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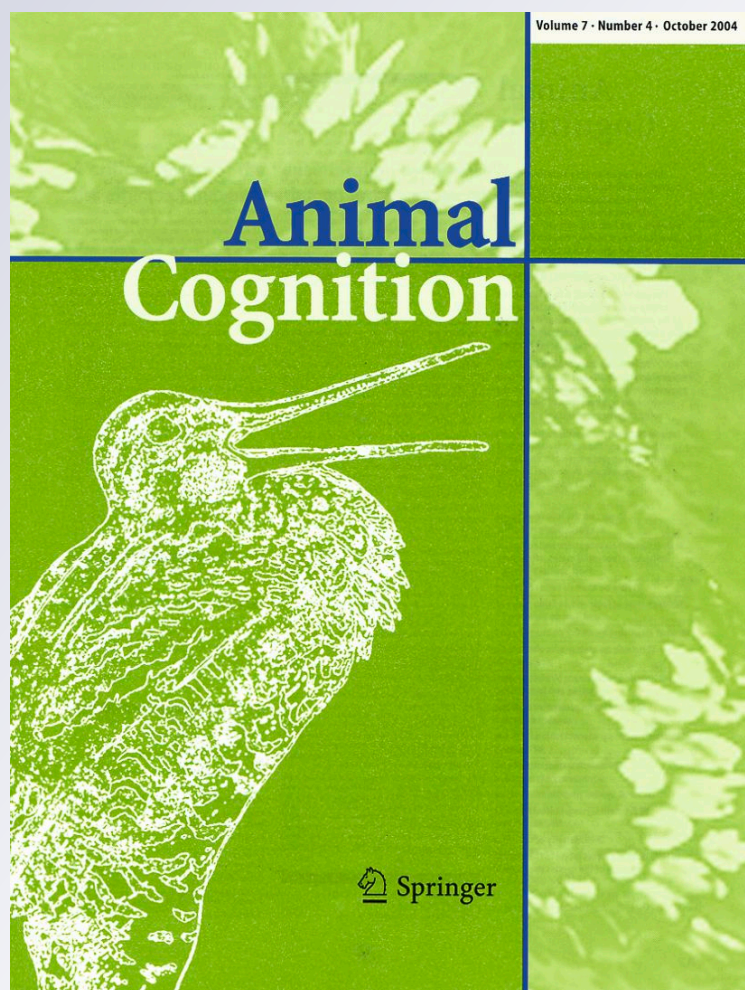
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Influence of spatial environment on maze learning in an African mole-rat

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Abstract In subterranean species where excavation is energetically expensive, efficient spatial navigation is vital to reducing the costs of locating important resources such as food and mates. While spatial navigational ability is positively correlated with sociality in subterranean mammals, we have a less clear understanding of the role of habitat complexity on navigational ability. We tested spatial navigational ability and memory in 12–18-month captive Natal mole-rats (*Cryptomys hottentotus natalensis*) maintained in a simple environment with no environmental enrichment and newly captured wild individuals from natural, complex burrow systems. In maze trials, mole-rats

captured freshly from the wild made significantly fewer navigational errors, were more likely to successfully navigate the maze, travelled shorter distances and as a consequence, completed the maze in less time. Male mole-rats from both experimental treatments were more likely to complete the maze than females. Memory retention of the maze was tested on day two, seven, 30 and 60, respectively. The results were variable, although both groups showed a significant memory retention 60 days after testing. Our results highlight the potential importance of the environment (microhabitat complexity) on spatial cognitive performance in mole-rats.

Keywords Mole-rat · Cognition · Memory · Learning · Navigation

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Introduction

Subterranean animals are not an obvious choice for spatial memory experiments because their visual systems are often regressed (Němec et al. 2007), and compared to surface dwelling animals, they have a limited range of cues for navigating their environment (Burda et al. 1990a; Sherry 1998). Efficient spatial orientation and memory is, however, critical for fossorial species in their search for food patches or mates, as underground locomotion and excavation is comparatively expensive (Lovegrove 1989; Vleck 1979, 1981; Zelová et al. 2010). In the absence of light, subterranean species use olfactory (Heth et al. 2002) and somatosensory stimuli (Kimchi and Terkel 2004b), as well as the earth's magnetic field (Burda et al. 1990b; Kimchi and Terkel 2004a) and path integration (Kimchi and Terkel 2002), to orientate themselves. Not surprisingly, these species possess remarkable abilities both in spatial

orientation and memory (Costanzo et al. 2009; Kimchi and Terkel 2002, 2003). For example, blind *Spalax* mole-rats perform better in learning and memorizing a complex maze than both laboratory rats and Levant voles (Kimchi and Terkel 2001).

African mole-rats of the family Bathyergidae are subterranean rodents that display a striking spectrum of sociality (Skinner and Smithers 1990). The geometry of the tunnels in which mole-rats live is a function of the level of sociality they display, with solitary species inhabiting simpler tunnel systems and more social species inhabiting a complex labyrinth of tunnels (Le Comber et al. 2002; Sichilima et al. 2008). Mole-rats are therefore a model species group with which to examine the role of the environment on spatial cognition. Recently, Costanzo et al. (2009) demonstrated that the eusocial Damaraland mole-rat (*Fukomys damarensis*) performs better at spatial memory tasks than the solitary Cape mole-rat (*Georychus capensis*). It therefore appears that a more complex spatial environment necessitates a better spatial memory in order for the animal to effectively and inexpensively navigate its way around its home range. Nevertheless, we need tests of how environmental complexity might affect spatial cognition within a species. This has been well studied in laboratory rats (Harris et al. 2009), but is currently poorly understood for wild rodents that navigate complex environments.

Another key issue in spatial cognition studies is the influence of sex. An increasing number of studies have found that males have better spatial cognitive ability than females in spatial tasks such as maze completion (Perdue et al. 2011) in part because of ranging behaviour. During the breeding season, males of many species increase their home range in their quest to locate multiple females (range size hypothesis, Gaulin and Fitzgerald 1986), and this presumably either stimulates cognitive ability to a greater degree than in females and/or provides a selective pressure for greater spatial cognitive ability in males. While males of many species have greater spatial cognitive ability and learning retention, this is not always the case. For example, in two species of subterranean mole-rats, the eusocial Damaraland (*Fukomys damarensis*) and solitary Cape mole-rat (*Georychus capensis*), males and females performed equally well in spatial and memory retention tasks (Costanzo et al. 2009). Similarly, monogamous voles show no sex difference in spatial cognitive ability, while males have better spatial cognition in a promiscuous species (Gaulin and FitzGerald 1989). We therefore need to test more species with varying ecological requirements to better understand sex differences in spatial cognition.

We used the Natal mole-rat (*Cryptomys hottentotus natalensis*) as a model to test whether the superior spatial

navigational ability displayed by social mole-rats is related to the complexity of the tunnel systems they inhabit (Hickman 1979b). In the wild, mole-rat tunnel systems continually change as colony members expand the tunnels through their foraging efforts. Conversely, captive mole-rats are maintained in simple rectangular containers and are provided with food by their caregivers. They lack the opportunity or need to enrich their spatial environment through the digging of a tunnel system. Captive animals therefore represent a unique opportunity to study the influence of habitat complexity on spatial navigational ability. We hypothesized that captive animals will have a decreased ability to navigate a complex maze when compared to conspecifics recently captured from the wild. We also asked whether there is a difference in spatial cognitive ability between males and females.

Methods

Study animals

We collected 14 male and ten female adult Natal mole-rats (*Cryptomys hottentotus natalensis*) from Glengarry Park in KwaZulu-Natal Province, South Africa (29°19'24"S, 29°42'55"E) in July 2005. Individual mole-rats were trapped using modified Hickman live traps baited with sweet potato (Hickman 1979a). Additionally, 12 male and 12 female mole-rats, originating from the same area/population but collected in 2004, were selected from a single existing laboratory population (range in captivity: 16–18 months). The animals were of indeterminate age; however, none were visibly juvenile or elderly. Subordinate animals belonging to sub-species in the *Cryptomys hottentotus* group typically remain physically small well into adulthood (Skinner and Smithers 1990). According to Oosthuizen (2007), female Natal mole-rats range between 47–127 g and males between 40–162 g. Therefore, the large range of weights seen in the study sample (56.9–164.9 g for field mole-rats, and 88.2–162.4 g for laboratory mole-rats) are within the normal range of variation reported in the literature. None of the animals used were born in captivity, and all animals were sexually mature. Animals were housed in plastic containers (colonies 100 × 50 × 50 cm; single animals 50 × 30 × 30 cm) in climate controlled rooms (25 ± 1 °C) at the University of Pretoria. A reversed light regime of 12 h dark: 12 h light was enforced for 3 weeks prior to commencement of the experiment in order to switch the activity patterns of the animals from nocturnal to diurnal (Hart et al. 2004). Untreated wood shavings were available as nesting material. The mole-rats were fed fresh vegetables ad libitum, from which they obtained sufficient water, since they do not drink.

Experimental groups and maze

Freshly caught adult wild mole-rats ($n = 24$) were compared to long-term laboratory animals ($n = 24$) to determine whether differences in their spatial environments (complex vs. simple) affect their ability to learn and remember spatial tasks. We constructed a complex maze, with six choice points and one correct path leading to a food reward at the end of the maze opposite to the entrance (Fig. 1; Kimchi and Terkel 2001). The maze covered an area of 100×120 cm, the floor consisted of a plywood board covered with vinyl sheeting, and the maze itself was constructed from dark opaque Perspex sheeting with a transparent Perspex lid. The tunnels of the maze pathway were 10 cm wide and 10 cm high. The entrance and exit to the maze were each fitted with a plastic tube (25 cm long, 8 cm diameter) with a removable door. A food reward was placed in the tube fitted to the maze exit.

At the completion of each trial, the floor, the roof and walls of the maze were cleaned with 50 % ethanol (Costanzo et al. 2009; Kimchi and Terkel 2001). The experiment was performed in a room with no external windows, and lighting was provided by a single red light (60 W) positioned above the maze. All trials were recorded by a single observer tracing the path of the animal on a diagram of the

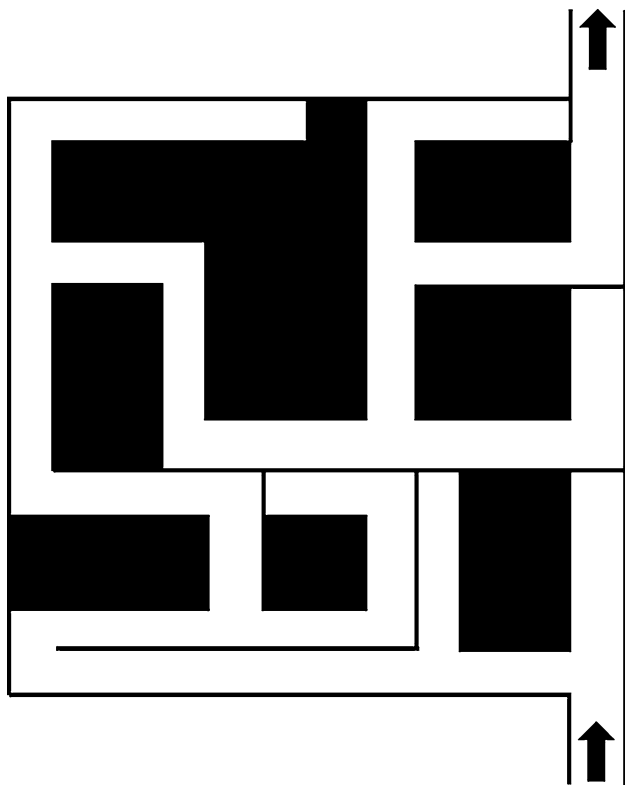


Fig. 1 Maze used to test spatial learning and memory in wild living and captive mole-rats

maze and recording the time taken to complete the maze. We also videoed all trials.

Learning experiment

The test procedure, adapted from Kimchi and Terkel (2001), was the same for all the animals. One day prior to the trial, the animal was removed from its home cage and housed individually in a plastic container ($50 \times 30 \times 30$ cm). We restricted food intake until completion of either the three-day learning experiment or the memory test because food deprivation has been shown to increase motivation to explore (Kimchi and Terkel 2001). A trial began when the animal entered the maze and was terminated when the animal reached the maze exit, or after a maximum of 20 min if it failed to complete the maze. Animals that successfully completed the maze were rewarded with a small piece of sweet potato (0.5 cm^3). At the end of each trial, the animal was returned to the plastic container, and after a complete set of trials, it was returned to its home cage. The experiments were conducted between 0900 and 1600 hours. Three parameters were recorded: (1) time required to correctly complete the path in the maze; (2) number of errors made; and (3) total distance travelled during each trial.

Each animal performed five trials daily for three consecutive days, and no more than four animals were tested per day. At the end of each day, the animals were provided with a small amount of food. The animals were returned to their home cages and received food ad libitum at the end of the three-day period.

Memory (retention) experiment

To determine how well the animals retained the maze learning, each animal was tested on its ability to navigate the maze only once at either 2, 7, 30 or 60 days from the end of the learning experiment. Six animals randomly selected from each treatment were tested for each time period. The groups consisted of three males and three females, or four males and two females (2 and 7 day groups for wild mole-rats and 7 day group for laboratory mole-rats). Mole-rats were housed individually, and food was restricted 1 day prior to the trial, and returned to their home cages and regular feeding cycle at the end of the single-day experiment.

Data analysis

Since the experiment concerned the time period until a certain event, where the event in this case was the completion of the maze, a survival analysis approach was used to analyse the duration data from the experiment. In conventional survival analysis problems, the normal variable

of interest is the time to death, but this can be replaced by any measure of duration. The data can be considered as 'right-censored', as experiments where the mole-rat did not complete the maze within 20 min were terminated. We constructed a probability model that a mole-rat would complete the maze in 20 or fewer minutes using the following factors: the day on which the maze was attempted, the body mass of the mole-rat, the mole-rat's group and the sex of the mole-rat.

In survival analysis, this probability distribution is referred to as the hazard function, which usually refers to the rate of death at a particular point in time. In this case, the hazard function describes the rate of completion of the maze over time. A common approach to obtaining the hazard function is through a non-parametric method referred to as the Cox proportional hazards model, which requires few assumptions regarding the probability distribution function (Tableman and Stahel 2009). The disadvantage of this method is that interactions between variables cannot be included, which makes this method inappropriate for this study. Alternatively, the hazard function can be modelled as a generalized linear model, but in this case, a density function needs to be chosen to describe the hazard function (Crawley 2005). The simplest choice is the exponential distribution, which requires only one estimated parameter, but this assumes that the probability of completing the maze remains constant throughout the duration of the experiment. A more flexible density function is the Weibull distribution that requires the estimation of two model parameters and can allow the rate of completing the maze to increase or decrease over time. In modelling the data, we found that the additional parameter required to fit the Weibull over the exponential distribution was significant and therefore used the Weibull distribution. If the mole-rats showed a learning effect, we would expect a reduction in both the distance travelled and the frequency of errors as a function of the number of trials performed. To test whether there was a decrease in the distance and number of errors from the first day of the experiment to the third day, we used conventional linear regressions, including 'group', sex and body mass as additional predictors.

Results

During the first day of the acquisition phase, 83 % (99 of 120 runs) of all wild caught animals completed the maze within the 20 min time limit compared to 81 % (97 of 120 runs) on the second day, and 90 % (108 of 120 runs) on the third day. Similarly, during the first day of the acquisition phase, 81 % (97 of 120 runs) of all laboratory animals completed the maze within the 20 min time limit compared

to 74 % (89 of 120 runs) on the second day, and 73 % (88 of 120 runs) on the third day.

In modelling the hazard function of the time to completion of the maze, we considered all combinations of the four variables of interest, up to the fourth level of interaction. Models were then selected based on the significance (5 % level of significance) of the terms in the model and the results of the Deviance tests, which compares the current model to the null model and maximal model (model with all possible combinations of variables). The most parsimonious model, containing only those interaction terms that were significant, was the model fitted with three-way interactions between day, sex and body mass, between day, sex and group and between group, sex and body mass (Table 1). This model fit as well as the maximal model (Deviance test: $P = 0.31$) fitted significantly better than the null model (Deviance test: $P < 0.0001$).

A plot of the hazard function (Fig. 2) shows that the rate at which mole-rats completed the maze increased with time, for all groups. However, freshly caught field mole-rats completed the maze at a significantly faster rate than laboratory mole-rats (Table 1). The difference in

Table 1 Generalized linear model results for hazard function, modelling the time it takes to complete the maze

Effect	Coefficient estimate	SE	z Statistics
Intercept	7.466	0.759	9.84***
Group: laboratory	7.768	1.380	5.63***
Day: 2	-2.232	0.985	-2.27*
Day: 3	-5.064	1.001	-5.06***
Sex: male	-1.070	0.889	-1.20
Weight	-0.007	0.009	-0.75
Group: laboratory*day: 2	-1.272	0.675	-1.88
Group: laboratory*day: 3	-1.751	0.671	-2.61**
Group: laboratory*sex: male	-10.972	1.617	-6.79***
Day: 2*sex: male	0.649	1.172	0.55
Day: 3*sex: male	2.104	1.176	1.79
Day: 2*weight	0.023	0.012	1.98*
Day: 3*weight	0.051	0.012	4.30***
Sex: male*weight	0.006	0.001	0.63
Group: laboratory*weight	-0.054	0.011	-4.89***
Group: laboratory*day: 2*sex: male	1.543	0.770	2.00*
Group: laboratory*day: 3*sex: male	2.660	0.762	3.49***
Day: 2*sex: male*weight	-0.011	0.013	-0.82
Day: 3*sex: male*weight	-0.036	0.013	-2.65**
Group: laboratory*sex: male*weight	0.089	0.013	6.76***

z Statistics marked (*) are significant at the 5 % level, (**) at the 1 % level and (***) at the 0.1 % level

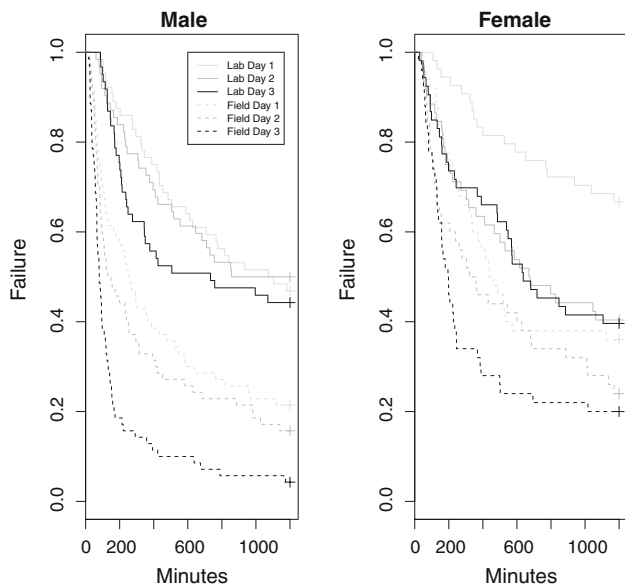


Fig. 2 Hazard plot for completion of maze times. The plot describes the proportion of mole-rats that are still to complete the maze at each minute into the trial

completion rates between field and laboratory mole-rats is different for males and females, with the difference being smaller for female rats. Overall, the field mole-rats had higher completion rates compared to the laboratory rats (Fig. 2).

The coefficients estimated for the model (Table 1) indicate that the effect of body mass on the rate at which the maze was completed depended on sex, group and day. For female mole-rats in the field group, the rate of completing the maze tended to decrease with increasing body mass, with the opposite being true for male field mole-rats. For laboratory mole-rats, increasing body mass of female rats tended to result in increased rates of completion, while for males increased body mass resulted in decreased rates of completion.

An examination of the p-values of the terms in the linear model for distance show that the day on which the trial was carried out did not have a significant effect (Table 2), unless in interaction with group, sex and body mass. The fact, that the main effect for day is not significant, does not imply that the day on which the trial was performed is not important. The importance of day comes through in the interaction effects, which shows that once these other effects are accounted for, then there is a significant difference between the distance travelled on these days. If group, sex and body mass were not accounted for, then the effect of the day on which the trial was carried out would be lost. Box plots of the distance data from the learning experiment (Fig. 3) illustrate that day does not have any noticeable effect on the distance travelled, except in the case of laboratory females where the median

Table 2 Coefficient estimates from linear model for the distance travelled by the mole-rat in the maze

Effect	Coefficient estimate	SE	t Statistics
Intercept	658.133	1,156.900	0.57
Day: 2	-481.784	1,135.061	-0.42
Day: 3	-1,041.365	1,135.059	-0.92
Sex: male	1,637.592	1,168.112	1.40
Group: laboratory	-2,904.452	2,340.113	-1.24
Weight	21.187	13.273	1.60
Day 2: sex: male	-312.338	545.623	-0.57
Day 3: sex: male	-1,395.599	544.829	-2.56*
Group: laboratory*day: 2	7,601.065	2,383.482	3.19**
Group: laboratory*day: 3	9,403.531	2,393.748	3.92***
Group: laboratory*sex: male	-7,165.066	2,261.977	-3.17**
Day: 2*weight	4.453	11.887	0.38
Day: 3*weight	16.315	11.886	1.37
Sex: male*weight	-22.649	12.644	-1.80
Group: laboratory*weight	29.533	21.928	1.35
Group: laboratory*day: 2*sex: male	-57.939	20.813	-2.78**
Group: laboratory*day: 3*sex: male	76.617	20.923	-3.66***
Group: laboratory*sex: male*weight	71.259	21.053	3.39***

t Statistics marked (*) are significant at the 5 % level, (**) at the 1 % level and (***) at the 0.1 % level. Residual degrees of freedom are 658

distance travelled, in fact, increased from day 1 to day 3. Furthermore, the plot shows that the laboratory group had higher median distances compared to the field group, and this difference was enhanced for heavier mole-rats, as indicated by the positive and significant coefficient of the laboratory group and weight interaction term in the model (Table 2).

The estimated linear model for the number of errors shows that, as for the distance model, day was not significant unless in interaction terms with other predictors (Table 3). The number of errors made during the course of the maze was significantly affected by the mole-rat's sex, group, and body mass. The strongest trend in the data was that laboratory mole-rats tended to perform more errors compared to field mole-rats. Box plots of the number of errors (Fig. 4) show no obvious trend over time within any of the groups.

Based on the data collected during the retention trials, a hazard function was estimated for the time to complete the maze, including the time between trials as an additional predictor. In the retention trials, there was a significant effect of time between trials on the performance of mole-rats in the maze (Table 4). As expected, mole-rats that

Fig. 3 Box plots of the distance travelled grouped according to sex, 'group' and body mass

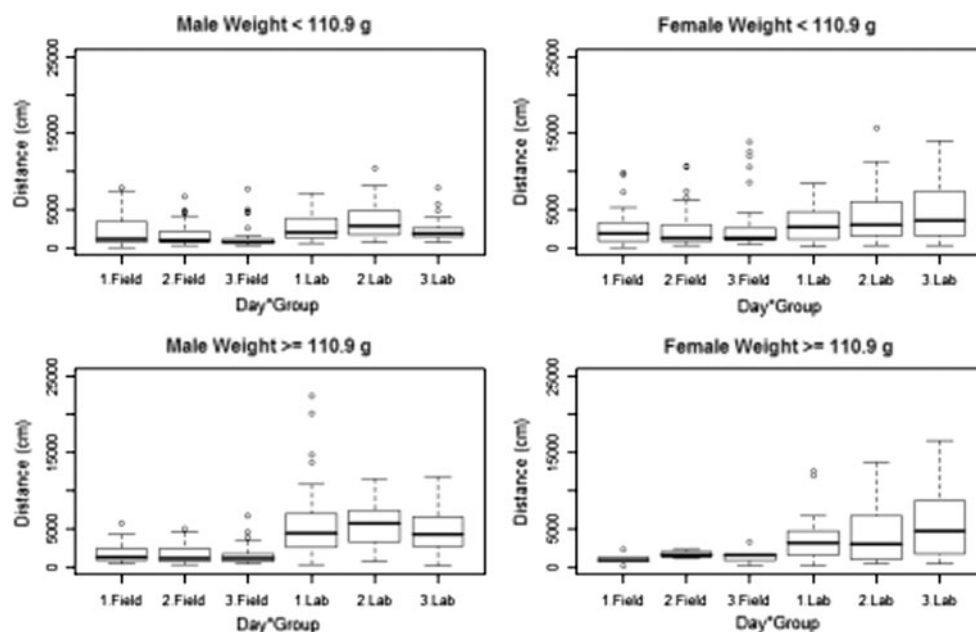


Table 3 Coefficient estimates from linear model for the number of errors made by the mole-rat in the maze

Effect	Coefficient estimate	SE	t Statistics
Intercept	0.909	13.086	0.07
Day: 2	-5.714	12.839	-0.45
Day: 3	-16.369	12.839	-1.28
Sex: male	17.118	13.213	1.30
Group: laboratory	-1.266	26.470	-0.05
Weight	0.296	0.1501	1.97*
Day 2: sex: male	-0.722	6.172	-0.12
Day3: sex: male	-14.055	6.163	-2.28*
Group: laboratory*day: 2	81.946	26.960	3.04**
Group: laboratory*day: 3	109.937	27.076	4.06***
Group: laboratory*sex: male	-106.995	25.586	-4.18***
Day: 2*weight	0.0319	0.134	0.24
Day: 3*weight	0.225	0.134	1.67
Sex: male*weight	-0.269	0.143	-1.88
Group: laboratory*weight	0.035	0.248	0.14
Group: laboratory*day: 2*sex: male	-0.628	0.235	-2.67**
Group: laboratory*day: 3*sex: male	-0.934	0.237	-3.95***
Group: laboratory*sex: male*weight	1.073	0.238	4.50***

t Statistics marked (*) are significant at the 5 % level, (**) at the 1 % level and (***) at the 0.1 % level. Residual degrees of freedom are 658

returned after 60 days showed the lowest retention, with approximately 60 % of mole-rats not completing the maze within the 20 min period in this group (Fig. 5). The results

for mole-rats returning to the maze after two, seven and 30 days are not as clear. In the case of the laboratory mole-rats, the retention of maze information after a two day return was approximately the same as that for 60 days (Fig. 5). The laboratory mole-rats also show a higher retention of maze information after 30 days compared to 7 days. In the case of the field mole-rats, retention of maze information by the mole-rats completing the maze appears to be similar after 2, 7 and 30 days return, and with a much lower retention after 60 days. The generalized linear model of the hazard function shows that there are significant interactions between the number of days between maze trials, sex, group and body mass, with significant two-way interactions between days between maze trials and sex, days between maze trials and group, and sex and body mass (Table 4). The distance travelled and the number of errors made by the mole-rats during the course of the maze was not significantly affected by the time interval between trials. The only significant predictor of the distance travelled or the number of errors made was the mass of the mole-rat, with the distance travelled and number of errors increasing with the mass of the mole-rat (estimated coefficients of 50.99 and 0.573 for the models of distance and number of errors, respectively, both significant at the 5 % level).

Discussion

We hypothesized that freshly captured wild mole-rats would perform better at spatial tasks than their captive counterparts, and the results from this study confirmed our expectations. The rate of successful completion of the

Fig. 4 Box plots of the number of errors grouped according to sex, 'group' and body mass

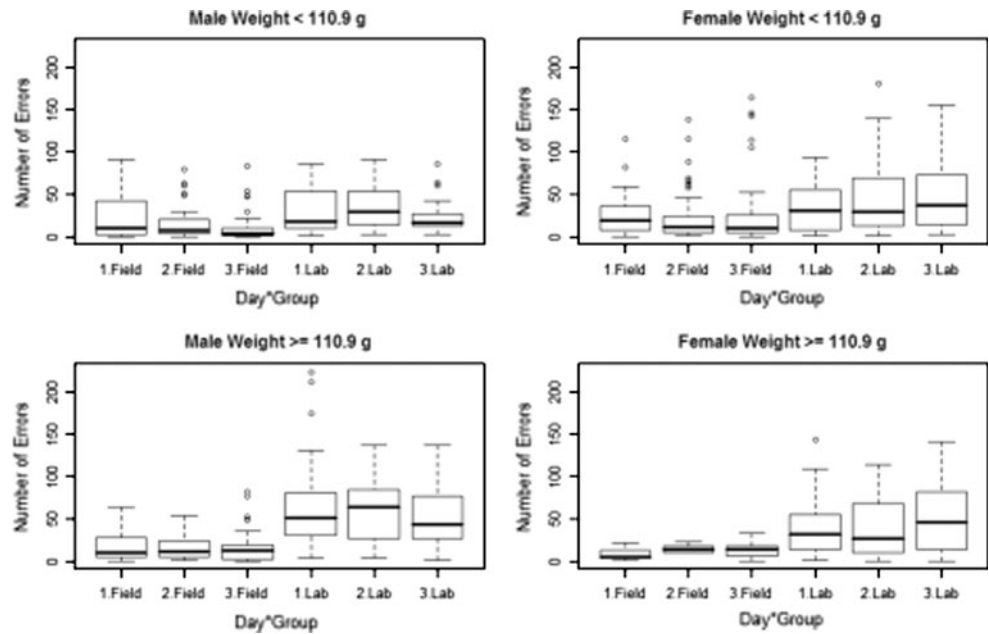


Table 4 Generalized linear model results for hazard function, modelling the time it takes to complete the maze

Effect	Coefficient estimate	SE	z Statistics
Intercept	5.729	1.005	5.70***
Day: 7	2.494	0.932	2.68**
Day: 30	1.153	0.690	1.67
Day: 60	3.332	0.872	3.82***
Sex: male	-2.761	1.374	-2.01*
Group: laboratory	3.331	0.944	3.53***
Weight	-0.018	0.013	-1.40
Day 7: sex: male	-1.904	0.940	-2.03*
Day 30: sex: male	-2.444	0.874	-2.80**
Day 60: sex: male	-2.326	1.290	-1.80
Group: laboratory*day: 7	-3.675	1.119	-3.29**
Group: laboratory*day: 30	-2.665	0.980	-2.72**
Group: laboratory*day: 60	-3.440	1.149	-2.99**
Sex: male*weight	0.047	0.016	3.02**

z Statistics marked (*) are significant at the 5 % level, (**) at the 1 % level and (***) at the 0.1 % level

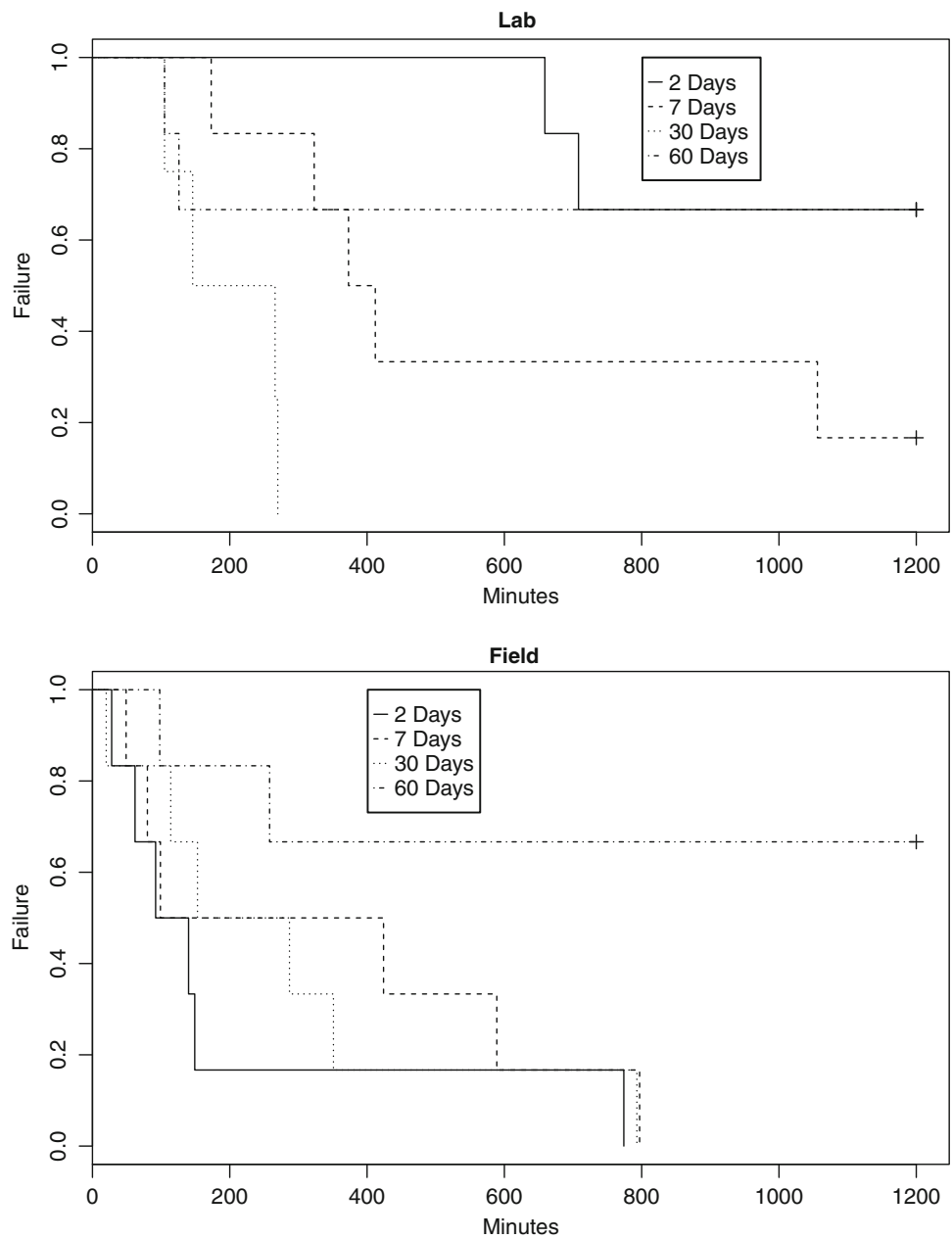
maze increased with time for both groups; however, field mole-rats showed higher overall rates of completion than laboratory mole-rats. Field mole-rats also committed fewer errors and ran shorter distances in the process of completing the route. The most obvious factor that sets captive mole-rats apart from wild ones was the simplicity of the artificial habitation. It is, however, important to note that this is not the only potential cause for the apparent cognitive decline observed in the laboratory animals. Captive mole-rats could lack the motivation to explore, as

they are used to food being provided. Food deprivation has been shown to heighten motivation to explore a maze (Kimchi and Terkel 2001); however, both groups received identical treatment prior to testing; therefore, lack of motivation probably does not play a major role here. It is possible that some other physiological or behavioural response to captivity correlates with reduced activity or reduced cognition.

Animals in captivity differ from conspecifics inhabiting their natural habitat in several key features that could influence their behaviour and cognition. Captive animals are provided with food and shelter, thereby negating the need for the animal to forage or to seek or construct a home for itself. Additionally, laboratory cages are often barren, and lack most of the sensory stimuli animals living in a natural setting would be exposed to. An enriched environment has been associated with increased spatial abilities as well as use-dependent plasticity in brain morphology in several species (for reviews see Clayton 1995; Van Praag et al. 2000; but see Harris et al. 2009). Cognition has also been found to change with age, and while we could not determine the absolute age of the adult mole-rats from our two cohorts, it is possible that laboratory maintained mole-rats may have been older and as a consequence suffered slightly from a reduced cognitive ability.

Sex differences in the spatial abilities of rodents are not straight forward. Although males generally perform better than females, there are significant exceptions to this trend (for a review see Harris 1978; Halpern 2000; Gaulin and Hoffman 1988). Extrinsic (e.g. study design; Roof and Stein 1999) and intrinsic (e.g. sex differences in home range size; Gaulin and Fitzgerald 1986; 1989), exploration

Fig. 5 Plot of hazard functions for the number of days after familiarizing the mole-rats with the maze, separated by group



levels, activity levels or motivation factors (Joseph 1979; Joseph and Gallagher 1980; Van Haaren et al. 1987) have been postulated as possible explanations for this phenomenon. In microtine voles, spatial abilities correlate with sex only when the mating system and reproductive tactics employed by each sex are taken into consideration (Gaulin and FitzGerald 1989). Interestingly, in the bathyergid mole-rats studied to date, no sex differences in spatial learning have been found in either solitary or social species (Costanzo et al. 2009). Our results show that for both laboratory and field mole-rats, males generally performed better than females. Home range cannot play a role here, as males and females share the same tunnel system and therefore have identical home ranges. Another possible

explanation might be gender differences in dispersal rates. If subordinate males were more prone to disperse from their natal colonies than females, it may necessitate better spatial capabilities. It is currently unknown whether Natal mole-rats display sex differences in dispersal rates. However, male-biased dispersal has been reported in the Damaraland mole-rat, *Fukomys damarensis* (Hazell et al. 2000). Natal mole-rats can now be added to the growing list of species (see Jones et al. 2003; Jozet-Alves et al. 2008 for partial reviews) that show sex differences in cognitive spatial ability including, for example, humans (reviewed in Coluccia and Louse 2004), fishes (Sovrano et al. 2003), birds (Vallortigara 1996), giant pandas (Perdue et al. 2011) and cuttlefish (Jozet-Alves et al. 2008).

In female field mole-rats and male laboratory mole-rats, the rate of completion decreased with increasing body mass. However, in male field and female laboratory mole-rats, the converse was true. In terms of the numbers of errors (see Table 3), body size had a negative effect on the ability of the animal to complete the maze, with smaller mole-rats performing better than larger mole-rats. This is counterintuitive as the tunnels of our maze were probably not of optimal size for the smaller mole-rats. Mole-rats dig their own tunnel systems, with the diameter of the tunnels closely approximating the size of their cylindrical bodies (Bennett and Faulkes 2000), while leaving space for animals to turn around in tunnels (White 2005). This not only keeps excavation costs down (Vleck 1979, 1981), but ensures close contact between the sensory hairs on the animal's body and the wall of the tunnel (Burda et al. 1990a; Kimchi and Terkel 2004b). Subterranean animals are very dependent on somatosensory input in their spatial orientation. They perform better in mazes that are small enough for their bodies to touch the sides of the maze. Laboratory rats, on the other hand, do not show improved orientation with heightened somatosensory input, but rely more on visual cues for orientation (Kimchi and Terkel 2004b). In our study, the range of body size was reasonably broad: 57–165 g. Smaller animals would have more difficulty staying in close contact with the walls of the maze, yet they performed better in the maze than larger animals. One possibility is that smaller individuals are more affected by food deprivation and are therefore more motivated to search for the food reward compared to larger individuals.

Interestingly, neither field nor laboratory mole-rats improved their maze running abilities over the course of the three day learning experiment. Although rates of completion increased for all groups, the number of errors committed and the distance travelled did not decrease with experience. Therefore, although the mole-rats remembered the food reward, they did not learn faster ways of completing the maze. This counterintuitive observation could be explained by the fact that the diameter of the tunnels in the maze were too big to optimize the somatosensory impact that subterranean animals partially depend on for navigation (Kimchi and Terkel 2004b).

In summary, we demonstrate that wild mole-rats from complex environments perform better in maze tests of spatial ability than captive mole-rats maintained in simple environments. Our study suggests a role for environmental complexity, amongst other factors, in stimulating cognitive development and activity, and highlights the potential importance of an appropriate environment for providing adequate cognitive stimulation in captive animals.

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