

Learning and laterality in wild-caught Namaqua rock mice (*Micaelamys namaquensis*)

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Abstract

Individuals often exhibit differences in cognition and/or preferences for one side over the other. Such differences have been attributed to the mating system and lateralization of the brain hemispheres that can differ between the sexes, respectively. Despite the hypothesized significant effects on fitness, only a limited number of rodent studies addresses sex differences in laterality and most focus on laboratory rodents. Here we examined whether wild-caught Namaqua rock mice (*Micaelamys namaquensis*), a rodent widespread in sub-Saharan Africa, exhibit sex differences in learning and laterality in a T-maze. Food-deprived animals entered the maze significantly faster over subsequent learning trials, suggesting that the sexes learned to find the food reward at the end of the maze arms equally. Although we could not confirm a side preference at the population level, the animals were strongly lateralized at an individual level. When the sexes were considered separately, females exhibited a preference for the right maze arm while the opposite was observed in males. The lack of comparable studies of sex-specific lateralization patterns in rodents makes the generalization of our results challenging and highlights the need for more such studies in rodents at both the individual and population levels.

Keywords: Choice behaviour; learning; *Micaelamys namaquensis*; rodent; side-bias; wild-caught

1. Introduction

The left or right-hand dominance observed in humans is a well-known example of laterality, the asymmetry in brain hemispheres, that results in behavioural and physiological variations between individuals such as biases toward a particular direction (Franklin and Lima, 2001; Wiper, 2017). Laterality has been observed at both the individual and population levels. When the majority of the individuals within a population are lateralized to a specific side that is indicative of population-level laterality (Rogers, 2002). In fact, in some species between 60 and 90% of individuals in a single population showed the same bias toward a specific side (Ghirlanda et al., 2009). However, this may not always be the case (Manns et al., 2021). Nevertheless, lateralization might still be apparent at the individual level with some showing preference for one side while others will be lateralized to the opposite side (Rogers, 2002).

The presence of laterality in many vertebrate and invertebrate species suggests that it is linked to biological fitness (Ghirlanda et al., 2009; Rogers et al., 2004). For instance, laterality is considered important because, in addition to allowing both hemispheres to analyse information simultaneously, it can make information processing more effective by preventing both brain hemispheres from processing the same information (Rogers et al., 2004). For example, the left hemisphere is oriented towards foraging tasks, while the right hemisphere perceives and responds to threatening stimuli such as a predator (Rogers, 2014). Such lateralization enables animals to improve their multitasking ability along with their fitness-related behaviours such as reproduction and foraging (McLean and Morrell, 2021). Biased behaviour is modulated by brain lateralization, thus individual bias towards the left side suggests control by the right brain hemisphere (Rogers, 2014). The right hemisphere in vertebrates is often associated with emotions, novelty, threatening stimuli, and recognition. More precise attention and routines are assumed to be controlled by the left hemisphere, along with learning and recognition (Rogers, 2014).

Rodent studies of laterality have used a range of measures and experimental set-ups to assess biases. These include the assessments of paw preferences, and biases in the

direction of head movements or body turns (Mundorf et al., 2020). Rodent laterality has often been tested using a T-maze arena (Mundorf et al., 2020). In trials where rodent behaviour was assessed repeatedly, they were observed to switch the side of the arm entered in consecutive trials suggesting they remembered previous choices (Hussein et al., 2018; Lalonde, 2002).

The direction of the side biases varied widely among rodents studied. More than 80% of rats (*Rattus rattus*) and mouse species (*Mus musculus* and *Apodemus agrarius*) studied had an individual-level paw preference for either their left or right side (reviewed in Manns et al., 2021). Red squirrels (*Sciurus vulgaris*) demonstrated a significant population-level right-handed preference when handling pine cones (Polo-Cavia et al., 2015). Not only have previous studies found differences between species, but also between different laboratory strains (Andrade et al., 2001). Both Wistar (Andrade et al., 2001; Santín et al., 1996) and Sprague–Dawley (Castellano et al., 1987) rats showed a very strong population-level bias towards the right side. However, population-level left biases have been observed in both Purdue–Wistar rats (Sherman et al., 1980) as well as ICR mice (Korczyński and Eshel, 1979). Strain-specific differences in observed laterality can be caused by a range of factors which include experienced stress, differences in experimental procedure, motivation and rearing conditions (reviewed in Manns et al., 2021).

Besides population and individual-level effects, sex differences in laterality can be expected, as in many species males and females may experience different selection pressures and be motivated by different factors (Andrade et al., 2001; Ariyomo and Watt, 2013). For example, female mammals are mostly driven by food, while males will be more motivated by mating opportunities and these differences can ultimately result in anatomical changes to the brain (Ariyomo and Watt, 2013). Differences between males and females of a species include the difference in hippocampus size, with males of several species showing a larger and thicker right hippocampus while the opposite has been observed in females. Such differences could account for divergent laterality patterns between the sexes (Sardar et al., 2021; Tabibnia et al., 1999). Although this has been evaluated in a number of studies, this is

not the case for many rodent studies. In fact, according to a recent review, the bulk of laterality research on rodents is focused solely on males (Jordan, 2020) or the studies do not provide information regarding the sex of the study animals (Manns et al., 2021).

Similar to laterality, T-maze arenas have frequently been used to test learning and memory (Andrade et al., 2001). Learning and memory play a significant role in animal fitness since previous experiences can guide optimal behaviour in current circumstances. By using the knowledge gained from past experiences an individual can be more successful in future tasks that will require valuable time and energy (Mondoloni et al., 2022). Learning ability can also differ between males and females. Polygamous males have been observed to be superior in learning spatial tasks such as mazes when compared to females (Gaulin and Fitzgerald, 1989; Hegab et al., 2019). This has been linked to the fact that males increase their ranges in search of females, which enhances their spatial experiences and as a result they have a better learning ability compared to the more sedentary females (Gaulin and Fitzgerald, 1989; Hegab et al., 2019). Another explanation for sexual dimorphism in learning concerns the method through which the sex learns (Lugo et al., 2018). It has been suggested that females make use of landmarks and males are more prone to rely on the surrounding geometrical details (reviewed in Lugo et al., 2018). However, this is not always the case and the speed and accuracy at which the sexes learn may be dependent on the type of experimental setup they are subjected to (Forcano et al., 2009).

Many rodent studies are conducted on laboratory rodents and their applicability to wild rodents has received much less attention, particularly for rodents outside the northern hemisphere. In order to address this gap in our knowledge, we chose the Namaqua rock mouse, *Micaelamys namaquensis* (Family: Muridae), which is widely distributed throughout southern Africa (Skinner and Chimimba, 2005), for our study. As their name suggests, these rodents are considered rock specialists that are omnivorous generalists (Skinner and Chimimba, 2005; van der Merwe et al., 2014). These rodents are polygamous but display no morphological sexual dimorphism, they can have up to four offspring per litter and their

reproduction is strictly seasonal (Fleming and Nicolson, 2004; Skinner and Chimimba, 2005). During the mating season, males have substantially larger home ranges than females which is likely to give them greater experience in spatial navigation and social encounters while exposing them to higher predation risks than territorial females (Fleming and Nicolson, 2004). *Micaelamys namaquensis* are nocturnal rodents and to our knowledge laterality studies have not previously been conducted on a wild-caught African murid.

Our study aimed to determine whether *M. namaquensis* would learn how to navigate a T-maze to find a food reward within five trials. In addition, we aimed to assess whether our study species had an innate bias to either side during the first trial (i.e., laterality) and whether there would be a learned biases during subsequent trials. Additionally, we wanted to detect if the direction of the bias would differ between males and females. We predicted that the study animals would (1) learn the purpose of the maze - i.e., to find the food reward - by the end of the experiment. In addition, we (2) hypothesized that males would learn faster than females. With regards to laterality, we anticipated that *M. namaquensis* would (3) exhibit laterality, both an individual- and population-level bias. In addition, we predicted that, similar to other species, (4) males would be biased towards the left and expected the laterality of females to differ from that of males.

2. Materials and Methods

2.1 Animal trapping

For this study, we caught 24 (12 of each sex) *M. namaquensis* individuals from two study plots at Telperion Nature Reserve (S25.70827 E28.93005), Gauteng, South Africa. A total of 300 Sherman live traps (H. B. Sherman Traps Inc., Tallahassee, Florida) were spread over the two plots, using three trap lines of 50 traps each per plot for four days. We spaced all traps 10 m apart and baited each trap with a peanut butter and oats ball. At 16h00 each day we opened and baited the traps and inspected them the following morning at 06h00. When an animal was

trapped, it was taken back to the field laboratory to assess its body condition. Only animals in good condition, i.e., without external injuries, were included in the study. Chosen females were checked to be non-pregnant or lactating. We removed each animal from the trap, sexed it, and placed each individual into an animal cage (11 x 38 x 28.4 cm) lined with wood shavings. The animals were transported to the University of Pretoria for experimentation.

2.2 Animal housing in the animal room

At the University of Pretoria, animals were transferred to bigger cages (22.5 x 37.7 x 34 cm) and kept in an animal room under constant conditions (12h light/12h dark cycle; 24°C ± 1°C). The animal room was windowless with bare walls which would make uneven reflection of sounds from the walls unlikely. We covered the bottoms of all cages with wood shavings and provided them with tissue paper (1 ply, Twinsaver, Johannesburg) for nesting material. In addition, we gave each individual a rock, a toilet paper roll, and a piece of egg carton as enrichment. The animals had *ad libitum* access to water and were fed a combination of apple, carrot, and sweet potato pieces daily. We supplemented with rodent pellets once a week to prevent excessive weight gain. Animals were in captivity for approximately two months before the experiments commenced.

2.3 Experimental procedures

To test the learning ability (i.e., locating a food reward) and laterality of *M. namaquensis*, we observed them in a T-maze (Figure 1) over five consecutive days. The T-maze consisted of two arms of equal length and was covered with a wire grid to prevent animals from escaping. At the end of each arm was a chamber with a slice of sweet potato covered in peanut butter. To further motivate animals to explore the maze, we reduced their regular daily diet by three-quarters from the day prior to the first learning trial until all trials were concluded (Day 5). Animals were transferred from their holding cages to the start chamber (Figure 1) of the T-

maze and allowed three minutes to habituate to the experimental setup. Once this time had elapsed, we removed the divider separating the start chamber from the maze (Figure 1). The animal then had five minutes to explore the maze. The same procedure was used on the subsequent four days. Following previous studies, the orientation of the maze remained constant over all trials conducted (Andrade et al., 2001; Hegab et al., 2019; Maciejewska et al., 2016). The animal's behaviour in the maze was recorded with a video camera suspended over the maze (Sony Handycam, DCR-SX65, 70X zoom). After five minutes the animal was directed back to the start chamber and transferred to its cage. We disassembled the maze and cleaned all the parts with soap (anti-bacterial dishwashing liquid, Checkers house brand, Brackenfell, South Africa) and water after each trial to remove odours. All of the parts were dried using paper towels.

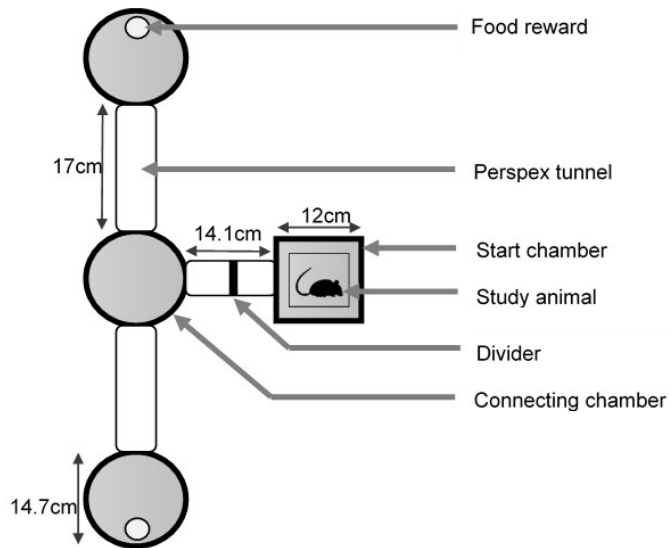


Figure 1: A visual representation of the T-maze used to conduct the experiment. All three circular chambers were of identical size. The animal was placed inside the start chamber through an opening at the top, the whole maze was covered with wire mesh to prevent escapees.

2.4 Data analyses

We examined all videos using the Observer XT v10.5 (Noldus Information Technology Inc., Wageningen, The Netherlands) to analyse four pre-defined observed behaviours (Table 1). None of the behavioural variables had a parametric data distribution (Shapiro-Wilk test: $p < 0.05$). Hence, we used generalized linear mixed models (GLMMs) with the “lmer” (Bates et al., 2015) package in R v3.6.1 (RStudio Core Team, 2019) for analyses. To test how long the animals took to enter the maze and the duration spent in the chosen arm, we used a Gamma distribution and log-link function. To determine whether there was an innate bias we analysed the latency to enter the arms during the first trial only. In order to evaluate whether the animals exhibited a learned bias of the maze, we repeated this analysis across all trials. These two models were run using the Gamma distribution and log-link function. Lastly, to analyse the frequency with which the animals entered the arms we used a Poisson distribution and log-link function. All models included the animal identity as a random variable to account for the repeated measurement of individuals. We started with the most saturated models which included the sex of the animals, the trial number (trial 1 to 5), the arm (i.e., left or right), and all interaction terms. To determine the most parsimonious models for each dependent variable we used the “drop1” function that drops non-significant variables in a stepwise manner. We selected the best-fitting models as those with the lowest AICc and highest weight values (Supplementary table) and the results produced from those models are reported here. The “emmeans” package (Lenth et al., 2020) was used to carry out post-hoc comparisons. To further evaluate laterality, we calculated the population-level lateralization using the laterality index (LI) by subtracting the number of total right turns (across the five trials, the number of times the animals entered the right arm) from the number of left turns (number of times the left arms were entered across all trials) and divided it by the sum of first left and the first right turns (total number of turns, Wiper, 2017). In addition, we determined the individual-level lateralization through the absolute laterality index (ALI) from which the strength of the laterality can be deduced (Wiper, 2017). Using a one-tailed t -test, we weighed all the animals’ LI and

ALI scores against each other (as done in previous studies, e.g., Jacobs and Oosthuizen, 2023; Rogers et al., 2004).

Table 1: Behaviours recorded during the experimental trials including the type of measurement (duration measured in seconds) and description of the behaviour.

Behaviour	Measure	Description
Latency to start	Duration	The time elapsed before the animal left the start chamber with more than half of their body to enter the T-maze
Latency to enter arms	Duration	The time elapsed before the animal entered the arm with more than half of their body
Frequency to enter arms	Frequency	The number of times the animal entered the arm with more than half their body
Duration in the arms	Duration	The total amount of time the animals spent in the arms

3. Results

3.1 Latency to enter the maze:

The final model to determine whether the animals learned the maze and found one of the food rewards contained only a single variable (Appendix 1). The trial number influenced the latency to start significantly (Table 2). Post-hoc tests showed that it was significantly higher during the first trial compared to all subsequent trials ($p \leq 0.036$, Figure 2A). In addition, trial 2 had a significantly higher latency than all subsequent trials ($p \leq 0.012$, Figure 2A). There was no significant difference in the latency to start between any of the other trials ($p \geq 0.210$, Figure 2A).

Table 2. Results of the principal component analysis for the exploration, aggressive response, and boldness tests (N = 22). Note that only PC1, explaining more than 50% of the observed variance is reported and was used in all subsequent analyses. Values larger than 0.5 are highlighted in bold.

Variable	Exploration test	Aggressive response test	Boldness test
	PC score	PC score	PC score
Latency to move (s)	-0.435	-0.644	-0.667
Stationary (s)	-0.891	-0.940	-0.900
Sniffing (s)	0.289	-	-
Touching divider/object (frequency)	0.898	0.840	0.783
Grooming (frequency)	0.283	-	-
Rearing (frequency)	0.957	-	-
Approaching object (s)	-	0.946	0.930
Retreating from object (s)	-	0.812	0.762
Time close to object (s)	-	0.708	0.653
Latency touching (s)	-	-0.857	-0.857
Speed (cm/s)	0.888	-	-
Distance (cm)	0.916	-	-
Eigenvalue score	4.497	4.794	4.474
Variance explained	56.2%	68.5%	63.9%

PC: Principal Component score, -: variable not measured for this test.

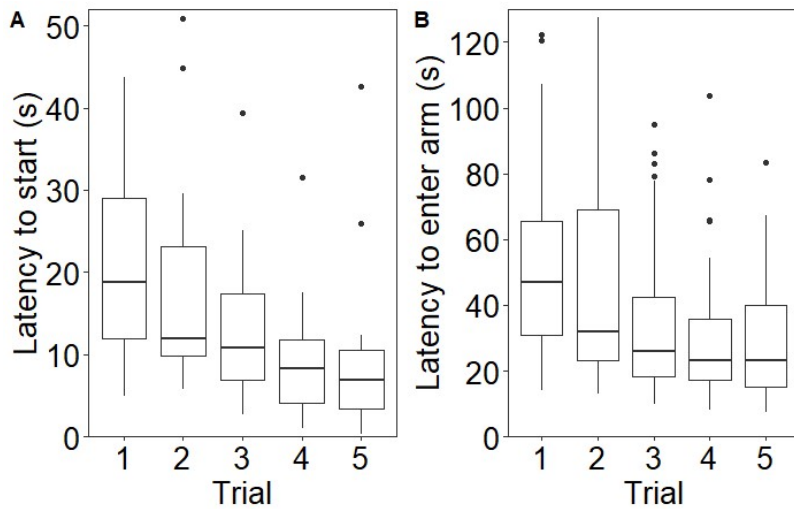


Figure 2: The influence of the trial number on (A) the latency to leave the start chamber and (B) the latency to enter an arm. The graph contains the medians (indicated in bold), the quartiles (top and bottom of the box) and the ranges (top and bottom ends of the lines).

3.2 Latency to enter arms:

The innate bias model showed that neither of the main effects, arm (left or right entered) and sex, influenced the latency to enter an arm significantly when only Trial 1 was considered (Table 2). In contrast, the two-way interaction between arm and sex was significant (Table 2). However, the pairwise comparisons revealed no significant differences ($P \geq 0.060$).

Our most parsimonious model for the learning bias (all five trials included) revealed that once again the main effects of arm entered and sex had no significant influence. However, the latency to enter the arms differed significantly between trials (Table 2). It was significantly higher during the first compared to trials 3, 4, and 5 ($p < 0.001$ for all, Figure 2B). Furthermore, it was significantly higher during trial 2 compared to trial 3 ($p = 0.030$, Figure 2B). None of the other pairwise comparisons were significant ($p \geq 0.053$, Figure 2B).

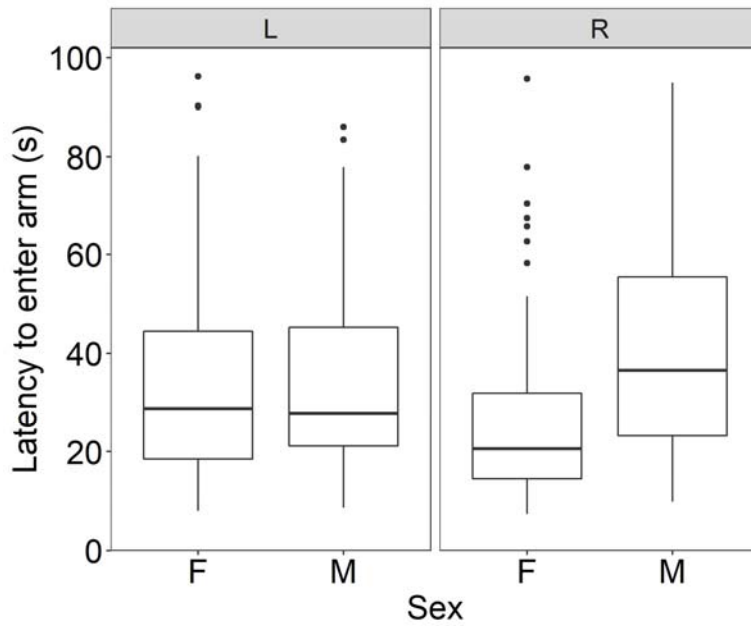


Figure 3: The influence of the sex and arm on the latency to enter the side chambers, including the separate medians (indicated in bold), quartiles (top and bottom of the box), and ranges (top and bottom ends of the lines).

The interaction between sex and arm was significant (Table 2). Females took significantly longer to enter the left arm compared to the right arm ($p = 0.015$, Figure 3). However, none of the other comparisons was significant ($p \geq 0.113$, Figure 3). None of the other variables was retained in the most parsimonious model (Appendix 1).

3.3 Arm first entered:

The most parsimonious model showed that the arm first entered was significantly influenced by trial (Table 2). During trial 2, animals were significantly more likely to enter the left arm compared to the animals in subsequent trials ($p \leq 0.012$). None of the other trials showed a significant difference in the arm first entered ($p \geq 0.063$). The sex of an individual significantly affected the arm first entered (Table 2) with females being significantly more likely to enter the right arm first (mean \pm SE: 74.6 ± 40.0). Males, however, entered the left arm first more frequently (-60.6 ± 35.7). None of the other variables was retained in the final model (Appendix 1).

3.4 Frequency to enter arms:

The most parsimonious model showed that the frequency to enter the arms was significantly affected by trial (Table 2). Animals entered the arms significantly more frequently during trial 4 compared to trial 1 ($p = 0.0007$) and trial 5 ($p = 0.012$, Figure 4A). In general, the animals entered the left arm significantly more frequently (169 ± 17.1) compared to the right arm (153 ± 17.1 , Table 2). Yet, it did not differ significantly between males and females (Table 2).

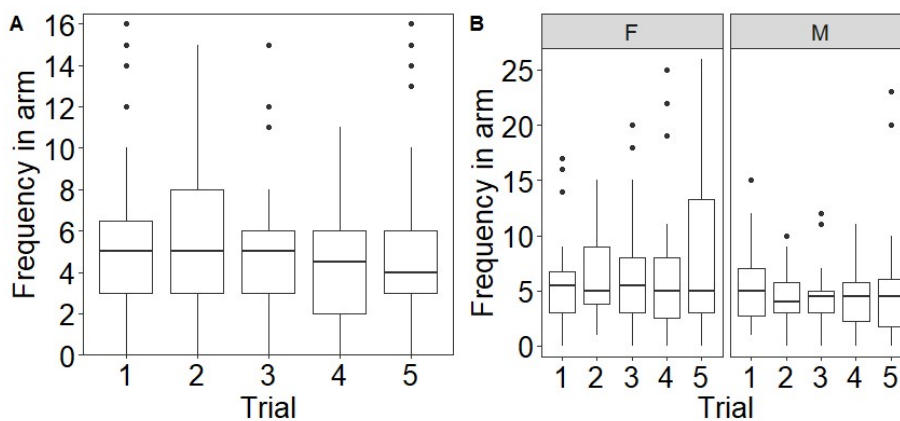


Figure 4: The effect of (A) trial number and (B) trial number and sex on the frequency to enter an arm.

The boxplot includes the medians (indicated in bold), quartiles (top and bottom of the box), and ranges (top and bottom ends of the lines).

In addition, the interaction between sex and trial number was significant (Table 2). Females entered the arms significantly more frequently during trial 4 compared to females in trials 1, 2, and 3 ($p \leq 0.036$, Figure 4B). In contrast, males entered the arms significantly less frequently during trial 1 compared to males in trials 2, 3, and 4 ($p \leq 0.035$, Figure 4B). Furthermore, males entered the arms significantly less frequently during trial 5 compared to males in trials 2, 3, and 4 ($p \leq 0.035$, Figure 4B). None of the other comparisons was significant ($p \geq 0.102$, Figure 4B). Neither the main effect arm nor its interaction terms were retained in the final model (Appendix 1).

3.5 Time spent in the arms:

Neither trial nor arm had a significant effect on the time spent in an arm (Table 2). However, the interaction between the trial and arm was significant (Table 2). The animals spent significantly more time in the left arm during trial 1 compared to the right arm during trial 2 ($p = 0.038$, Figure 5). In addition, animals spent significantly more time in the right arm during trial 3 compared to the time spent in the right arm during trial 2 ($p = 0.043$, Figure 5). None of the other comparisons was significant ($p \geq 0.058$). Sex as well as the interaction terms between sex and any of the other variables were dropped from the most parsimonious model (Appendix 1).

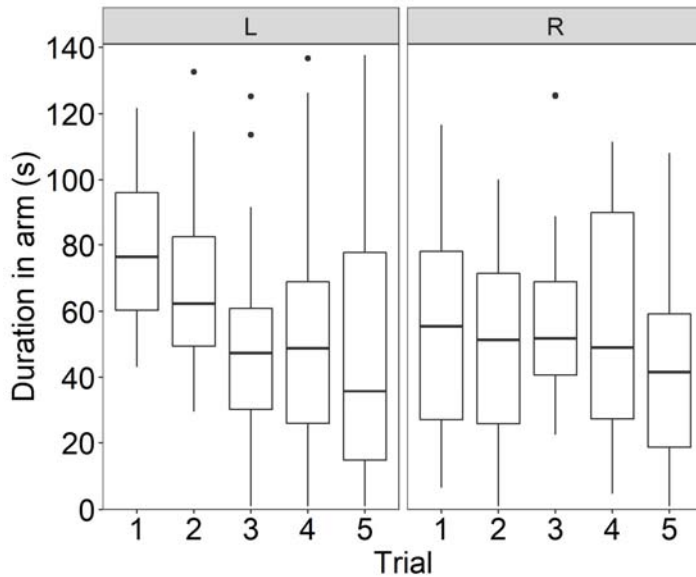


Figure 5: The effect of trial number and arm entered on the duration spent in the arms. The boxplots include the medians (indicated in bold), quartiles (top and bottom of the box), and ranges (top and bottom ends of the lines).

3.6 Laterality indices:

The individual-level laterality ALI was significant ($t = 20.235$, $df = 23$, $p < 0.001$). However, the calculated population-level laterality LI indicated no significant bias to a specific side ($t = -0.455$, $df = 23$, $p = 0.653$, Supplementary figure).

4. Discussion

Our study focussed on learning and laterality including the potential sex biases in wild-caught *M. namaquensis*. In support of our first hypothesis, the decreasing latencies to enter the maze and the first arm from trial 1 to subsequent trials clearly indicated that the animals had learned the maze (Valentinuzzi et al., 2004). This may also be an indication of reduced fear as the animals become acclimated to the experimental conditions (Lamanna and Martin, 2016), although these two mechanisms are not mutually exclusive. The latter hypothesis is further

supported by the observation that animals increased their frequency of entering a side as this could be an indication of increased exploratory behaviour, specifically inquisitive exploration (Dellu et al., 2000; Oosthuizen et al., 2013). However, our results indicated the possible presence of conditioned learning in the study species as the animals could have associated a food reward with the experimental maze and entered the different parts less frequently across trials as a result (Hammond et al., 2012). A possible explanation for this observation could be that the animals experienced boredom, as the task became monotonous with no added novelty or stimulus (Burn, 2017). However, contrary to our second prediction, we did not observe significant effects of sex on learning. The latency to enter the maze did not differ between the sexes, and the main effect of sex did not influence the latency to enter an arm. This could be a result of testing that occurred outside of the breeding season, thus the sexes could have experienced lower drivers for sex-specific exploration (Hegab et al., 2019). Interestingly, this effect was more pronounced in males than females, as females took longer to enter one of the arms. Males in polygynous species are generally thought to maximize their reproductive output by mating with as many females as possible and this often involves roaming over large areas which leads to overall more experience finding resources and interacting with conspecifics (Gaulin and Fitzgerald, 1989; Vanden Broecke et al., 2019). Conversely, females are more territorial due to their reliance on knowledge of the distribution of resources such as food and shelter in time and space which has been reported for our study species (Fleming and Nicolson, 2004). Hence, the exploration of male *M. namaquensis* may have been more motivated by the search for females while females may have been more food driven.

We found mixed evidence for our third hypothesis, that laterality would be apparent in our study species, and while the laterality indices indicated lateralization at an individual level, this was not supported at the population level. The lack of laterality at the population level based on the LI contrasts with the results considering the other variables measured. The animals entered the left arm of the maze significantly faster, more frequently and were more

likely to enter it first than the right arm during the second trial. The increased frequency of entering the left compared to the right side suggests that the study species has a lateralized right hemisphere (Rogers, 2014). Although this was not apparent from the population level LI, this could be attributable to the type of assessment we carried out in the current study. Laterality may be present depending on the kind of measure used (e.g., spatial orientation vs. paw preference) but also depend on the study species. Past studies are mostly biased toward laboratory rodents and they showed population-level biases to both right (Andrade et al., 2001; Castellano et al., 1987) and left sides (Korczyński and Eshel, 1979; Sherman et al., 1980). Available studies on wild-caught rodents showed population-level biases to the left side for two mole-rat species (Jacobs and Oosthuizen, 2023, 2021). For one of these species, Damaraland mole-rats (*Fukomys damarensis*), Jacobs and Oosthuizen (2023) showed that captivity can affect such lateralization with wild-caught mole-rats not exhibiting a bias at the population level, while their captive counterparts did. The authors attributed these changes to the potential stress and aggression caused by handling to which captive animals are likely more acclimated to it compared to their wild counterparts (Jacobs and Oosthuizen, 2023). However, the dearth of studies of lateralization in wild-caught rodents and the lack of clear distinctions between individual- and population-level lateralization in many of those available (Wiper, 2017), does currently not allow for a generalization, instead it highlights the need for further studies on wild-caught rodents.

Some authors have employed rotation of the maze between trials to ensure that any side preferences observed are not simply generated by responses of the study animals to external cues such as the Earth's magnetic field or directional sounds (Franklin and Lima, 2001; Jacobs and Oosthuizen, 2021; Kight et al., 2008). However, while there is currently no information available on the use of magnetic orientation in *M. namaquensis*, we are confident that although we chose not to rotate our maze between trials, we could largely exclude other potential external cues. Experiments were conducted in a room without windows and tiled surfaces that largely blocked outside stimuli and provided similar stimuli from all sides inside

the room. Our approach is in accordance with that employed in a number of previous studies of laterality in rodents (Andrade et al., 2001; Hegab et al., 2019; Maciejewska et al., 2016).

In accordance with our last predictions, we found a distinct sex bias in laterality for the side first entered. Females were more likely to enter the right side first while the opposite applied to males. Similar sex differences were not apparent for the frequency to enter the sides, or the time spent in an arm. This difference is striking but somewhat difficult to interpret due to the limited number of rodent studies considering both sexes (Jordan, 2020). At the same time, a lateralization study on male Wistar rats in a T-maze has reported right biases (Andrade et al., 2001; Castellano et al., 1987). One of the few available studies looking at both sexes on plateau zokors (*Eospalax baileyi*), plateau pikas (*Ochotona curzoniae*) and laboratory rats (*Rattus norvegicus*) did not find any bias in which of the T-maze arms they entered (Hegab et al., 2019). The authors suggested that this could be a result of experimenting with the animals during their non-breeding season. However, they did not elaborate on why this might be the case in rats that normally have a year-round breeding season (Hegab et al., 2019). Conversely, several studies in primates, fish and domestic animals have investigated the effect of sex on the direction of laterality. Tufted capuchins (*Sapajus apella*) showed similar sex biases seen in our study species, with females being more right-handed and males more left-handed (de Andrade and de Sousa, 2018). Similarly, male zebrafish (*Danio rerio*) showed a biased use of their left eyes when compared to females (Ariyomo and Watt, 2013), similar to the pattern observed in our study. In both cases the authors suggested that links between ecological and sexual selection pressures on behaviour and/or brain development affected their foraging behaviour, interactions with potential mates and predators (Ariyomo and Watt, 2013; de Andrade and de Sousa, 2018). Three-spined sticklebacks (*Gasterosteus aculeatus*) showed no population side bias in either sex (McLean and Morrell, 2021). However, the degree of lateralization did differ, with males – the parent caring for offspring – being more strongly lateralized compared to females. The authors suggested that in this case, the caring parent has higher reproductive costs and demands and

thus, stronger selection pressure on the ability to multitask. By multitasking, the caring parent can spend ample time on both reproductive efforts along with survival tasks such as feeding (McLean and Morrell, 2021). Conversely, this usually applies to females in mammals such as our study species (Bales, 2017). Sex-specific selection pressures could also account for male rock mice entering the arms more frequently during the first and females during the fourth trial. Reduced neophobia would bear sex-specific fitness pay-offs for males that are more likely to venture into unfamiliar territories in search of mates while this is not the case for females (Best et al., 2020).

In conclusion, we showed that in *M. namaquensis* both sexes learn a T-maze equally fast, but males may lose interest in a food incentive sooner than females. Strong individual-level lateralization was apparent in our study species, but received mixed support at a population-level. Similar to findings from other taxa, we show that the direction of laterality differs between the sexes with females exhibiting right while males show left-biased laterality. This is possibly related to sex differences in the morphology of the left and right brain hemispheres, physiology and evolutionary trajectories of the sexes. These hypotheses require further corroboration in follow-up studies. Overall, our results suggest that future studies of lateralization, particularly in rodents, should include individuals of both sexes to further tease apart the mechanisms and general applicability of our findings in rodents.

5. Ethics number

NAS065/2019

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7. CRediT authorship contribution statement

Tasha Oosthuizen: Animal acquisition, Conceptualization, Methodology, Data collection and analyses, Manuscript writing.

Heike Lutermann: Conceptualization, Writing, Editing, Supervision, Project administration, Funding acquisition.

8. Declaration of Competing Interest

The authors report no declarations of interest.

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10. References

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