



Contents lists available at ScienceDirect

Physiology &amp; Behavior

journal homepage: [www.elsevier.com/locate/phb](http://www.elsevier.com/locate/phb)

## Spatial learning and memory in African mole-rats: The role of sociality and sex

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### ARTICLE INFO

#### Article history:

Received 29 February 2008

Received in revised form 3 September 2008

Accepted 5 September 2008

Available online xxx

#### Keywords:

Cryptomys

*Fukomys damarensis*

*Georychus capensis*

Sociality

Spatial learning

Spatial memory

Sex differences

Species differences

### ABSTRACT

Spatial learning and memory is an important skill for the survival and fitness and may vary between the sexes depending on differences in space use. This is particularly true for animals that explore the subterranean niche as it is associated with high travelling costs. In subterranean rodents the complexity of burrow systems varies with differing degrees of sociality possibly posing stronger selective pressures regarding spatial abilities on species with more complex burrow structures. This could lead to superior abilities in spatial learning and memory in social compared to solitary subterranean species. We tested this hypothesis in two species of subterranean mole-rats, the eusocial Damaraland (*Fukomys damarensis*) and solitary Cape mole-rats (*Georychus capensis*) by comparing their ability to locate food in an artificial maze. Measurements of the time taken to the goal chamber, the number of wrong turns taken, and the average velocity at which animals travelled were used to compare performance between animals. We did not find marked sex-specific differences in either study species during the assessment of learning and memory retention. In accordance with our hypothesis significant differences between the species were apparent during both learning and memory trials with the social species exhibiting superior performances. However, in both species memory retention was generally high suggesting that the fossorial lifestyle poses a strong selective pressure on spatial abilities in subterranean mammals.

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### 1. Introduction

Orientation and spatial memory have a significant impact on many aspects of animal behaviour, including foraging activities [1,2] and reproduction [3,4]. Due to differences in strategies of optimising their reproductive success spatial abilities often differ between the sexes. Promiscuous males tend to maximize their reproductive success by roaming around widely during their search for receptive females and this is aided by advanced spatial skills e.g. [4,5]. As a result, sex differences in spatial ability have been recorded for a number of promiscuous rodents and correlate with differences in home range size between the sexes [3,6]. In contrast, in species with sexually isometric home range sizes no sex differences in spatial abilities were found [6].

Animals living above ground have access to a variety of mechanisms such as landmark recognition to facilitate navigation [7]. In contrast, sensory input in subterranean animals is limited resulting in the use of alternative cues such as the earth magnetic field for orientation [8,9]. At the same time it is posited that digging below ground is associated with largely increased energetic costs compared to locomotion above ground [10]. The limitations of the subterranean

niche should thus pose a strong selection pressure for effective orientation and avoidance of unnecessary digging costs on fossorial animals. Previous studies on the blind mole-rat, *Spalax ehrenbergi*, have indeed found that these subterranean rodents exhibit a well-developed mechanism of spatial orientation and memory that is superior to those of two other rodent species that do not restrict their foraging activities to a tunnel system below ground [11]. Those superior spatial abilities also enable blind mole-rats to reduce energy expenditure when circumnavigating obstacles [12].

Foraging related constraints of the subterranean niche are thought to have led to the evolution of sociality in another group of fossorial rodents, the African mole-rats (Bathyergidae), which exhibits a unique range of social structures [13,14]. The aridity food-distribution hypothesis proposes that arid habitats are associated with increased energetic costs of digging and patchy food plant distribution compared to mesic habitats [15]. The risk of unsuccessful foraging in such arid habitats may decrease when large numbers of animals forage cooperatively and thus select for sociality [16]. Successful foraging in fossorial rodents is strongly related to burrow structure and those with higher fractal dimensions are more successful in locating food items than burrows with low fractal dimensions [17,18]. Burrows of social species and larger groups show indeed larger fractal dimensions and higher food mass [18,19]. The suggestion is therefore that social mole-rat species forage more efficiently than solitary ones.

In the present study we aimed to assess how differences in sociality and corresponding levels of complexity in burrow geometry

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affect the spatial abilities of two mole-rat species, the eusocial Damaraland mole-rat, *Fukomys damarensis* (formerly named *Cryptomys damarensis*), and the solitary Cape mole-rat, *Georchus capensis*. The burrow system of the Damaraland mole-rat is complex and similar to the design found in other species of social mole-rat species [20,21]. In contrast, the Cape mole-rat exhibits a burrow system that has a linear and rather simple tunnel geometry [20,22]. In addition to differences in sociality the two study species are characterised by different mating systems with the social species being monogamous and the solitary one promiscuous [14]. In this study, we aimed to explore possible sex and species-specific differences by investigating learning and memory retention in Damaraland and Cape mole-rats. With regard to the differences in mating system between the two species we predicted sex-specific differences in navigational skills for the promiscuous Cape mole-rat but not the monogamous Damaraland mole-rat. Furthermore, we hypothesized that the social species would exhibit superior spatial abilities due to the higher navigation demands of its burrow system.

## 2. Materials and methods

### 2.1. Animals

Damaraland mole-rats were captured at Hotazel in the Northern Cape Province, South Africa (27°17'S 22°58'E). Cape mole-rats were captured near the town of Darling in the Western Cape Province, South Africa (33°22'S 15°25'E). All individuals had been resident in the laboratory for a period of at least a month prior to the experiment. Individual Damaraland mole-rats and Cape mole-rats were housed in plastic containers with wood shavings and fed a diet of sweet potato, carrot, gem squash and apple *ad libitum*. The animals were kept in a temperature-controlled room (25 °C ± 1 °C) and maintained on a 12L:12D light cycle.

Due to differences in the activity patterns of the two study species [23–25], individuals from both study species were tested at different times of the light cycle. This is unlikely to affect performance of the two species since although they are not blind and do entrain to light bathyergids are poorly equipped for visual orientation in the three-dimensional environment [26] and probably largely rely on tactile cues for spatial orientation as has been shown for blind mole-rats [27]. For the diurnal Damaraland mole-rats both learning and memory (retention) trials were conducted during the light component of the 12L:12D light cycle. A total of 34 animals were trained to complete the maze and were tested once at only one of the three periods of the memory retention trials. The nocturnal Cape mole-rats were conditioned and tested during the dark cycle. A single red light was used to facilitate observation by the experimenter in the dark. Animals appeared to be undisturbed by the presence of this weak light source. A total of 23 individuals were trained to learn the maze and used at only one of the periods of the memory retention trials. This smaller sample size was due to the constraint of limited availability of study animals.

### 2.2. Apparatus and procedure

A clear Perspex maze comprising interlocking sections (approximately 20 cm in length with a diameter of 8 cm) was used (Fig. 1). The maze was cleaned using 30% ethanol prior to commencing each of the animal's two days of conditioning and before the memory trial. The maze was not cleaned between trials of the same individual on the same day. This was done to allow the animal to become conditioned to the maze using natural mechanisms of learning, including olfaction. For all experiments animals were introduced into the top chamber by means of a small transfer jar or by the use of handling tweezers, while the food (a piece of apple) was placed in the bottom left chamber. Care was taken not to cause undue stress in the transfer of the animal. Once an animal had completed the maze, the food

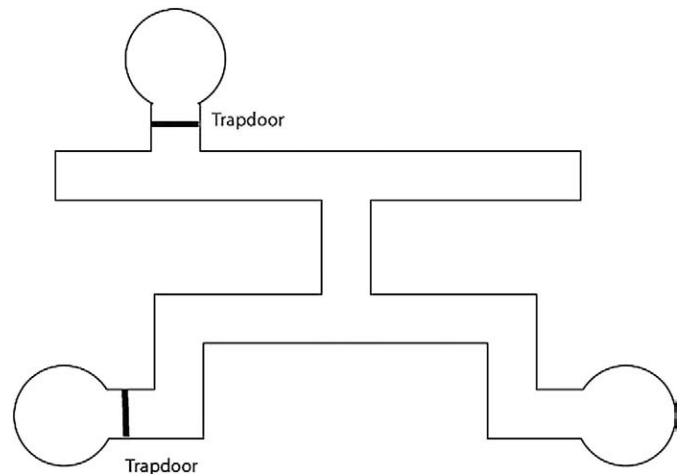


Fig. 1. Maze used to test spatial learning and memory in mole-rats.

chamber was separated from the rest of the maze using a metal trapdoor that was manually inserted in the tunnel leading to the food chamber. The animal was allowed to eat for 15 s, thus ensuring that it was indeed aware of the presence of the food and that hunger was a motivating factor. After 15 s the trial was terminated, and the animal was removed and returned to its home cage while the maze was reset, after which the animal was placed in the top chamber again.

### 2.3. Learning experiment

Following the protocol of previous experiments exploring spatial abilities (e.g. [11]) animals were deprived of food 24 h prior to learning and memory experiments in order to keep them motivated. In between the two days of learning animals were fed enough to keep their body mass stable. Animals lost between 10 and 20% of their body mass as a result of food deprivation and fully recovered their initial body mass after the experiments. During the learning phase of the experiment each animal underwent eight consecutive trials per day for two consecutive days (learning trials), after which the animals were left undisturbed in their home cages for their respective test periods.

During their trials animals were timed using a Timex stopwatch and the data were recorded on a custom-made data sheet. The following parameters were measured to assess learning performance during the trials: time taken from entering the maze to reaching the goal chamber (time to goal), the number of wrong turns taken while travelling from entry to the first encounter with the food (wrong turns) and the average velocity with which an animal travelled during the trials (velocity), as determined by distance/time to first encounter with food.

Unlike Damaraland mole-rats, Cape mole-rats were reluctant to enter the maze and very rarely consumed the food upon first discovery but tended to assess the maze further and then return to the food. To evaluate whether this behavioural difference may be related to anxiety or stress experienced by the animals we measured the time taken to enter the maze from the start chamber (time to entry), the time taken from reaching the goal chamber till first handling the food (time to food handling) and the distance travelled from the entry chamber to first encountering food (distance). In addition, for Cape mole-rats we assessed the additional distance travelled between first encountering and first handling the food (distance 2-1).

### 2.4. Memory experiment

To assess memory retention of spatial information learned during the first part of the study five individuals of each sex for Damaraland mole-rats and between three and five individuals of each sex for Cape mole-rats were then subjected to a single trial. Those trials were run

after an interval of two, seven, or fifteen days after the learning trials, respectively (memory trials).

### 2.5. Statistical analysis

We performed separate analyses for sex-specific differences within a species and lumped the data together for species-specific analyses if no sex-specific differences were found. Data were transformed logarithmically ( $\lg(x)$  or  $\lg(x+1)$ ) before employing multiple measurement ANOVAs. The response variable was the respective variable measured (time to entry, time to goal etc.) and the explanatory variables were sex or species as well as the combined variable Day-trial (for example, Day-Trial 15 is Trial 5 on Day 1 and Day-Trial 21 is Trial 1 on Day 2) and the interaction terms. For comparisons between the sexes and species on particular Day-Trials we used *t*-tests. Furthermore we evaluated the learning performance of the study animals according to sex and species by estimating the best learning curve fit for each species with Table Curve 2D version 5.01 (Systat Software Inc, 2002).

To examine medium-term memory performance during the learning period we used Wilcoxon matched-paired test for dependent samples comparing the performance of the first trial of the second day (trial 9) and the last trial of the first day (trial 8). For the comparison of sex- and species-specific differences in performance we calculated the difference between trial 9 and 8 and tested for differences between the sexes or among same-sex members of the two study species with a Mann-Whitney *U* test.

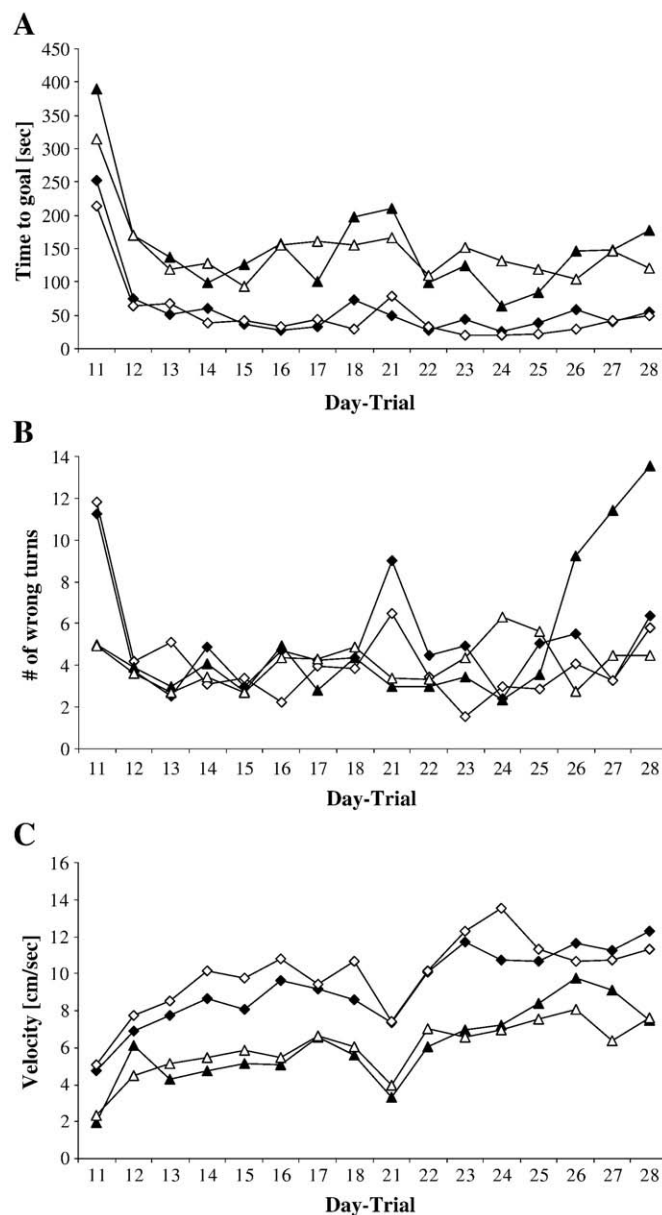
Memory retention was determined by comparing the performance during the memory trial on either day 2, 7 or 15 with that during the last learning trial (DT 28) employing Wilcoxon-tests. Differences between the sexes of the two study species were tested with a Mann-Whitney *U* test. A Bonferroni correction was applied to correct for multiple comparisons. All analyses were carried out with SPSS 15.0.

## 3. Results

### 3.1. Learning

All animals exhibited a clear pattern of learning and Day-Trial was a significant variable in all analyses performed to assess learning ( $p \leq 0.025$ ). Time to goal declined with the number of trials while at the same time velocity increased (Fig. 2A and C). However, this trend was not as clear for the number of wrong turns (Fig. 2B) with particularly female Cape mole-rats exhibiting rather erratic performances (see below). With the exception of one variable measured no significant sex-specific differences in learning in Damaraland mole-rats or Cape mole-rats were apparent (Table 1). However, female Cape mole-rats demonstrated a large number of wrong turns during the last three of the learning trials and those were significantly higher than those of conspecific males during trial 26 ( $t=3.027, p=0.007$ ) and 28 ( $t=2.453, p=0.023$ ) and tended to be higher during trial 27 ( $t=2.011, p=0.058$ ).

The interspecific comparison revealed significant differences in learning for time to goal and velocity (Table 1) with Damaraland mole-rats reaching the goal chamber sooner (Fig. 2A) and travelling at a faster speed (Fig. 2C). We found no systematic significant species-specific differences for the number of wrong turns observed in our study animals (females:  $F=0.567, p=0.460$ ; males:  $F=0.700, p=0.410$ ). However, significant species-specific differences were apparent for both sexes for the number of wrong turns during particular trials (females:  $F=1.723, p=0.046$ ; males:  $F=0.1954, p=0.017$ , Fig. 2B). Both, female and male Damaraland mole-rats made significantly more wrong turns during the first learning trial than their same-sex counterparts of the Cape mole-rat (females:  $t=2.879, p=0.008$ ; males:  $t=2.282, p=0.030$ ). Furthermore, female Cape mole-rats showed significantly more wrong turns during trial 27 ( $t=-2.760, p=0.011$ ) while male Cape mole-rats performed signifi-



**Fig. 2.** Learning performance for mole-rats A. Mean time required to enter the maze B. number of wrong turns C. velocity while travelling the maze. Black diamonds: female Damaraland mole-rats, white diamonds: male Damaraland mole-rats, black triangles: female Cape mole-rats, white triangle: male Cape mole-rats.

cantly more wrong turns than Damaraland mole-rat males during trial 23 ( $t=-2.187, p=0.041$ ) and 24 ( $t=-2.578, p=0.016$ ). The learning curves for the different groups were correlated with an exponential growth regression expressed by the formula:  $Y=a+be^{cx}$  (Table 2), however the correlation was weak ( $R^2 > 0.35$ ). Nevertheless these learning curves confirm the lack of sex differences in performance for all but number of wrong turns in Cape mole-rats and corroborate the species differences.

### 3.2. Anxiety assessment

With the exception of distance travelled for Cape mole-rats ( $F=1.602, p=0.071$ ) all measures of anxiety were significantly affected by Day-Trial with the performance improving with increasing number of trials for both species ( $p \leq 0.044$ ). We found no significant effect of sex for any of the variables measured (Table 1). Cape mole-rats took significantly longer to enter the trial maze during the learning trials

**Table 1**  
Results of the generalized linear mixed model comparing sex- and species-specific performances during the learning trials

	Variable	Learning			Anxiety			
		Goal	Wrong turns	Velocity	Entry	Food	Distance	Dist2-1
Fd ♂ vs. ♀	Sex	F=0.278, 0.602	F=0.021, 0.886	F=0.176, 0.680	F=0.096, 0.759	F=0.541, 0.471	F=0.009, 0.925	–
	Sex*DT	F=0.645, 0.837	F=1.065, 0.387	F=1.170, 0.294	F=0.951, 0.507	F=0.862, 0.608	F=1.299, 0.199	–
Gc ♂ vs. ♀	Sex	F=0.405, 0.535	F=0.072, 0.791	F=0.422, 0.536	F=0.353, 0.559	F=1.071, 0.335	F=0.665, 0.423	F=3.853, 0.062
	Sex*DT	F=0.616, 0.858	F=3.101, <0.0001*	F=0.677, 0.802	F=1.165, 0.298	F=0.882, 0.652	F=1.491, 0.106	F=0.781, 0.699
Fd vs Gc	species	F=122.897, <0.0001*	See text	F=50.607, <0.0001*	F=18.112, <0.0001*	F=1.941, 0.174	F=0.177, 0.675	–
	Species*DT	F=1.268, 0.217		F=2.987, <0.0001*	F=2.275, <0.0001*	F=1.301, 0.198	F=2.128, 0.007*	–

Fd: *Fukomys damarensis*, Gc: *Georychus capensis*, \*: significant comparisons.

( $F=18.112$ ,  $p<0.0001$ ) and this applied to all learning trials ( $p\leq 0.002$ ). There were no significant differences between the time between first entering the goal chamber and first encountering the food between the two species or the distance travelled till first encountering food (Table 1). However, Cape mole-rats travelled a significantly shorter distance before their first contact with the food during trial 25 ( $t=2.267$ ,  $p=0.028$ ) and tended to travel a shorter distance during trial 26 ( $t=1.898$ ,  $p=0.064$ ). Although all Cape mole-rats eventually ate the food they often explored the maze further after first encountering food. The additional distance travelled ranged from 0 to 4405 cm and males were more likely to travel an additional distance (44.0% versus 22.4% of the trials) and tended to travel a longer additional distance ( $F=3.853$ ,  $p=0.062$ ), however, this was only significant during trial 22 ( $t=-3.149$ ,  $p=0.008$ ) but not for any of the other trials ( $p\geq 0.07$ ).

### 3.3. Medium-term memory

Neither Damaraland mole-rats nor Cape mole-rats exhibited significant differences between the sexes for any of the variables measured (all  $p>0.12$ , see Table 3) and data for both sexes were thus lumped together for further analyses. Damaraland mole-rats showed no significant difference in time to goal ( $Z=-1.347$ ,  $p=0.178$ ) and number of wrong turns ( $Z=-1.772$ ,  $p=0.076$ ) during trials 8 and 9. In contrast, Damaraland mole-rats travelled with significantly lower velocity during trial 9 compared to trial 8 ( $Z=-2.426$ ,  $p=0.015$ , Fig. 2C).

Similar to Damaraland mole-rats the Cape mole-rats did not exhibit a significantly poorer performance in time to goal ( $Z=-0.643$ ,  $p=0.520$ ) and number of wrong turns ( $Z=-1.010$ ,  $p=0.312$ ) during trial 9 compared to the previous one. However, as in Damaraland mole-rats the velocity while travelling the maze was significantly reduced during trial 9 compared to trial 8 ( $Z=-2.905$ ,  $p=0.004$ , Fig. 2C).

When comparing medium-term memory of the two study species Cape mole-rats took significantly longer than Damaraland mole-rats to reach the goal chamber during both trial 8 ( $Z=-4.413$ ,  $p<0.0001$ ) and 9 ( $Z=-4.833$ ,  $p<0.0001$ , Fig. 3A). We found no significant difference in the number of wrong turns during trial 8 ( $Z=-1.048$ ,  $p=0.295$ ) and 9 ( $Z=-1.230$ ,  $p=0.219$ ) between the two species (Fig. 3B). Cape mole-rats were significantly slower than Damaraland mole-rats during both trials 8 ( $Z=-3.960$ ,  $p<0.0001$ ) and 9 ( $Z=-4.907$ ,  $p<0.0001$ , Fig. 3C).

**Table 2**  
Learning curves estimated for learning trials

Variable	Species	Sex	Equation	R <sup>2</sup>
Goal	<i>C. damarensis</i>	Female	$y=39.4+11,902,033 * e^{-x}$	0.345
		Male	$y=35.4+10,038,714 * e^{-x}$	0.378
	<i>G. capensis</i>	Female	$y=132.3+14,073,536 * e^{-x}$	0.205
		Male	$y=130.0+10,247,288 * e^{-x}$	0.109
Wrong turns	<i>C. damarensis</i>	Female	$y=4.4+328,935.6 * e^{-x}$	0.051
		Male	$y=3.5+452,709.8 * e^{-x}$	0.141
	<i>G. capensis</i>	Female	$y=3.9+7.8 * e^x$	0.199
		Male	$y=4.0+30,215.9 * e^{-x}$	0.001
Velocity	<i>C. damarensis</i>	Female	$y=12.2-826.0 * e^x$	0.192
		Male	$y=12.4-711.9 * e^x$	0.135
	<i>G. capensis</i>	Female	$y=6.19-418.4 * e^x$	0.074
		Male	$y=6.59-520.2 * e^x$	0.148

### 3.4. Memory retention

We tested for differences in memory retention by comparing the performances of the experimental animals 2, 7 and 15 days after the learning experiment and the last learning trial. With the exception of time to goal ( $Z=-1.984$ ,  $p=0.047$ , females:  $104.8\pm 58.9$  s, males:  $34.8\pm 15.3$  s) and velocity ( $Z=-1.984$ ,  $p=0.047$ , females:  $4.7\pm 3.8$  cm/s, males:  $10.4\pm 5.1$  cm/s) during the memory trial on day 15 there was no significant difference between the performance of the sexes in Damaraland mole-rats ( $p\geq 0.34$ ) on any trial day. Similarly, there was a significant difference in the number of wrong turns during the learning trial for Cape mole-rats but during none of the other trials (see Learning section above). However, results did not differ qualitatively between analyses performed separately for the sexes and those with the sexes combined and hence, we only present the results for the latter. The performance of Damaraland mole-rats was not significantly poorer during any of the memory trials compared to the last learning trial for any of the variables measured (Table 4), however, there was a tendency for animals to travel with lower velocity during the memory trial on day 7 after the learning trials than during the last learning trial ( $Z=-1.955$ ,  $p=0.051$ ).

In contrast, Cape mole-rats took significantly longer to reach the goal during the memory trial on day 15 after the learning trials ( $Z=-2.023$ ,  $p=0.043$ , Fig. 4) and travelled with significantly lower velocity during the memory trial on day 7 after the learning trials than during the last learning trial ( $Z=-2.023$ ,  $p=0.043$ ), however, these differences were not significant after Bonferroni corrections. None of the other comparisons was significant for Cape mole-rats (Table 4). The comparison of the performance during the memory trials revealed significant differences between the two species for time to goal ( $p\leq 0.024$ , Fig. 4) and velocity ( $p\leq 0.04$ ) during all trials. However, this was not the case for number of wrong turns during any of the trials ( $p\geq 0.24$ ).

## 4. Discussion

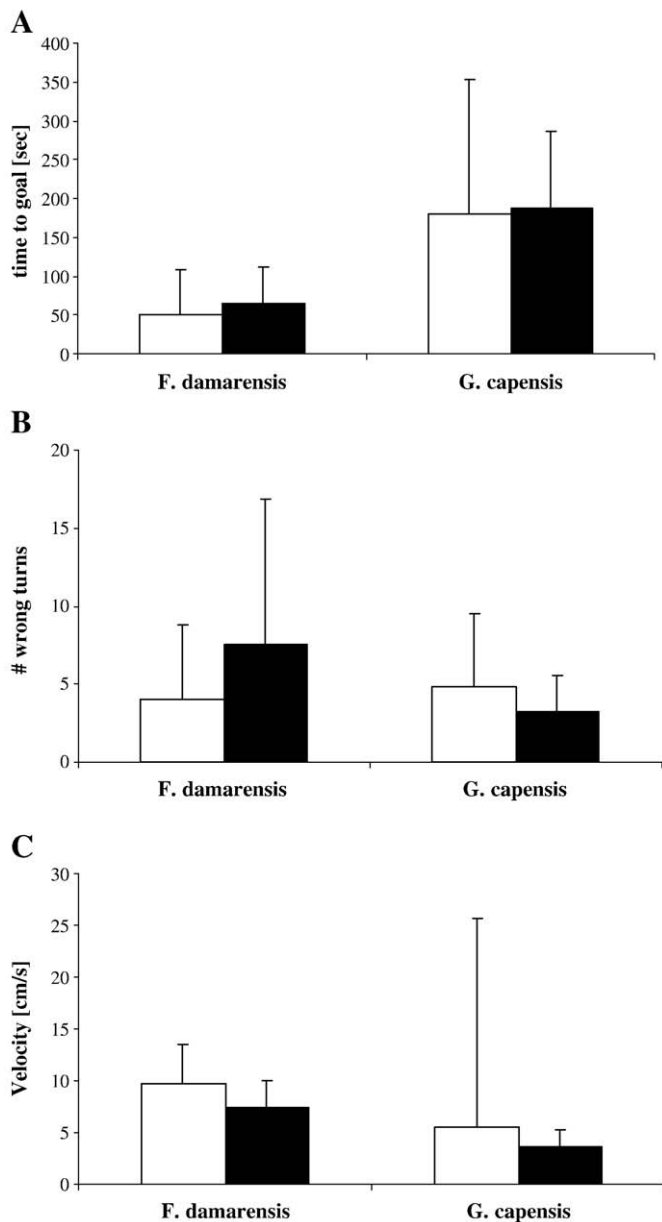
### 4.1. Sex-specific differences

Our study revealed no general significant differences between the performances of the sexes in our two study species in either their learning ability or memory although the sexes may differ during

**Table 3**  
Comparison of male versus female performance during trials 8 and 9 of the learning experiment

	Trial	Goal		Wrong turns		Velocity	
		8	9	8	9	8	9
Fd	U	100.5	90.0	126.5	140.5	68.5	126.5
	Z	-0.735	-1.416	-0.038	-0.139	-1.557	-0.038
	P	0.462	0.157	0.970	0.889	0.119	0.970
Gc	U	62.0	65.5	56.5	49.0	48.5	58.0
	Z	-0.550	-0.680	-0.135	-0.645	-1.334	-1.089
	P	0.582	0.496	0.896	0.519	0.186	0.276

Fd: *Fukomys damarensis*, Gc: *Georychus capensis*.



**Fig. 3.** Medium-term memory performance of Damaraland and Cape mole-rats during trial 8 (white bars) and trial 9 (black bars). A. Time required to enter the maze, B. Number of wrong turns until completion of task, C. Velocity while travelling through the maze. (Mean+SD).

particular trials. This contradicts our prediction of sex-specific differences for the promiscuous Cape mole-rat. Sex-specific differences in spatial abilities have been reported for some [28,29] but not for other rodent species [11,30] and may depend on the test situation [31]. To explain such differences a link between home range size and mating system has been proposed [3] in such a way that sex differences in spatial abilities will only be found in species in which males have larger home ranges than do females as is the case in promiscuous mating systems. Since Damaraland mole-rats are social and both sexes share the same burrow system [14] our results are in agreement with the spatial abilities that are linked to home range size. In contrast, their promiscuous mating system suggests differences in space use for Cape mole-rats. Home range size data for the solitary Cape mole-rat are lacking, however, with the exception of the solitary Namaqualand dune mole-rats (*Bathyergus janetta*, [32]) no sex-specific differences in home range size have been reported for subterranean rodents [33–35] suggesting that the same may apply

**Table 4**

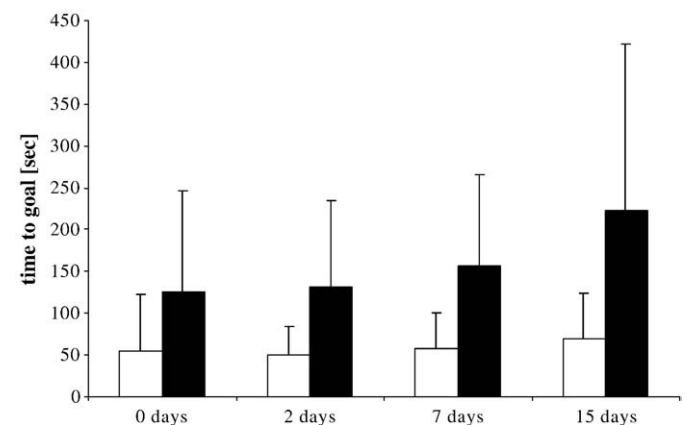
Results of the paired *t*-tests between performance during the last learning trial and the memory trials

Variable	Trials	Species	Z	p
Goal	DT28-MT2	<i>F. damarensis</i>	-0.553	0.594
		<i>G. capensis</i>	0.000	1.000
	DT28-MT7	<i>F. damarensis</i>	-0.153	0.878
		<i>G. capensis</i>	0.000	1.000
	DT28-MT15	<i>F. damarensis</i>	-1.172	0.241
		<i>G. capensis</i>	-2.023	0.043*
Wrong turns	DT28-MT2	<i>F. damarensis</i>	0.000	1.000
		<i>G. capensis</i>	-1.069	0.285
	DT28-MT7	<i>F. damarensis</i>	-0.350	0.726
		<i>G. capensis</i>	-1.187	0.235
	DT28-MT15	<i>F. damarensis</i>	-0.415	0.678
		<i>G. capensis</i>	-1.262	0.207
Velocity	DT28-MT2	<i>F. damarensis</i>	-1.572	0.116
		<i>G. capensis</i>	-1.461	0.144
	DT28-MT7	<i>F. damarensis</i>	-1.955	0.051
		<i>G. capensis</i>	-2.023	0.043*
	DT28-MT15	<i>F. damarensis</i>	-1.481	0.139
		<i>G. capensis</i>	-1.481	0.138

DT: Day-Trial, MT: memory trial, \*: significant comparison.

to Cape mole-rats. Female Cape mole-rats are probably less likely to enter foreign burrow systems and could thus be more reluctant to explore the maze, yet, although males tended to travel larger additional distances none of the other measures of learning or anxiety reflected such motivational differences between the sexes in Cape mole-rats. However, female Cape mole-rats performed significantly more wrong turns during the last learning trials. Since none of the anxiety measures indicates that this would be related to stress and the learning measures suggests a learning effect with increasing number of trials we have no explanation what might have caused this behaviour.

Sex-specific differences in home range size could be limited to the breeding season when males search for mates. In Cape mole-rats males need to dig to locate potential mates and although this is assisted by acoustic communication [36] it may require superior spatial abilities in males as has been reported for other rodent species [37,38,28]. This may explain the lack of sex-specific differences recorded for Cape mole-rats. Neither of the subterranean rodents studied so far exhibited any differences in spatial abilities between males and females [11,30] and the results of our study are in concordance with those findings. The lack in sex-specific differences in home range was invoked to explain these results [11]. This hypothesis awaits future validation for Cape mole-rats and excavation of mole-rat burrows during the breeding and non-breeding season of this species are necessary to evaluate this possibility. In general the



**Fig. 4.** Time taken to goal during by Damaraland (white bars) and Cape mole-rats (black bars) the last learning trial and 2, 7 or 15 days after the learning experiment (Mean time+SD).

high energetic costs of digging could pose a severe constraint on both sexes for the development of superior spatial abilities and no additional improvement may be necessary for mate searches in males.

#### 4.2. Species comparison

We expected Damaraland mole-rats to have superior spatial abilities compared to Cape mole-rats due to their more complex burrow structures [20] and higher digging costs [10,13]. Our results for the learning trials suggest that this is indeed the case with Damaraland mole-rats generally reaching the goal chamber sooner and travelling at a faster speed during both learning period and the assessment of memory retention. These differences may rather be a consequence of the divergent social systems of Damaraland and Cape mole-rats than a result of spatial abilities. Solitary mole-rats are highly xenophobic and aggressive towards each other [39,14,40]. This could make Cape mole-rats more reluctant to enter a new burrow system and indeed Cape mole-rats significantly delayed their entry to the maze compared to Damaraland mole-rats. Furthermore, although Damaraland mole-rats travelled larger distances till they first encountered food, Cape mole-rats frequently travelled additional distances instead of proceeding to eat the food immediately. The increased distress when being faced by an unfamiliar burrow system was furthermore expressed by the increased frequency of pumping sequences. Similarly, solitary blind mole-rats show stereotyped retracting during the first learning trials and performed poorly compared to two other rodent species [11]. In contrast, several animals are responsible for modifications to the tunnel system in Damaraland mole-rats and the geometry is constantly in a state of dynamic flux. Thus, the likelihood of encountering unfamiliar parts of a burrow system increases with colony size making them readily enter the experimental apparatus. Animals were allowed to use olfactory cues during the learning trials of our studies and if there are differences in olfactory properties of the two species this may explain differences in their performance. Little is known about olfactory senses in bathyergids and we can thus not exclude the effect of olfactory cues on performances in the maze. However, those differences persisted during the memory trials when olfactory cues were not available for navigation suggesting that such cues have played a minor role during the learning trials.

Although Damaraland mole-rats took longer to reach the goal chamber during the first learning trial and made more wrong turns during this trial, Cape mole-rats generally performed poorer than Damaraland mole-rats in all tests of their spatial ability. Both species demonstrated decreases in velocity during learning trial 9 compared to trial 8 but not for the other learning measures and memory decay during the assessment of long-term memory was high for both species. However, there was some indication of memory decay for Cape mole-rats during memory trial days 7 and 15 and for Damaraland mole-rats on day 7. Our memory trial period may have been too short to reveal significant differences in spatial abilities between Damaraland and Cape mole-rats. Kimchi and Terkel [11] found in their study of another solitary mole-rat steep learning curves and evidence of reduced performance during medium-term memory. However, up to 30 days after the learning trials blind mole-rats showed very little memory decay up to a period twice as long as the one we used in our experiment and only after more than 60 days fell the performance below 50%. Unfortunately, logistic constraints prevented memory trials beyond day 15 in our study.

Increased cognitive abilities have been attributed to ecological (i.e. foraging habitat characteristics, e.g. [41,42]) and/or social factors (i.e. group size, [43–46]). However, although spatial abilities have been explored with respect to social learning e.g. [47–50] this has not been tested before on an individual level. Our study does not allow us to differentiate between the effect of ecological and social factors on spatial abilities but the question whether superior spatial abilities in

the social species have developed purely as an adaptation to foraging constraints or as a by-product of superior cognitive abilities of social animals merits attention in future studies.

#### 5. Conclusion

When comparing spatial abilities among two species of mole-rats learning and memory appear to be correlated with sociality and the level of burrow complexity rather than the mating system. Sex-specific differences in spatial abilities were largely absent in both study species while they differed markedly between the two study species. We suggest that these findings may be explained by the high energetic demands of the subterranean niche exert a strong selection pressure on fossorial rodents irrespective of sex. Nevertheless sociality and the associated higher habitat complexity can impose larger adaptive advantages for superior spatial abilities in social species.

#### Acknowledgements

The study presented here complies with the laws and regulations of the Republic of South Africa. We thank the National Research Foundation and the University of Pretoria for research grants. We are grateful to Mr. and Mrs. J Duckitt Darling, Western Cape and Mr. and Mrs. J. Opperman Hotazel, Northern Cape for their hospitality. We thank the Western and Northern Cape Departments of Nature Conservation for permission to trap and collect the mole-rats on the respective properties. We also thank two anonymous referees for their suggestions and comments on the manuscript. M.S. Costanzo acknowledges a grant holder NRF bursary and H. Lutermann a postdoctoral research fellowship from the University of Pretoria.

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