasized in subterranean animals, due to the above mentioned high energy cost of excavation. Although the first comments on spatial behavior of subterranean mammals and its uniqueness is more than 50 years old (Eloff 1951), it has not received the attention of scientists for a long time. Almost all hitherto research on spatial orientation has been carried out only on surface-dwelling animals (for review see Healy 1998). Recent studies on subterranean rodents exaggerated outstanding navigational abilities of mammals living permanently in self-constructed underground burrows. For example, the blind mole-rat *Spalax ehrenbergi* is able to efficiently detour a disconnected tunnel in the field (Kimchi & Terkel 2003a; 2003b). In laboratory tests, in the absence of visual and olfactory cues, subterranean mammals also show superior navigational skills to surface dwelling mammals (Antinuchi & Schleich 2003; Kimchi & Terkel 2001b).

1.5. Sensory cues useful for navigation underground

Spatial tasks can be solved using allothetic cues, which are external and relatively independent to movements, or idiothetic cues, which come from vestibular or proprioreceptive systems (Whishaw et al. 1998). Animals utilize every possible external or internal cue for creating a cognitive map of their environment. For surface-dwelling animals the most important external cues are visual landmarks (Healy 1998). However, some sensory information is inaccessible or useless underground. Although subterranean mammals are able to perceive light for adjusting circadian activity or avoiding damaged tunnels, it seems they cannot use vision for navigation (Burda et al. 1990a; Němec et al. 2007).

Chemical signals play an important role in social interaction and food localization in subterranean animals (Heth & Todrank 2007). It can also have significance in topographic navigation. For example naked mole-rats are able to follow odor trails left by other family members (Judd & Sherman 1996). However, usage of chemical cues is limited by the absence of air currents necessary for scent transport.

Positional information about magnetic South and North could be another very useful source of information underground. In mammals, the usage of magnetic fields for direction finding were found first just for African mole-rats (Burda et al. 1990b). Similarly, some other subterranean rodents build their nests according to magnetic fields (Kimchi & Terkel 2001a; Marhold et al. 1997). Magnetic sense probably enables subterranean mammals to navigate within their extensive burrow systems. The blind mole-rat (*Spalax ehrenbergi*) assesses direction both through internal signals and by estimating its heading in relation to the earth’s magnetic field (Kimchi et al. 2004b). Although results from other experiments do not confirm usage of a magnetic sense in all subterranean rodents (Schleich & Antinuchi 2004) recent studies indicate that utilizing information obtained from magnetic fields, should be common not only in rodents (Deutschlander et al. 2003; Muheim et al. 2006) but also in other mammalian groups (Burda et al. 2008; Wang et al. 2007).

Due to the spatial isolation of solitary dwelling subterranean mammals, low-frequency signals are a good alternative for long-distance communication (Mason & Narins 2001). The Insectivorous subterranean golden mole (*Eremitalpa granti*) can use seismic waves for prey localization (Mason & Narins 2002). The silvery mole-rat (*H. argenteocinereus*) is able to detect vibrations from a distance of up to 6 meters (Šklíba et al. 2007). In addition, the blind mole-rat is able to estimate the location and physical properties of underground obstacles using reflected self-generated seismic waves. This specialized seismic echolocation system could be used to determine distance from an obstacle (or tunnel wall) without using vision (Kimchi et al. 2005).

Ability to navigate by relying mainly on self-motion cues and calculate a route through a process called path integration (Etienne & Jeffery 2004; Mittelstaedt & Mittelstaedt 1980) seems to be common in the African mole-rats. Nevertheless, for longer distances path integration is very sensitive to cumulative errors (Benhamou et al. 1990; Etienne et al. 1988; Etienne et al. 1998). The ability to detect and utilize magnetic fields could thus be a very useful tool in assessing stable external references for correcting this error (Kimchi et al. 2004b).

1.6. Factors influencing spatial learning performance

Complex interactions among society members like recognition and communication are fundamental for socially living animals. A social environment can encourage the evolution of increased learning and memory abilities in highly social species (Johnston 1982). The advanced learning and memory abilities associated with social life may also promote an increased capacity for learning other tasks, such as spatial learning (Dukas & Real 1991).

Only a few studies have focused on differences in learning and memory capacities between solitary and social animals. Bumblebees learn to distinguish between floral types of different quality more quickly than carpenter bees. It provides some evidence of superior spatial learning abilities in social species (Dukas & Real 1991). Variability in social systems and uniformity of their ecology made African mole-rats (at least among mammals) an ideal group for studying the influence of different degrees of sociality on the spatial learning processes. Costanzo (Costanzo 2005) denoted superior performance in the complex maze task by the eusocial bathyergid Damaraland mole-rat (*Fukomys damarensis*) to its solitary relative, the Cape mole-rat (*Georchychus capensis*).

2. Objectives

The main goal of this study was to test the navigational, exploratory and learning abilities of two mole-rats with different social systems in the absence of visual and olfactory cues in a complex maze simulating a natural burrow system. The burrow systems of social species (*Fukomys mechowii*) is continuously modified by other family members so we expect that this species possesses better short term spatial learning abilities. In contrast, the solitary mole-rats (*Heliophobius argenteocinereus*) build their burrow systems alone and the system is stable for longer periods. Therefore we expect better results from this species in the long term spatial memory tests.

3. Methods

3.1. Study animals

Giant mole-rat (*Fukomys mechowii*, Peters 1881)

The giant mole-rat *F. mechowii* is a social bathyergid with a mean colony size of about 10 individuals (Scharff et al. 2001; Sichilima et al. 2008). Among others members of the genus *Fukomys* (genus recently emancipated from genus *Cryptomys* see (Ingram et al. 2004; Kock et al. 2006), the giant mole-rat could be easily recognized because of its large size. It occurs in a variety of habitats in the Democratic Republic of Congo, Angola and Zambia (Burda 2001; Honeycutt et al. 1991; Scharff et al. 2001). The sexual dimorphism is displayed mainly in the size. Adult animals trapped in Zambia weighed 380 ± 95 g (mean ± SD), females 260 ± 35 g (Scharff et al. 2001), respectively in other locality 570.7 ± 20.7 g (males) and 391.3 ± 11.7 (females) (Sichilima et al. 2008).

Some of the animals tested were trapped in Zambia between the years 1995 -1999 (Ndola and Chichele). Others were born in captivity. Nine females, nine males and two subadults were used for testing.

Silvery mole-rat (*Heliophobius argenteocinereus*, Peters 1846)

The distribution of solitary silvery mole-rat covers southern Kenya, Tanzania, southeast Democratic Republic of Congo, Zambia, Malawi and northern Mozambique (Bennett & Faulkes 2000; Burda 2001). It prefers grassland or open forest and it can be found in variety of substrates, often in very compact soils (Jarvis 2003). There is low sexual dimorphism in the silvery mole-rats, weight of males 190 ± 58 g (range 63-331 g) and females 162 ± 47 g (51-271 g) (Šumbera et al. 2003).

The silvery mole-rats were captured in Malawi in localities Mpalanganga, Zomba (15°27´S, 35°15´E), Zomba plateau (15°20´S, 35°16´E) and Mulanje-Chitakali (16°02´S, 35°30´E) in 2005. Animals were kept at least six months in captivity before the beginning of the experiment. Five males, eight females and five subadults were used for testing.

3.2. Housing conditions

The Mole-rats were maintained at a constant temperature (25 ± 1˚C) and photoperiod (12L:12D). Colonies of *F. mechowii* were kept in large terrariums filled with horticultural peat. The silvery mole-rats were kept individually in systems of interconnected Perspex tubes with two nest boxes. All tested *F. mechowii* were housed in the similar system one month before the experiment to provide similar housing conditions, because the breeding environment could affect performance in spatial learning tasks (Seymoure et al. 1996; van Praag et al. 1999). Animals were fed *ad libitum* with potatoes, carrots, lettuce, apples and commercial rodent pellets. Water was not provided, because mole-rats do not drink free water.

3.3. Experimental equipment

The testing maze (110 cm x 100 cm x 9 cm) was made from transparent Perspex (fig. 1). This type of maze simulates the mole-rats' burrow system respecting also the diameter of natural tunnels (Scharff et al. 2001; Šumbera et al. 2008). The maze contains one correct route and six blind alleys. The shortest route to the reward box was 360 cm. We use a similar maze used in the study of (Kimchi & Terkel 2001b) to allow comparison of our data with unrelated subterranean rodents sharing a convergent way of life.

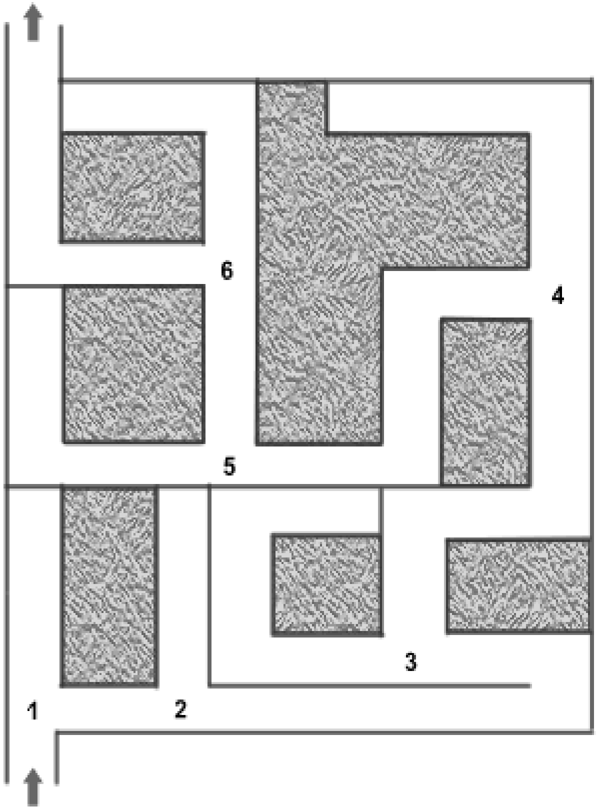

Figure 1. Diagram of the complex maze used to asses spatial learning and memory abilities (110 cm x 100 cm x 9 cm). The maze consisted of starting (home) box, reward box and 6 blind alleys. Wrong turns are numbered.

3.4. Motivation

Tested animals were food deprived for three days before beginning of experiment to decrease body mass to 80% of that original. A small piece of apple was provided to each animal once per day as source of water. This procedure is in agreement with other studies on subterranean rodents (Antinuchi & Schleich 2003; Kimchi & Terkel 2001a; 2001b). During our pilot study, the mole-rats weighing above 90% of their original weight failed the task, probably due to a lack of motivation. After completing the task, animals were rewarded with a small piece (0.5 cm^3) of an apple. Starvation didn't affect the mole-rats' health. All animals regained their pre-experimental weight within a few days.

3.5. The arrangement of the experiment

Animals were placed into Perspex boxes with lockable trapdoors three days before the beginning of the experiment. The box allowed connection to the experimental maze without handling of the animals. The number of errors (wrong turns), the time to complete the task and traveled distance were recorded from entering the maze to entering the reward box. Animals were divided into four groups with four animals.

The experiment consisted of two main parts. To test spatial learning, each animal made five trials daily for three consecutive days (trial 1, …, 15). After each trial, the maze surface was cleaned with 70% ethanol, washed with water and wiped down. All animals in the group finished their trial before next round started. To test spatial memory, each animal made an additional single trial after 30 (group 1), 60 (group 2, 3) or 120 (group 4) days (animals showed no retention of the maze in the 120 day memory test so we decided to use more animals for 60 days test). Individuals which did not finish all trials during learning experiment were excluded from analyses, because they were considered not to be sufficiently motivated.

3.6. Data analysis

Statistical analysis was performed with Statistica 8.0 (StatSoft 1999). The spatial learning data was analyzed using a repeated-measures analysis of variance (RM-ANOVA). Time, path length, number of errors and speed were the dependent variables with species (*F. mechowii*, *H. argenteocinereus*), sex (male, female) and age (subadult, adult) as categorical predictors and trials as the within-subject factor. The logarithmic transformation for path length

($\log(X)$), time ($\log(X)$) and the number of errors $\log(X+1)$ were used to attain a homogenous variance and normal distribution in the data.

Mann-Whitney U-Test was used on untransformed data to test species difference in exploration activity (first trial) for parameters time, path length and number of errors. Velocity was analyzed using T-test for dependent samples. To compare the mid term memory (the last trial of the day versus first trial of the following day) a Wilcoxon Matched Pairs Test (for time, path length and number of errors) and a T-test for dependent samples (for velocity) were applied. The T-test for dependent samples was applied to find out if there is a difference in performance between the first trial and the memory trial after 30, 60 or 120 days. To determine between species differences in long term memory the success rate was calculated, using the following formula:

$\left(\frac{a-b}{a-c}\right)$, where

a = performance in the worst out of all trials

b = performance in the memory experiment

c = performance in the best out of all trials

The success rate achieved by each animal of both species was compared by the T-test for independent samples.

4. Results

All animals entered the maze within less than one minute. After entering the maze, they started to explore it, especially the tunnel walls. Exploration begins with careful and slow outward trips followed by more rapid returns to the home box. A mix of common behaviors were observed in the maze including grooming, digging, scratching the maze with teeth and urination.

4.1. Sex and age differences

No sex or age differences in spatial performance were found for all four parameters (see appendix 1, 2 for test statistics and appendix 7-10 for absolute values of measured parameters). Therefore males, females and subadults were grouped together for following analyses.

4.2. Spatial learning

There were interspecific differences in time, path length and the number of errors in the first trial (Mann Whitney U-test: $Z=-4.30$; $p<0.001$, $Z=-4.45$; $p<0.001$, $Z=-4.32$; $p<0.001$, respectively, Fig. 2-4). No difference was found for velocity (T-test: $F=1.39$; $p=0.50$, fig. 5).

There was highly significant differences between both species in the spatial learning test for all measured parameters (RM ANOVA, time $F_{(1,32)}=121.84$; $p<0.001$, path length: $F_{(1,32)}=91.64$; $p<0.001$, number of errors: $F_{(1,32)}=70.00$; $p<0.001$, velocity: $F_{(1,32)}=59,60$; $p<0.001$). It is possible find (figures 2-5), that both species improved their performance with increasing number of passages through the maze (RM ANOVA, time: $F_{(1,36)}=16.04$; $p<0.001$; fig. 2, path length: $F_{(1,36)}=10.90$; $p<0.001$; fig. 3, number of errors: $F_{(1,36)}=13.08$; $p<0.00$; fig. 4, velocity: $F_{(1,36)}=9.15$; $p<0.001$; fig. 5).

No effects were found for interactions trial*species and path length (RM ANOVA, $F_{(14,448)}=1.56$; $p=0.09$; fig. 3) or trial*species and number of errors (RM ANOVA, $F_{(14,448)}=0.95$; $p=0.51$; fig. 4). Interestingly, a significant difference between species can be seen in combined effects of trial*species with time (RM ANOVA $F_{(14,448)}=2.13$; $p<0.05$; fig. 2) and trial*species with velocity (RM ANOVA $F_{(14,448)}=5.89$; $p<0.0001$; fig. 5).

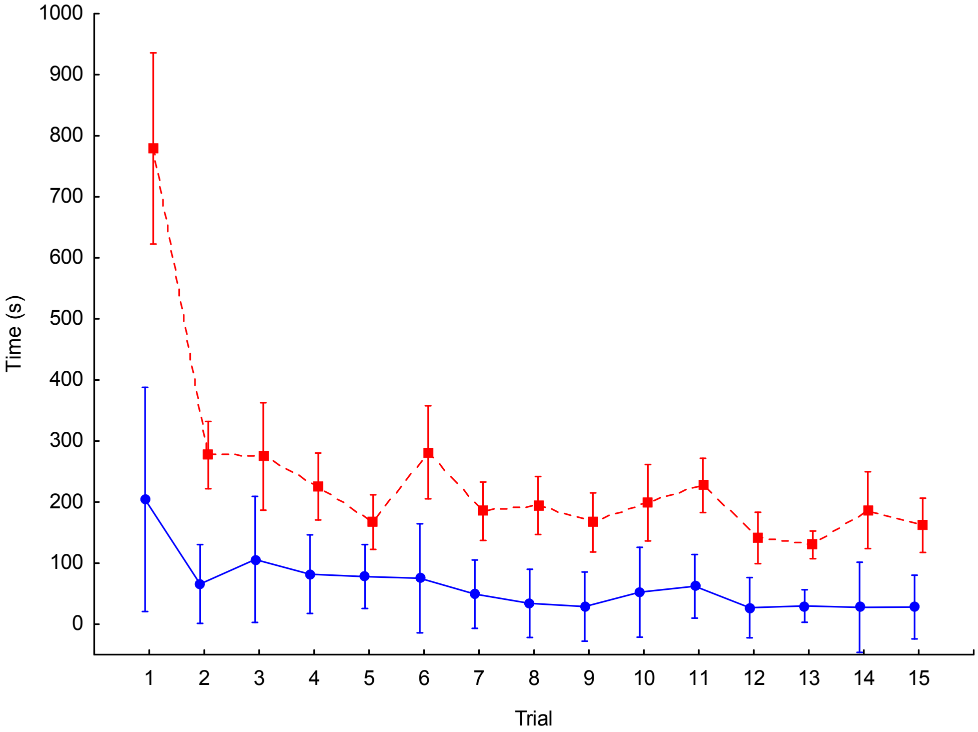

Figure 2. Time (mean ± 0.95 confidence int.) required to complete spatial learning task in 15 consecutive trials for solitary *H. argenteocinereus* (dotted line) and social *F. mechowii* (solid line).

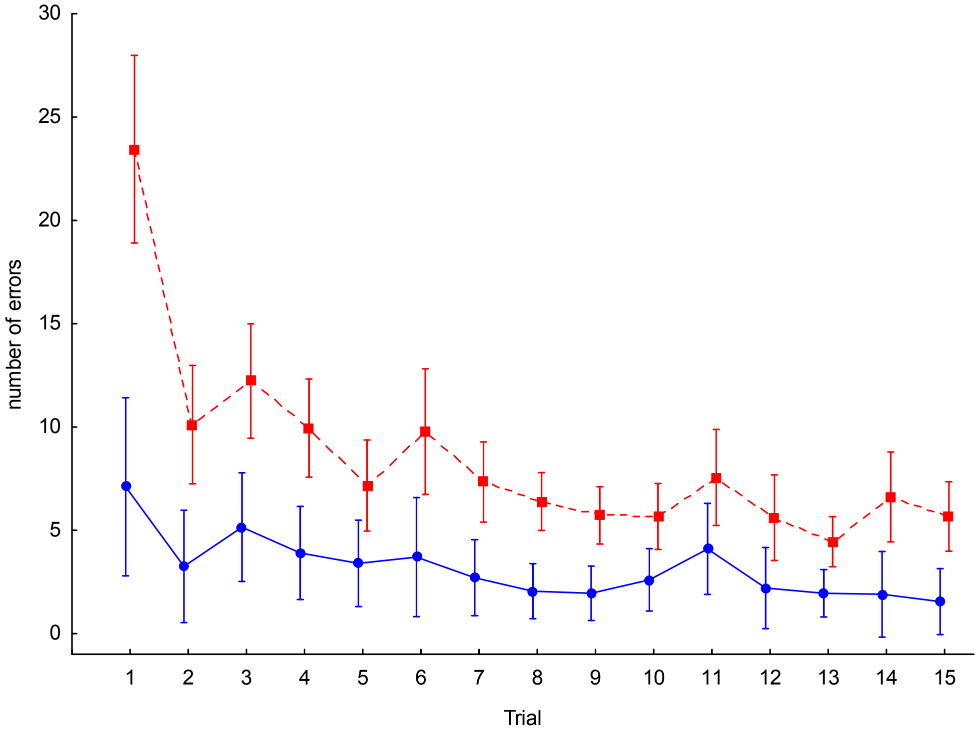

Figure 3. Number of errors (mean ± 0.95 confidence int.) required to complete spatial learning task in 15 consecutive trials for solitary *H. argenteocinereus* (dotted line) and social *F. mechowii* (solid line).

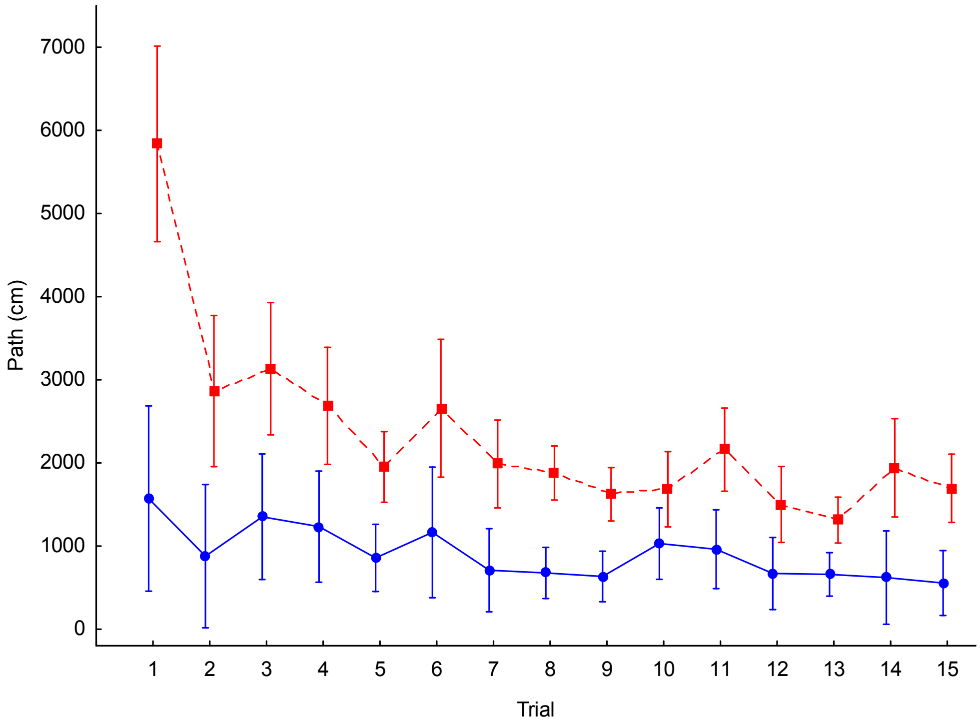

Figure 4. Path length (mean ± 0.95 confidence int.) required to complete spatial learning task in 15 consecutive trials for solitary *H. argenteocinereus* (dotted line) and social *F. mechowii* (solid line).

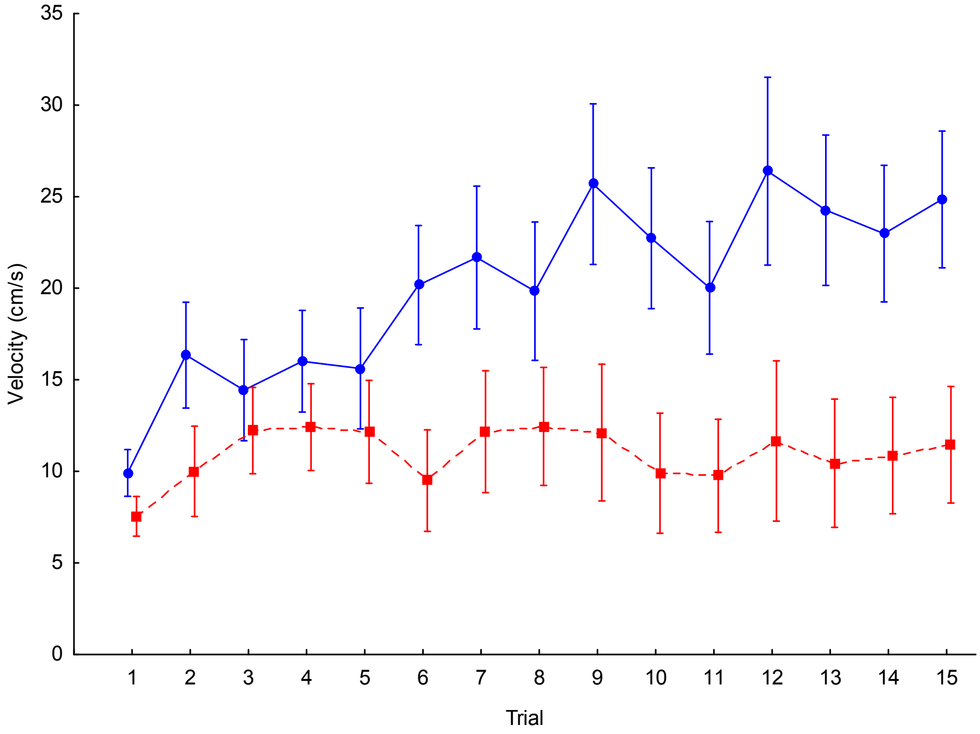

Figure 5. Velocity (mean ± 0.95 confidence int.) in 15 consecutive trials of spatial learning task for solitary *H. argenteocinereus* (dotted line) and social *F. mechowii* (solid line).

4.3. Spatial memory

No decrease in performance was found in the mid term memory test (i.e. last trial of the previous day and the first trial following day) in the giant mole-rats (fig. 6). In contrast, there were several differences between these trails in the silvery mole-rat (fig. 7). Results of the statistical tests are presented in appendix 3.

No significant results were found between species in the long term memory experiments after 30, 60 and 120 days (appendix 4). Differences between the first trial and memory trials are significant only in *H. argenteocinereus* after 60 days for all parameters and after 30 days for time (for T-test scores see appendix 5 and 6 and figures 8 and 9)

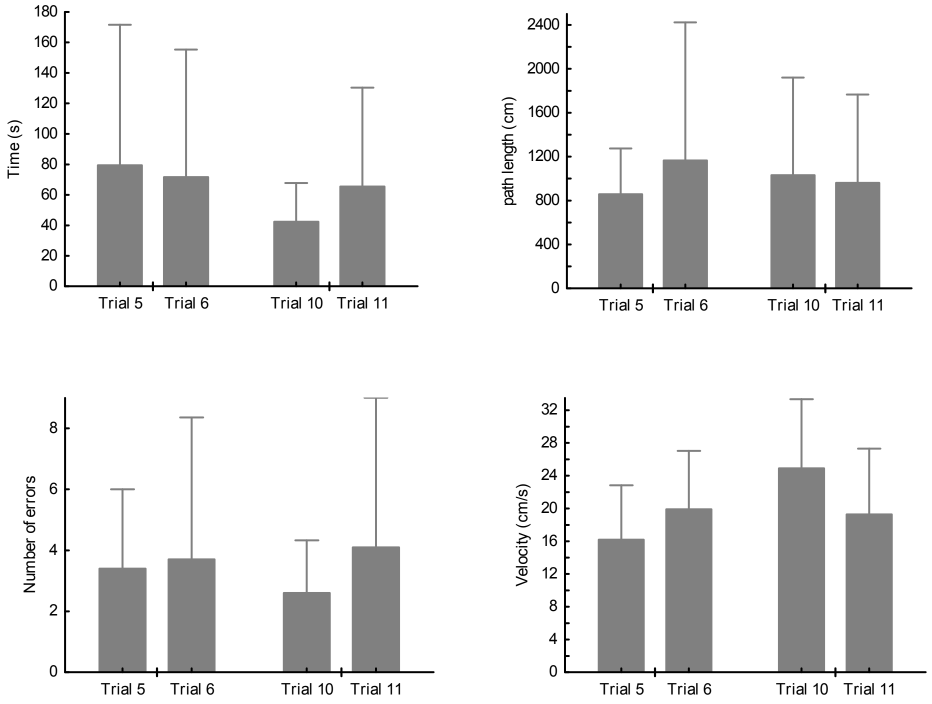

Figure 6. Comparison of performance (mean ± SD) between trials 5 x 6 and 10 x 11 in the mid term memory test in F. mechowii for all parameters (.* $p < 0.05$).

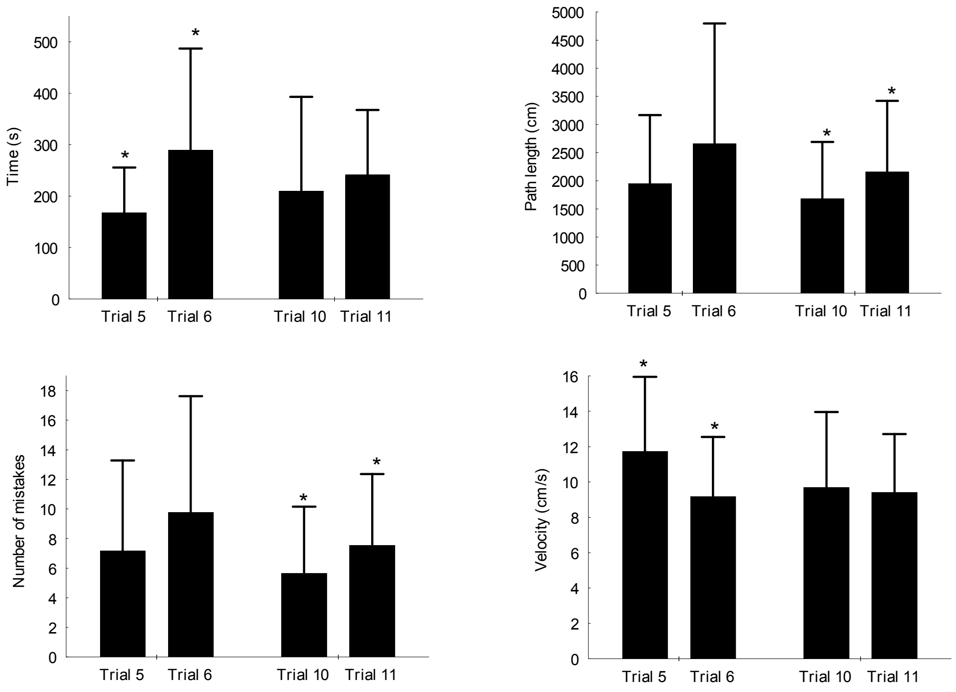

Figure 7. Comparison of performance (mean ± SD) between trials 5 x 6 and 10 x 11 in the mid term memory test in *H. argenteocinerues* for all parameters (.* $p < 0.05$).

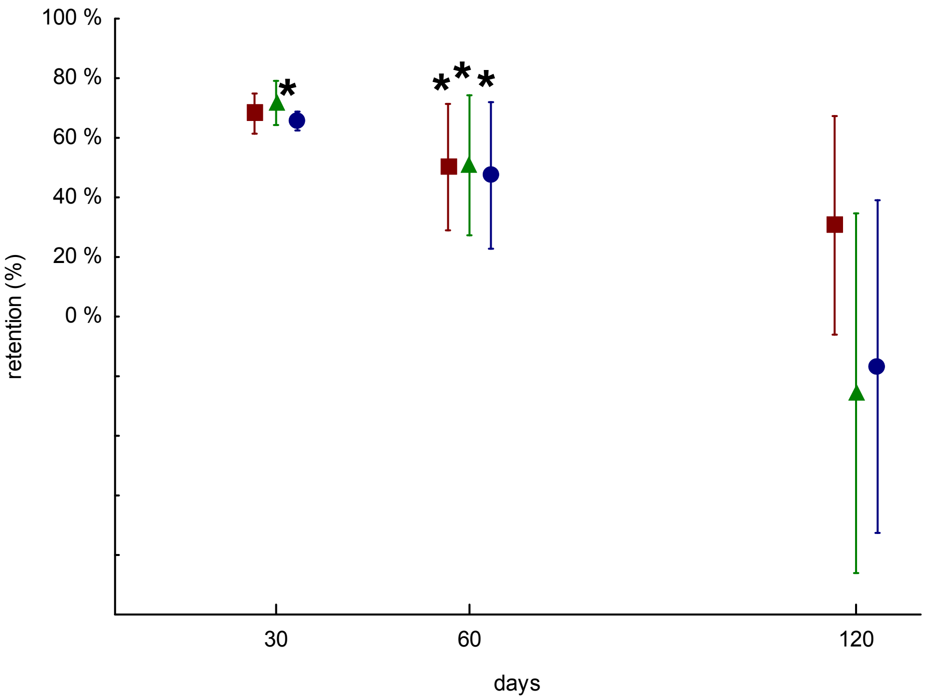

Figure 8. Performance (mean ± SD) in the repeated trial after 30 (N=3), 60 (N=8) and 120 (N=4) days for number of errors (square), path length (triangle) and time (circle) in the long term memory retention for *H. argenteocinerreus*. On the Y axis a 100 % score points to the best performance in the learning experiment and 0 % represents result in the worst (exploratory) trial. Significant difference between first trial and repeated trials are indicated by * (p < 0.05).

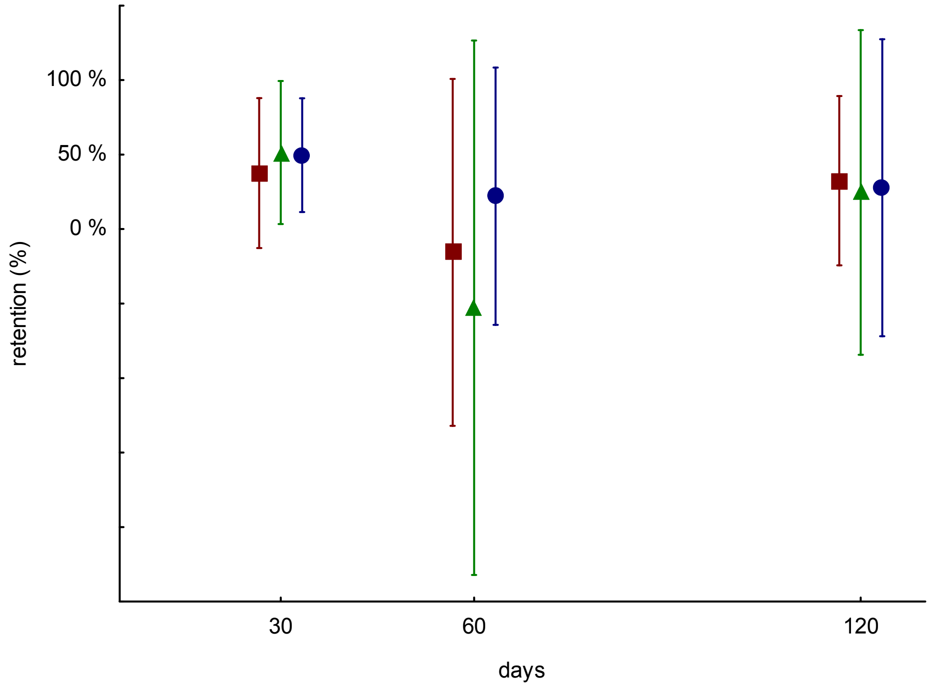

Figure 9. Performance (mean ± SD) in the repeated trial after 30 (N=4), 60 (N=6) or 120 (N=4) days for number of errors (square), path length (triangle) and time (circle) in the long term memory retention graph for *F. mechowii*. On the Y axis a 100 % score points to the best performance in the learning experiment and 0 % represents the result in the worst (exploratory) trial. Significant differences between first trial and repeated trials are indicated by * (p < 0.05).

5. Discussion

Our results bring evidence for remarkably different behavior in the complex maze in two closely related species of African mole-rats. The solitary silvery mole-rats were extremely cautious during the first exploration trial and this trend was maintained also in further passages. In contrast, the giant mole-rats' exploration was faster.

The process of exploration in both bathyergids was comparable to other subterranean mammals (Antinuchi & Schleich 2003; Costanzo 2005; Kimchi & Terkel 2001b; 2004) and other rodents (for review see Whishaw et al. 1998). However, each species used a specific exploration technique upon entering the maze in the first trial. The solitary silvery mole-rat spent more time in the maze, made more errors and traveled a longer distance during the first trial. The giant mole-rat explored the maze with similar velocity, but made less errors, traveled a shorter distance and the time needed to enter the reward box was shorter. It was possible to observe also notable interspecific difference in the process of habituation in the maze. After a few trials, the giant mole-rats showed no slowdown or escape movements (retracing steps) while entering the reward box. In contrast, the silvery mole-rats were very cautious and moved slowly around the trapdoor in the all trials. Similar exploration patterns as in the silvery mole-rat can be seen in other strictly subterranean solitary rodents as *S. ehrenbergi* and *G. capensis* (Costanzo 2005; Kimchi & Terkel 2001b). Surprisingly, the behavior of the giant mole-rats during exploration was closer to the behavior of the aboveground dwelling rats in the similar maze. More rapid passage through the maze in the first trial was also observed in the eusocial bathyergid *F. damarensis*. Results on low trapping success (12%) of the silvery mole-rats from their natural habitat and its behavior during radiotracking also suggested a much higher level of caution in the solitary species (Šklíba et al. 2008). Trapping success reported for a social bathyergid *Cryptomys hottentotus* was 75% (Hickman 1979) and in another highly social bathyergid, the naked mole-rat (*Heterocephalus glaber*), a capture rate as high as 10–15 individuals per day using the same type of traps was reported (Brett 1991). All these facts together indicate a higher level of caution in the solitary animals.

Remarkable progress in maze performance from the first to the second trial confirms the ability to learn and memorize the maze in the absence of visual and olfactory cues. It means that African mole-rats are able to navigate using path integration based on self-generated signals, similarly to other mammals (for review see Etienne & Jeffery 2004). Usage of magnetic orientation cannot be ruled out in our experiment. The Geomagnetic field has been already shown to act as a directional reference in the blind mole-rat (Kimchi & Terkel 2001a; Marhold et al. 2000) and African mole-rats (Burda et al. 1990b; Marhold et al. 1997). Out of both tested species in our experiment, minimally the giant mole-rat showed spontaneous preferences to build nests according to alternation of geomagnetic field (Oliveriusová 2008 in preparation). The earth's magnetic field could also influence the path integration process in blind mole-rats, but only for longer distances (approx. 10 meters) (Kimchi et al. 2004a). The Length of the shortest route in our experiment is only 3,6 meters, so there is the question if animals use it for these short distances also. The size of the natural burrow systems inhabited either by *F. mechowii* and *H. argentecinereus* is very long and complex (Sichilima et al. 2008; Šumbera et al. 2008), so magnetic navigation for longer distances provide an advantage in navigation in highly branched systems of tunnels. Magnetic navigation could also be very useful in combination with other senses during homing in on expected surface activity during mating season (Šumbera et al. 2007, Patzenhauerová et al. 2008). The silvery mole-rat males search aboveground for females for distances of up to several hundred meters. They probably return to their burrow systems, so combination of good spatial memory, magnetic sense and using scent marking could assist them on the way back. However, it is only speculation and it should be tested.

The mole-rats' performance in the third trial was not better than in second one in both species as expected if only learning is involved. The worse performance in the third trial could reflect attempts to explore the maze more carefully after the second passage or to avoid being trapped in the reward box. Efforts to find an alternate route to the food source in the maze tests were registered also in other African mole-rats (Costanzo 2005). The pattern of behavior in which the rats failed to explore from a secure starting position and were increasingly likely to run away as security decreased, suggests that a primary function of locomotor behavior in a novel environment is to optimize security (Whishaw et al. 2006). Performance for subsequent trials increased again. Interestingly, Levant voles, laboratory rats and blind mole-rats in the study with the same type of maze showed stable progress with no fluctuation for any of the animals (Kimchi & Terkel 2001b).

No difference for the parameters of time, path length and velocity with combined interactions species*trial shows a similar pattern of change in performance with repeated passages through the maze in both species (on a different level of absolute values for each species). It means the difference between social and solitary animals remain constant in all trials.

Although no difference was found in spatial performance for sex or age categories, the difference still cannot be ruled out. Sex differences in spatial ability are observed in numerous species. In navigational ability males usually outperform females (Jonasson 2005; see reviews of Jones et al. 2003). One of the hypotheses explaining sex divergence in navigation is polygyny-range size hypothesis suggests the existence of sex differences in spatial abilities dependent on an unequal home range between males and females in polygynous species (Gaulin 1992; Gaulin & Fitzgerald 1986). Home range size in subterranean animals is equal to the size of their burrow system Males and females of social *F. mechowii* live together in one burrow. In the solitary *H. argenteocinereus* i.e. species with very low sex dimorphism (less than 15%), the size of systems is comparable between sexes (Šumbera et al. 2007; 2008). I suppose, there is no reason for divergence in spatial learning in sexes in both tested species. No differences have been found in any tested subterranean rodents so far, African mole-rats, *Spalax* or South American fossorial rodent *Ctenomys talarum* (Antinuchi & Schleich 2003; Costanzo 2005; Kimchi & Terkel 2001b).

The age of the animals could be another factor affecting performance. Decrease in performance and velocity in radial mazes is known in senescent animals (Punzo & Chavez 2003) and also in pre-weaned juveniles (Galea et al. 1994). However, all our tested animals were adult.

A method for examination of spatial performance is the comparison of learning rates derived from slopes of learning curves. However, if tested animals differ in other parameters than learning abilities (like exploration activity), using regressions could lead to confusing results providing evidence for superior navigational abilities in the species with a high level of exploration in the first trial(s). It was the reason for the differences found in the study comparing subterranean blind mole rats to aboveground laboratory rats and fossorial voles (Kimchi & Terkel 2001b). Slopes of learning rates were steeper in blind mole rats which displayed extremely cautious exploratory behavior in the first trial similarly to the silvery mole-rats in my study. However, the absolute values of the tested parameters were almost identical in the last trials (see appendix 11). Since the first (exploratory) trial is responsible for significant differences in the learning curves, this should not be considered as a difference in learning abilities.

It seems that remarkable interspecific difference does not necessarily evidence better learning abilities in the giant mole-rat. A high number of errors in the last trial from the silvery mole-rat (i.e. six wrong turns in six blind alleys) is probably a too poor result for assessing it as a learning performance. However, if home range size is responsible for interspecies differences, this factor should also be considered for comparison between two species It can be assumed that the home range size of Giant mole-rats is larger (see above) and this should have an impact on their overall behavior in the maze tasks.

For interaction of velocity with species*trial a different pattern could be seen in the change of locomotor activity in the maze. In the first trial, the speed of exploration was comparable in both species. Later, the giant mole-rats increased speed, whereas the speed of the silvery mole-rats remained almost same as in the first trial (fig. 5). It means that solitary silvery mole-rats moved slowly in the labyrinth and repeated passages have no effect on this behavior.

There was also a difference in mid term memory. While reentering the maze on the next day was not followed by a decrease of performance in the giant mole rats, the silvery mole-rats' performance was worse (see figures 2 and 3), because the silvery mole-rat spent more time by re-exploring blind alleys. Nevertheless, this behavior could be also attributed to caution rather than learning abilities. Interestingly, very similar results were found in a recent study also comparing the navigation of social Damaraland mole-rats with solitary Cape mole-rats (Costanzo 2005). In agreement with our findings, the author also suggests that the social mole-rat's superior learning and memory retention could be an artefact of the more cautious Cape mole rat's behavior in a maze.

There is a problem in understanding the results of the long-term memory test, since no clear trend was observed in the retention of the maze. High variability of the data and low sample size was probably the main reason for insignificant differences between species. Based on my own observation, I suppose, that navigational behavior in both mole-rats was probably superimposed simply by exploratory motivation. It could be the reason why we cannot distinguish between the performances in the first trial in the learning experiment and in the repeated trials after 30, 60 or 120 days in the memory experiment in the *F. mechowii*. For *H. argenteocinereus* it possible to see (fig. 8) some pattern in a declining retention of the maze (significantly better performance in the 60 day trial, when compared to the first trial in the learning experiment), but clear conclusions cannot be made from these incoherent results.

To test genuine navigational or learning abilities in very cautious mammals like solitary mole-rats some other types of tests could be more useful. One of the most frequently used tests, the water maze (Morris 1981) is probably less sensitive to differences in activity and exploration (Lindner 1997). Nevertheless, this type of test cannot be used simultaneously with preservation of natural conditions as we wanted. A more promising tool is probably the method of combining appetitive and aversive motivation, like passive and active place avoidance (Cimadevilla et al. 2000; Stuchlík 2004).

Behavioral differences in the maze performance between both species could be caused by different modes of social life in both species. Solitary mole-rats live singly in self-constructed burrow systems. They are well familiarized with burrow architecture, so very cautious reaction to new stimulus/environment (maze) seems to be very important, since it could be connected with predator activity. Social species may have been under less severe selection pressure from predators than the solitary species, because the non-reproductive colony members benefit more from an indirect component of their inclusive fitness. The giant-mole rats are probably more accustomed to burrow environment modification i.e. new tunnels built by other family members. In any case, the differences in exploratory behavior and caution between solitary and social animals need to be examined in a larger number of species.

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7. Appendix

Appendix 1. Differences between males and females in four parameters of spatial performance in both species (RM - ANOVA).

	H. argenteocinereus	*F. mechowii*
Time	$F_{(1.11)} = 2.57; p = 0.14$	$F_{(1.16)} = 0.85; p = 0.37$
Path length	$F_{(1.11)} = 0.12; p = 0.73$	$F_{(1.16)} = 1.31; p = 0.27$
Number of errors	$F_{(1.11)} = 0.10; p = 0.76$	$F_{(1.16)} = 1.68; p = 0.21$
Velocity	$F_{(1.11)} = 1.71; p = 0.22$	$F_{(1.16)} = 0.02; p = 0.89$

Appendix 2. Differences between adults and juveniles in four parameters of spatial performance in both species (RM - ANOVA)

	H. argenteocinereus	*F. mechowii*
Time	$F_{(1.16)} = 1.93; p = 0.18$	$F_{(1.18)} = 0.08; p = 0.78$
Path length	$F_{(1.16)} = 0.43; p = 0.52$	$F_{(1.18)} = 0.67; p = 0.86$
Number of errors	$F_{(1.16)} = 0.08; p = 0.78$	$F_{(1.18)} = 0.10; p = 0.75$
Velocity	$F_{(1.16)} = 4.35; p = 0.06$	$F_{(1.18)} = 0.07; p = 0.80$

Appendix 3. Mid term memory test in two mole-rats for time, path length, number of errors (Wilcoxon Matched Pairs Test) and for velocity (T-test for dependent samples). Significant results ($p < 0.05$) are indicated by *.

		H. argenteocinereus		*F. mechowii*	
	Trial	Z	p	Z	p
Time	5 x 6	2.55	0.01*	0.46	0.64
	10 x 11	1.46	0.15	1.53	0.13
Path lenth	5 x 6	1.72	0.09	0.56	0.57
	10 x 11	2.07	0.04*	0.08	0.93
Number of errors	5 x 6	1.71	0.09	0.28	0.78
	10 x 11	1.97	0.05*	1.44	0.15
		t	p	t	p
Velocity	5 x 6	2.45	0.03*	-1.66	0.11
	10 x 11	0.41	0.69	2.06	0.05

Appendix 4. Success rates from 0 to 1 (means ± SD) for both species in the long term memory test (T-test, * p < 0.05).

		F. mechowii	*H. argenteocinereus*	T-test	
		Mean ± SD	Mean ± SD	t-value	p
30 days	Number of errors	0.38 ± 0.50	0.68 ± 0.07	-1.02	0.35
	Path legth	0.51 ± 0.48	0.72 ± 0.07	-0.71	0.51
	Time	0.50 ± 0.38	0.66 ± 0.03	-0.71	0.51
60 days	Number of errors	-0.16 ± 1.16	0.50 ± 0.21	-1.58	0.14
	Path legth	-0.53 ± 1.79	0.51 ± 0.23	-1.64	0.13
	Time	0.22 ± 0.86	0.47 ± 0.25	-0.80	0.44
120 days	Number of errors	0.33 ± 0.57	0.31 ± 0.37	0.06	0.96
	Path legth	0.25 ± 1.09	-0.26 ± 0.60	0.81	0.45
	Time	0.28 ± 1.00	-0.17 ± 0.56	0.78	0.47

Appendix 5. Number of errors, path length and time needed to complete spatial memory task by *F. mechowii* and scores of T-test for dependent samples between 30, 60 or 120 days and first learning trial (* p < 0.05).

		Mean ± SD	t-value	p
30 days	Number of errors	5.0 ± 2.4	-1.45	0.24
	Path legth	1310.0 ± 688.6	-1.76	0.18
	Time	79.8 ± 15.3	-1.58	0.21
60 days	Number of errors	8.0 ± 7.4	-0.05	0.97
	Path legth	2355.0 ± 2228.5	0.35	0.74
	Time	130.7 ± 131.0	-0.89	0.42
120 days	Number of errors	5.3 ± 2.9	-1.59	0.21
	Path legth	1472.5 ± 1192.4	-1.06	0.37
	Time	111.0 ± 84.6	-1.23	0.31

Appendix 6. Number of errors, path length and time needed to complete spatial memory task by *H. argenteocinereus* and scores of T-test for dependent samples between 30, 60 or 120 days and first learning trial. (* p < 0.05).

		Mean ± SD	t-value	p
30 days	Number of errors	11.3 ± 6.8	-2.80	0.11
	Path legth	3170.0 ± 1276.4	-2.92	0.10
	Time	239.3 ± 61.7	-6.23	0.02 *
60 days	Number of errors	12.4 ± 5.0	-4.49	0.00 *
	Path legth	3093.8 ± 917.4	-3.54	0.01 *
	Time	423.3 ± 145.2	-4.98	0.00 *
120 days	Number of errors	16.5 ± 5.3	-1.73	0.18
	Path legth	5787.5 ± 670.0	0.62	0.58
	Time	776.0 ± 178.9	-0.02	0.98

Appendix 7. Time in seconds (mean ± SD) required to complete spatial learning task in 15 consecutive trials.

	Fukomys mechowii			*Heliophobius argentecinereus*		
Trial	Females	Males	Subadults	Females	Males	Subadults
1	360 ± 482	177 ± 147	75 ± 30	794 ± 310	611 ± 209	933 ± 298
2	93 ± 110	79 ± 56	26 ± 8	225 ± 163	141 ± 77	465 ± 133
3	122 ± 71	136 ± 149	61 ± 52	357 ± 289	268 ± 149	325 ± 224
4	104 ± 71	93 ± 85	50 ± 45	191 ± 73	178 ± 145	212 ± 179
5	107 ± 130	53 ± 36	74 ± 42	170 ± 99	207 ± 99	124 ± 44
6	84 ± 114	56 ± 43	86 ± 101	331 ± 191	262 ± 245	252 ± 189
7	48 ± 52	31 ± 13	70 ± 1	207 ± 124	201 ± 181	155 ± 95
8	39 ± 26	31 ± 14	32 ± 1	195 ± 147	215 ± 145	139 ± 148
9	36 ± 40	23 ± 7	28 ± 19	250 ± 180	104 ± 60	152 ± 114
10	43 ± 24	34 ± 22	81 ± 11	266 ± 258	199 ± 89	131 ± 55
11	81 ± 88	53 ± 39	53 ± 56	313 ± 125	219 ± 115	152 ± 72
12	26 ± 15	37 ± 27	18 ± 4	148 ± 109	208 ± 186	73 ± 36
13	34 ± 23	22 ± 6	34 ± 13	169 ± 82	127 ± 83	63 ± 23
14	35 ± 31	25 ± 13	23 ± 4	265 ± 253	149 ± 81	144 ± 104
15	30 ± 18	17 ± 5	38 ± 29	264 ± 175	117 ± 77	105 ± 66

Appendix 8. Path length in cm (mean ± SD) required to complete spatial learning task in 15 consecutive trials.

	Fukomys mechowii			*Heliophobius argentecinereus*		
Trial	Females	Males	Subadults	Females	Males	Subadults
1	1613 ± 1066	1670 ± 1438	940 ± 339	4960 ± 2156	3660 ± 824	9420 ± 3924
2	872 ± 551	962 ± 598	535 ± 78	2808 ± 3592	1274 ± 751	4546 ± 1131
3	1570 ± 895	1237 ± 745	895 ± 686	3303 ± 2831	2880 ± 1911	3118 ± 2005
4	1484 ± 928	1128 ± 773	575 ± 191	2150 ± 1317	2100 ± 1424	4134 ± 2745
5	861 ± 417	808 ± 408	1065 ± 700	1570 ± 822	2658 ± 1822	1854 ± 937
6	1502 ± 1736	776 ± 417	1400 ± 1457	2511 ± 1728	2734 ± 2625	2814 ± 2696
7	591 ± 105	671 ± 228	1410 ± 240	1666 ± 1422	2280 ± 2058	2208 ± 1543
8	798 ± 488	598 ± 236	485 ± 106	1494 ± 618	2484 ± 1184	1892 ± 814
9	691 ± 248	587 ± 159	595 ± 318	2075 ± 1078	1190 ± 625	1334 ± 818
10	1216 ± 1244	780 ± 456	1325 ± 35	1660 ± 894	1920 ± 1509	1480 ± 720
11	987 ± 1091	948 ± 516	915 ± 771	2384 ± 1230	2424 ± 1758	1534 ± 594
12	751 ± 580	633 ± 257	475 ± 7	1444 ± 1158	2102 ± 2011	992 ± 485
13	733 ± 489	561 ± 182	770 ± 424	1656 ± 927	1176 ± 527	898 ± 312
14	742 ± 690	531 ± 151	475 ± 7	2416 ± 2405	1556 ± 987	1568 ± 908
15	590 ± 260	456 ± 86	850 ± 594	2018 ± 1234	1116 ± 775	1756 ± 1567

Appendix 9. Number of errors (mean ± SD) required to complete spatial learning task in 15 consecutive trials.

	Fukomys mechowii			*Heliophobius argentecinereus*		
Trial	Females	Males	Subadults	Females	Males	Subadults
1	8.1 ± 5.9	6.7 ± 6.3	4.5 ± 3.5	20.4 ± 8.6	15.4 ± 4.2	36.4 ± 14.0
2	3.9 ± 3.7	3.1 ± 1.7	1.0 ± 0.0	9.0 ± 10.0	5.0 ± 3.4	17.0 ± 2.3
3	5.7 ± 3.2	5.1 ± 3.0	3.0 ± 4.2	12.6 ± 8.7	13.0 ± 9.4	10.8 ± 5.7
4	4.3 ± 2.8	4.0 ± 2.6	1.5 ± 0.7	8.6 ± 4.0	7.4 ± 4.5	14.6 ± 10.1
5	4.2 ± 3.4	2.4 ± 1.3	4.0 ± 2.8	5.1 ± 2.6	11.6 ± 9.8	6.0 ± 4.1
6	4.2 ± 6.3	2.9 ± 2.0	5.0 ± 7.1	9.0 ± 5.6	11.0 ± 9.8	9.8 ± 10.4
7	2.6 ± 1.8	2.2 ± 1.0	5.5 ± 0.7	7.3 ± 5.9	6.6 ± 6.7	8.2 ± 5.4
8	2.1 ± 1.6	2.0 ± 1.2	2.0 ± 0.0	5.1 ± 4.2	9.0 ± 4.6	5.8 ± 2.3
9	2.4 ± 2.2	1.6 ± 0.7	1.5 ± 2.1	6.6 ± 4.1	4.0 ± 2.4	6.0 ± 4.7
10	2.7 ± 1.2	2.0 ± 1.9	5.0 ± 0.0	5.8 ± 5.0	6.8 ± 5.8	4.4 ± 2.2
11	5.7 ± 6.8	2.7 ± 1.5	3.5 ± 4.9	8.5 ± 4.8	8.6 ± 6.6	5.0 ± 1.9
12	2.2 ± 3.3	2.4 ± 1.9	1.0 ± 0.0	5.6 ± 5.2	8.8 ± 7.8	2.4 ± 2.3
13	2.4 ± 1.9	1.4 ± 1.0	2.0 ± 1.4	6.4 ± 3.9	4.0 ± 1.4	1.8 ± 1.5
14	2.4 ± 3.1	1.6 ± 1.5	1.0 ± 0.0	8.5 ± 8.2	4.8 ± 4.1	5.4 ± 3.8
15	1.9 ± 2.0	0.9 ± 0.8	3.0 ± 2.8	7.3 ± 5.7	3.6 ± 3.8	5.2 ± 4.2

Appendix 10. Velocity in cm*s^{-1} (mean ± SD) required to complete spatial learning task in 15 consecutive trials.

	Fukomys mechowii			*Heliophobius argentecinereus*		
Trial	Females	Males	Subadults	Females	Males	Subadults
1	7.9 ± 3.4	9.3 ± 1.4	12.6 ± 0.5	6.2 ± 1.0	6.4 ± 1.7	10.0 ± 2.7
2	13.5 ± 6.0	13.3 ± 5.3	22.3 ± 10.3	10.9 ± 4.6	9.1 ± 2.1	10.0 ± 2.3
3	14.1 ± 4.7	13.6 ± 6.9	15.6 ± 2.1	9.9 ± 2.0	12.6 ± 4.7	14.2 ± 3.6
4	16.1 ± 5.1	15.3 ± 5.0	16.6 ± 11.1	10.5 ± 3.9	12.6 ± 4.1	14.2 ± 3.0
5	16.3 ± 9.5	16.5 ± 3.6	14.0 ± 1.4	9.7 ± 3.6	12.0 ± 4.2	14.8 ± 3.9
6	22.2 ± 7.1	17.4 ± 7.0	21.0 ± 7.7	7.6 ± 2.9	10.4 ± 2.6	10.5 ± 4.2
7	21.3 ± 10.6	23.4 ± 6.1	20.3 ± 3.7	8.7 ± 3.6	11.3 ± 3.8	16.5 ± 5.0
8	24.0 ± 9.4	20.4 ± 6.0	15.1 ± 2.6	9.4 ± 4.0	10.6 ± 3.7	17.4 ± 7.1
9	27.6 ± 10.2	26.3 ± 7.8	23.2 ± 4.5	10.4 ± 4.4	12.3 ± 4.5	13.7 ± 8.5
10	27.6 ± 10.8	24.1 ± 5.0	16.5 ± 1.9	8.7 ± 4.3	9.4 ± 5.2	11.7 ± 3.3
11	16.7 ± 7.5	21.2 ± 8.5	22.2 ± 8.9	7.7 ± 2.5	10.6 ± 3.6	11.0 ± 3.3
12	28.8 ± 12.4	23.2 ± 11.5	27.1 ± 6.0	9.8 ± 3.0	9.7 ± 3.7	15.5 ± 4.9
13	23.8 ± 7.4	26.8 ± 11.0	22.2 ± 3.7	9.6 ± 3.9	8.6 ± 4.1	13.1 ± 2.6
14	23.7 ± 8.5	23.9 ± 7.0	21.4 ± 3.7	10.0 ± 5.7	10.9 ± 3.9	11.7 ± 4.0
15	23.2 ± 10.3	27.8 ± 5.2	23.6 ± 2.4	9.5 ± 5.1	9.6 ± 2.3	15.3 ± 3.9

Appendix 11. Graph indicating performance for laboratory rats, Levant voles and blind mole-rats from Kimchi and Terkel study (Kimchi & Terkel 2001b)

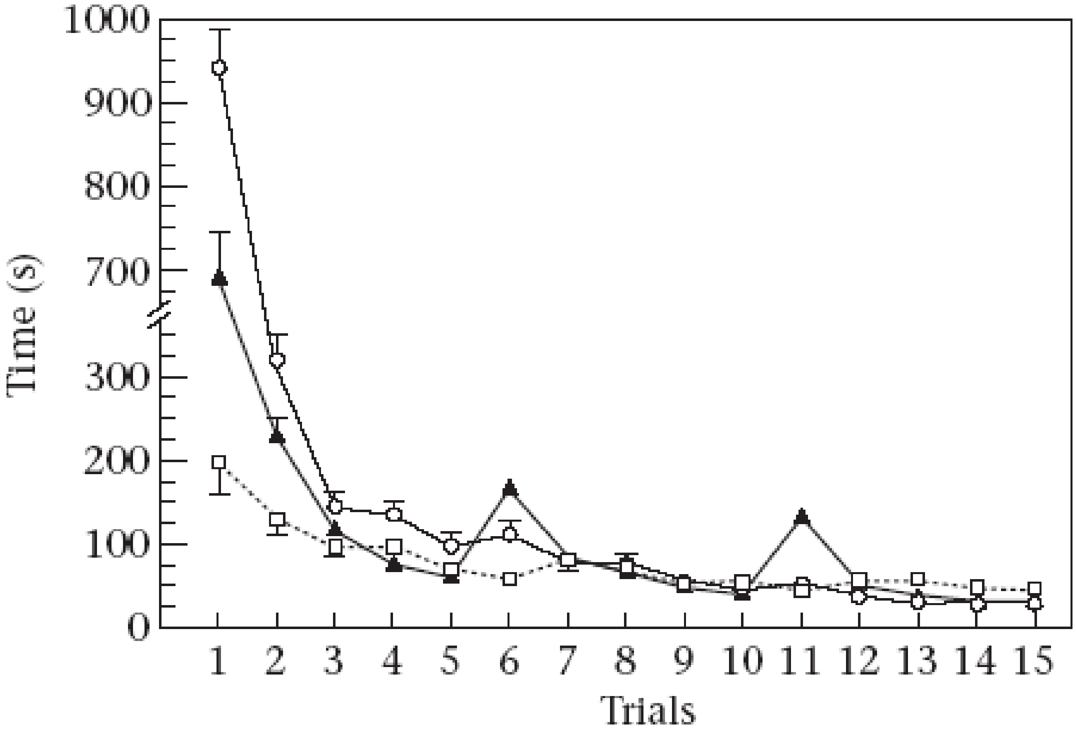

Figure 2. Time (s) ±SE required by the mole-rats (○), rats (▲) and voles (□) to reach the end of the complex maze in 15 trials.