

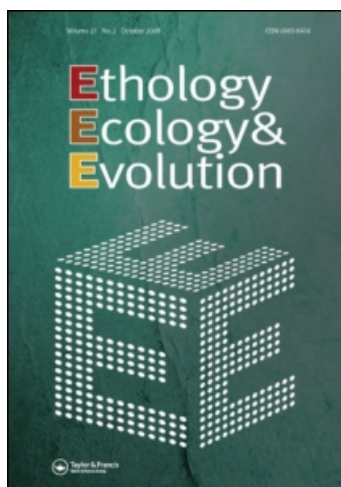
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Spatial learning abilities in males and females of the subterranean rodent *Ctenomys talarum*

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Few studies have focused on sex differences in spatial learning in subterranean rodents. *Ctenomys talarum* inhabits complex burrow systems, with males occupying larger areas than females. We assessed spatial learning ability by measuring the capacity of *C. talarum* individuals to solve appetitive radial or longitudinal spatial tasks during the non-reproductive season. We found that, regardless of sex differences in home-range size, males and females performed similarly in both tasks, rapidly improving their spatial performance after the initial trials and maintaining an accurate performance during subsequent trials. Our results show that sex differences in home-range sizes may not always lead to the evolution of sexually dimorphic spatial abilities.

KEY WORDS: spatial learning, space use, sex, subterranean rodents, *Ctenomys talarum*, Tala's tuco-tuco.

INTRODUCTION

Survival and successful reproduction are contingent upon individuals learning the spatial and temporal characteristics of their environment to find mates and food, to avoid predators, and to defend territory. Spatial learning and memory enable animals to build representations of their environment and thus to achieve proper orientation and navigation, especially in structurally complex habitats (KIMCHI & TERKEL 2001). Almost all research to date examining these cognitive functions has been conducted on surface-dwelling rodents; however, more recent studies have focused on the spatial ability of subterranean rodents. It is expected that these species present well developed capacities to process spatial information which

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would contribute to navigate accurately in the intricate underground tunnels (ANTINUCHI & SCHLEICH 2003).

Tala's tuco-tuco is a small subterranean rodent found in South America that inhabits a system of closed galleries parallel to the surface. The complex burrow system of *C. talarum* has a branching structure, consisting of a main axial tunnel and a variable number of lateral branches and feeding tunnels, all of them plugged with soil (ANTINUCHI & BUSCH 1992). Spatial orientation inside these burrow systems must be based on restricted sensory input when compared with surface habitats: the limited use of auditory and olfactory cues, the restricted use of visual cues to only the proximity of burrow openings, and the absence of a magnetic sense in this species to orient underground (FRANCESCOLI 2000; SCHLEICH & ANTINUCHI 2004; SCHLEICH et al. 2007). In spite of these sensory limitations, a previous study has shown that individuals of *C. talarum* were able to solve a complex spatial task accurately for a period between 30 and 60 days after the last training session (ANTINUCHI & SCHLEICH 2003). Special sensory adaptations found in subterranean rodents (e.g. somatosensory systems or internal information; NEVO 1999) were not described for *C. talarum*.

Highly developed spatial abilities are required for an accurate orientation in the intricate tunnel structures in order to improve the localisation of other individuals during intra-specific interactions (i.e. courtship, search of pups) and to decrease the high energetic costs associated with digging when extending the burrows for foraging. Besides this subterranean navigation, tuco-tucos are also active aboveground, when they emerge short distances from burrow openings to cut grasses and forbs growing in the soil and run back into the burrows where they later consume the collected food (BUSCH et al. 2000; DEL VALLE et al. 2001). During these excursions, animals become vulnerable to terrestrial and aerial predation (VASSALLO et al. 1994; BUSCH et al. 2000). Hence, both under and aboveground activities require the ability to rapidly acquire new spatial information and build transitory representations of the environment during the search of conspecifics or food within the tunnels or while foraging aboveground to reduce the time exposed to predators (MASTRANGELO et al. 2009).

In this species, animals of both sexes and all ages maintain exclusive territories. Previous studies have shown that home-range size differed between sexes, with *C. talarum* males occupying larger areas than females (ANTINUCHI & BUSCH 1992; CUTRERA et al. 2006). This difference has been attributed to variations in energetic demands between males and females, with males being heavier than females and thus requiring larger foraging areas. Additionally, it has been related with the mating system of *C. talarum*: a resource-defence polygyny in which males monopolise resources (territory and foraging areas) that will then be used by reproductive females (ZENUTO et al. 1999). Therefore, by occupying larger territories, males could have access to a larger number of females.

Sexually dimorphic home-range size has usually been associated to differential spatial learning abilities of both sexes in response to the increased spatial requirements of the widely ranging sex (GALEA et al. 1996). Therefore, we studied the spatial learning ability of males and females of the subterranean rodent *C. talarum* during the non-breeding season to discover whether the variation in home-range size between sexes is correlated with differential spatial capacities in this species. We evaluated spatial learning ability by measuring the capacity of individuals to solve appetitive spatial tasks that require different types of spatial learning capacities: radial maze and longitudinal labyrinths.

MATERIALS AND METHODS

Experimental individuals

We captured adults of both sexes (32 males and 36 females) in Mar de Cobo (37°46'S, 57°26'W, Buenos Aires province, Argentina) using plastic live traps set at fresh surface mounds. Then, we transported them to the laboratory and housed them in individual plastic cages (25 × 32 × 42 cm). The cages contained wood shavings for bedding and food was provided ad libitum, consisting of carrots, sweet potatoes, lettuce and sunflower seeds. The temperature in the animal room remained constant (23 ± 1 °C) and a 12L:12D illumination cycle was maintained. Animals were maintained at 75–80% of the initial body mass during the experiments to increase their motivation to explore and learn the mazes. At the end of the experiments the animals were fed ad libitum, recovered the initial body mass after a few days, and remained in good physical condition. They were then returned to their site of capture.

Labyrinths

Both labyrinths were constructed of white PVC tubes with transparent acrylic sheets on the top to allow observation of the animals. At the end of each trial, the labyrinths were dismantled and washed with tap water and odourless detergent, wiped with ethanol and then allowed to air dry to ensure that no odours from previous trials remained.

- (a) Six-arm radial maze. Each arm was 55 cm long and 10 cm in diameter, and diverged from the central start point constituted by a cylindrical recipient (35 cm in diameter and 40 cm in height). A small food reward (0.2 g of sweet potato) was placed at the end of each arm into a small cup to avoid the visual detection of food from the entrance. Plastic inserts with different colours and textures were placed at the entrance of each arm and served as intramaze visual and tactile cues. A spatial error occurs when an animal entered an arm of the maze that it had previously visited in the same test trial.
- (b) Longitudinal maze. This comprised a series of dead-end paths and one correct path leading to the goal point at the opposite end of the start point (Fig. 1). A food reward (5 g of sweet potato) was placed at the goal point. A spatial error occurs when the animal entered a dead-end path during the test trial. The total length of the artificial labyrinth (9–10 m) was within the range of burrow lengths of individuals of *C. talarum* from Mar de Cobo (mean 14 ± 8 m, ANTINUCHI & BUSCH 1992), being therefore representative of the natural burrows of this subterranean rodent.

Learning performance

We trained animals in two daily trials (one in the morning and one in the afternoon) until ten trials were completed. Before starting each trial, the animal was transported in a transfer tube from its home cage to the start point of the labyrinths, where it remained in the dark for a habituation period of 2 min. Then, it was allowed to enter to the six-arm radial or longitudinal labyrinths and the trial ended when the animal reached the food reward or when 10 min had elapsed, if the reward was not obtained. At the end of each trial, the animal was weighed and returned to its home cage in the transfer tube. The time spent to complete the task (latency) and the number of errors made by individuals (spatial performance parameters) were recorded during each trial.

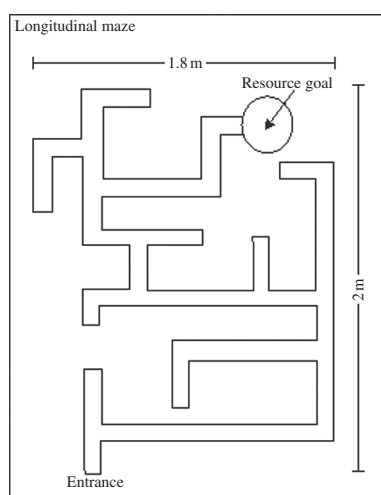


Fig. 1. — Design of the longitudinal maze used to evaluate spatial learning performance, which resembled the complex tunnel system that tuco-tucos inhabit in the field.

Data analysis

For radial and longitudinal mazes, spatial learning performance parameters between males and females were compared using a two-way ANOVA test (with “trial number” as the repeated factor), while a post-hoc Tukey test was performed to analyse differences between sexes at different trials.

Ethical note

The experimental procedure (food restriction and handling) did not affect the neutrophils: lymphocytes (N:L) ratio, indicating that the methodology did not increase the animal's chronic stress levels (MASTRANGELO et al. 2009).

RESULTS

Radial arm maze

Tuco-tucos showed a clear improvement in their spatial learning performance after the first trials, and the number of errors and the latency to reach the goal declined as the number of trials increased (Fig. 2(a)–(b) two-way (one RM factor) ANOVA, $n = 42$, $df = 9$, $F = 10.96$, $P < 0.001$; $F = 10.34$, $P < 0.001$, for number of errors and latency, respectively). No overall effect of sex on the number of errors was observed (Fig. 2(a), two-way (one RM factor) ANOVA, $n = 42$, $df = 1$, $F = 0.21$, $P = 0.652$). There was a significant effect of sex on the latency (Fig. 2(b), $n = 42$, $df = 1$, $F = 6.43$, $P = 0.01$), and a statistically significant interaction with the number of trials was also observed ($n = 42$, $df = 9$, $F = 2.88$, $P = 0.003$). However, the post hoc analysis

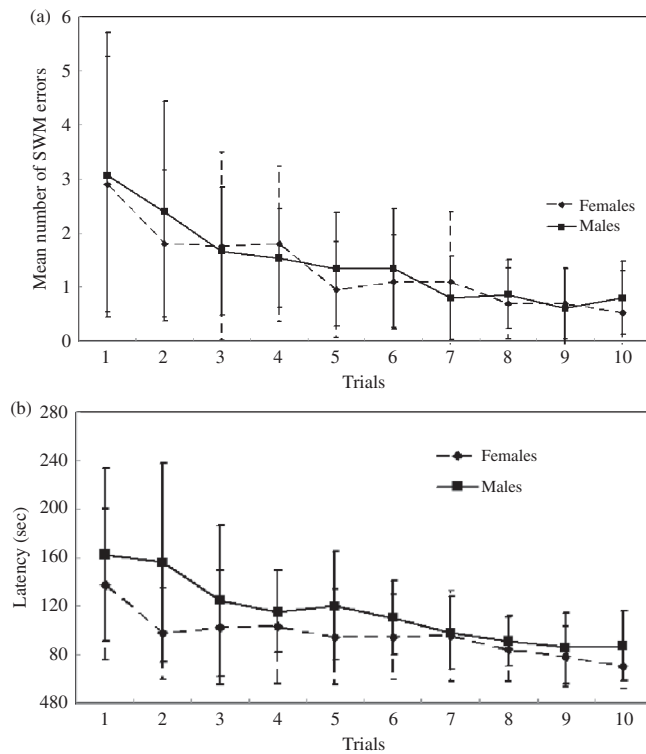


Fig. 2. — Mean number (\pm SD) of errors (a) and latency (b) to reach the goal during each trial of spatial learning in the six-arm radial maze.

revealed that there were no significant differences in the latency to reach the goal between sexes at the same trial number ($P > 0.05$).

Longitudinal maze

Similar to the other maze, individuals showed an improvement in their spatial learning performance after the first trials, and both spatial parameters declined as the number of trials increased (Fig. 3(a)–(b), two-way (one RM factor) ANOVA, $n = 33$, $df = 9$, $F = 39.65$, $P < 0.001$; $F = 48.49$, $P < 0.001$, for number of errors and latency, respectively). No effect of sex on the number of errors (Fig. 3(a), two-way (one RM factor) ANOVA, $n = 33$, $df = 1$, $F = 1.85$, $P = 0.183$) nor the latency to reach the goal was observed (Fig. 3(b), $n = 33$, $df = 1$, $F = 0.72$, $P = 0.401$). A significant interaction between sexes and both performance parameters was observed ($n = 33$, $df = 9$, $F = 3.08$, $P = 0.002$ for number of errors; $n = 33$, $df = 9$, $F = 3.2$, $P = 0.001$ for latency), although post hoc analysis also revealed that there were no significant differences in the number of errors nor the latency to reach the goal between sexes at the same trial number ($P > 0.05$).

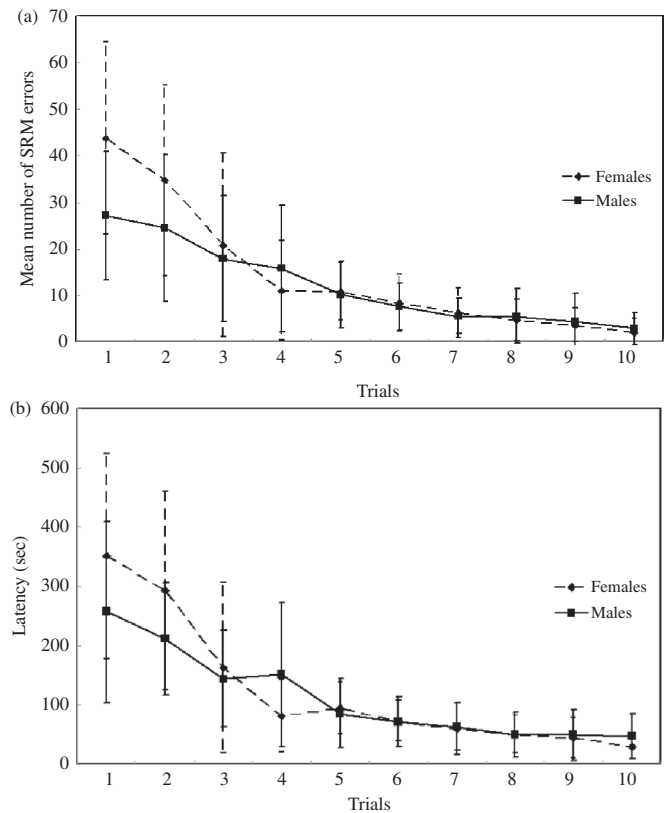


Fig. 3. — Mean number (\pm SD) of errors (a) and latency (b) to reach the goal during each trial of spatial learning in the longitudinal labyrinth.

DISCUSSION

It is expected that spatial learning ability is under a strong selective pressure in species that inhabit structurally complex habitats. This is the case of subterranean rodents which construct, use and maintain extensive and elaborate burrows which contain multiple chambers and openings (NEVO 1999; BENNETT & FAULKES 2000; BURDA 2003). In these species, proper orientation is crucial to decrease the high energetic costs of digging while extending the burrows for foraging. Moreover, in species which present some surface activity it is also important to reduce the time exposed to predators on the surface by relocating burrow openings rapidly (MASTRANGELO et al. 2009). The results obtained here showed that *C. talarum* has a highly developed capacity to learn structurally complex labyrinths in a radial task as well as in a longitudinal task, since individuals rapidly improved their spatial performance after the initial trials and maintained an accurate performance during the rest of the study period.

Sex differences in spatial learning capacities have been shown to be related to variations in home-range sizes between sexes due to differences in the amount of

spatial information needed to be processed in the wild (GALEA et al. 1996). Regarding subterranean rodents, KIMCHI & TERKEL (2001) did not find any sex differences in the ability to learn and navigate in a complex maze in *Spalax ehrenbergi*, a solitary species that showed no differences in the size of male and female home ranges throughout the year. Similar results were obtained in the solitary Cape mole-rat (*Georychus capensis*), although in this case females made a larger number of wrong turns during the last learning trials (COSTANZO et al. 2009). However, no information of home-range sizes in this species was provided, making any comparison with the situation observed in other species difficult. Radiotelemetry studies carried out during the non reproductive season showed that male home-range sizes of *C. talarum* are significantly larger than that of females (minimum convex polygon method, males: $70.10 \pm 31.60 \text{ m}^2$, females: $34.91 \pm 8.49 \text{ m}^2$; CUTRERA et al. 2006). However, home-range sizes estimated from excavated burrows indicated that differences in home range size between sexes are not as significant as estimated by radiotelemetry studies, although still different (minimum convex polygon method, males: $18.01 \pm 11.74 \text{ m}^2$, females: $11.04 \pm 13.18 \text{ m}^2$; ANTINUCCI & BUSCH 1992). Therefore, it is possible that, although males of *C. talarum* occupy larger areas than females, due to larger foraging areas required for conforming the energetic demands of the heavier sex (ZENUTO et al. 1999; CUTRERA et al. 2006), such difference in home-range sizes may not be large enough to require the evolution of differential spatial abilities in order to process the dissimilar amounts of spatial information required by males and females.

Spatial learning ability has also been shown to be modulated by the reproductive status of the individuals. Differences in this behaviour, for instance, have been shown in seasonally breeding polygynous rodents. These differences have been mostly observed during the breeding season when males have expanded home ranges for the purpose of controlling mates (GAULIN & FITZGERALD 1986; GALEA et al. 1996). For example, reproductively active males of deer mice (*Peromyscus maniculatus*) and meadow voles (*Microtus pennsylvanicus*) out-perform females in a spatial reference memory task (Morris water-maze) (GALEA et al. 1996). For this reason, it has been hypothesised that sex differences in spatial learning capacities are proximately related with the reproductive condition of individuals, which ultimately leads to male–female differences in space use and home range size. Future studies measuring spatial learning performance of *C. talarum* during the breeding season must be conducted in order to see whether spatial abilities are differentially affected by the reproductive status of individuals, since higher levels of circulating gonadal hormones have been shown to affect spatial abilities (GALEA et al. 1995, 1996).

Finally, the spatial complexity of the labyrinths must also be considered regarding the lack of differences in spatial learning capacities between sexes. In our experiments, we challenged animals with two complex spatial tasks that resemble natural burrows in their structure and size. Although increasing the complexity of these labyrinths could reveal potential sex differences in spatial learning capacities, using more challenging spatial tasks would not be representative of the situation that this species encounters in nature.

In conclusion, the results of this work showed that, although home-range sizes differed between sexes, spatial learning capacities are similar in males and females of *C. talarum*. Contrary to previous suggestions, this outcome shows that sex differences in home-range sizes may not always lead to the evolution of sexually dimorphic spatial abilities.

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