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Received: 26 March 2024 | Revised: 11 September 2024 | Accepted: 12 September 2024

DOI: 10.1111/eth.13509

RESEARCH ARTICLE

ethology | WILEY

Personality may modulate learning and memory differences in two taxa of the African striped mouse genus *Rhabdomys*

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Funding information
National Research Foundation; University of the Witwatersrand, Johannesburg

Editor: Luis Ebensperger

Abstract

Different environments place different cognitive demands on constituent taxa. Learning and memory involve cognitive processes with associated costs, and it is expected that different levels of learning will occur in taxa from different environments. Greater memory loads linked to increased environmental complexity require greater learning and memory capacities. We investigated the variation in learning and memory in sister taxa of striped mice (genus *Rhabdomys*). We studied two populations each of the mesic grassland-occurring *R. d. chakae* and the mostly arid-occurring *R. pumilio*. We conducted two sets of experiments. (1) In a novel object recognition (NOR) test, we assessed memory by recording the duration of exploration of similar and novel objects by test mice. (2) In an associative learning task, we assessed whether mice could associate specific scents with or without a food incentive or with different quantities of the food incentive in previous training phases. We measured the latency of mice to contact scents in a two-sample choice in the test phase. In the NOR test, *R. pumilio* spent less time investigating similar objects in a training trial than *R. d. chakae* but increased absolute exploration of the novel object when presented with a novel and a familiar object in the retention trial, suggesting a sensitization to the novel object by *R. pumilio*. In the associative learning experiments, *R. pumilio* approached the stimuli faster than *R. d. chakae*, whereas mice from both taxa preferred scents associated with a seed versus no seed and scents associated with 5 seeds versus 1 seed. The data provide evidence of taxon-level differences in learning and memory, likely related to environmentally modulated personality differences between the taxa.

KEYWORDS
associative learning, memory, novel object recognition, personality, *Rhabdomys*

1 | INTRODUCTION

Learning is an adaptation to changing environments (Johnston, 1982) and involves the acquisition of information based on experience, which is then integrated into memory (Shettleworth, 2009). Dunlap and Stephens (2009) hypothesised that learning is less likely in stable environments since individuals rarely encounter novel challenges. In contrast, novel challenges are more likely to arise in more variable environments, and individuals in these environments benefit from the ability to learn and modify their responses to novel situations

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(Dunlap & Stephens, 2009). Learning and memory (i.e., the ability to recall knowledge gained through experience) allow for more appropriate behavioural responses to a previously encountered situation without repeating inappropriate choices (Dukas, 2013). Therefore, learning and memory would be expected to occur when environmental conditions are variable but relatively predictable within an individual's lifetime (Stephens, 1991) and not when prior experiences are no longer appropriate (Dunlap & Stephens, 2016; Moran, 1992).

Complex environments are likely to drive selection for greater learning and memory because of increased cognitive demands and memory loads (Mettke-Hofmann, 2014). Increased physical complexity of the environment or increased social complexity stimulates and thus enhances both general and social learning and memory (Dunbar, 1998; van Praag et al., 2000). Structurally complex environments result in better memories, most likely because of the increased cognitive demand of navigating through the environment (Mettke-Hofmann, 2014). For example, juvenile Belding's ground squirrels *Urocitellus beldingi* from more complex environments (i.e., those with more visual navigational cues) learned to associate visual cues with an escape tunnel more quickly than those from less complex environments with sparse visual navigational cues (Bruck & Mateo, 2010). Similarly, larger group sizes necessitate greater cognitive abilities to remember more information about group members, enabling group cohesion (Croney & Newberry, 2007). For example, Võikar et al. (2005) found that C57BL/6J and DBA/2 lab mouse strains showed greater novel object recognition when housed in groups, whereas such recognition was impaired in solitary-housed mice.

Studies of learning and memory have largely focused on within-species variation (Liefting et al., 2019), linked to variation in personality (Mazza et al., 2018; White et al., 2017), and some have investigated the neural mechanisms that mediate cognition (reviewed by Chittka & Niven, 2009). For example, bolder individuals are less successful at learning to navigate a maze than less bold individuals in brook trout (*Salvelinus fontinalis*; White et al., 2017). Neural mechanisms involved in cognition occur in the splitter neurons in the hippocampus of C57/BL6 mice, which remain active for longer and retain more consistent spatial information than other neurons during the recall of a navigational route (Kinsky et al., 2020). However, the studies comparing variation in learning and memory between closely related taxa from different environments are rare. While understanding intraspecific variation in learning and memory between populations is important, by investigating differences between closely related species that occur in different environments we can assess environmental and/or phylogenetic influences in species that occur in specific but different environments.

Personality is the stable suite of behavioural traits an individual shows over time and different contexts (Réale et al., 2007) and describes differences in behaviour between individuals and between populations and taxa. Personality traits may differ between individuals from complex and simple environments (Mesa-Gresa et al., 2013) and the sexes (Frick & Gresack, 2003). For example, Trinidadian guppies (*Poecilia reticulata*) from populations living in high predation streams were bolder than those from populations in low predation streams (Harris et al., 2010). Similarly, mountain chickadees (*Poecile gambeli*) from high elevations explored novel environments slower than mountain chickadees from populations at low elevations (Kozlovsky et al., 2014). Female Wistar rats in proestrus or oestrus showed greater exploration of novel objects than familiar ones compared to metestrus or dioestrus females (Van Goethem et al., 2012).

Individuals in a population can differ in boldness, activity level and exploration, which can influence the speed at which they learn, as well as how effectively they remember (Dougherty & Guillette, 2018; Sih & Del Giudice, 2012). For instance, a fast explorer (i.e., an individual that explores their environment superficially and thus quickly; Careau et al., 2009) will explore its environment more quickly than a slow explorer but may be a less flexible learner (Benus et al., 1990). For example, bolder and more active bank voles (*Myodes glareolus*) responded faster than less bold and less active conspecifics in associative learning tests but were also less flexible in reversal learning tests (Mazza et al., 2018). Thus, individuals will also benefit from learning faster and/or having better memory capacities in more open environments where bolder and more exploratory personality types would be favoured. In contrast, learning should be comparatively slower where personality types that are less bold and less exploratory would be selected.

We studied levels of variation in learning and memory in two taxa of the murid striped mouse *Rhabdomys* occupying different habitat types. The African striped mouse (genus *Rhabdomys*) is a small (40-50 g), diurnal, generalist omnivore with an opportunistic diet, specific to each species' habitat (Monadjem et al., 2015). Members of the genus *Rhabdomys* are widely distributed throughout eastern and southern Africa, and species are phylogeographically distributed along an east–west rainfall gradient (Monadjem et al., 2015). Our study focuses on *R. pumilio* from comparatively arid western parts of South Africa and *R. d. chakae* from the mesic grasslands.

Rhabdomys pumilio in the Succulent Karoo is facultatively group-living with groups comprised of a single reproductive male, multiple breeding females and their non-reproductive adult offspring (Schradin & Pillay, 2005). The social organization can change in response to habitat saturation (Schradin et al., 2010), with groups disbanding at lower population densities and both males and females changing to a solitary lifestyle (Schradin et al., 2012). In contrast, *R. d. chakae* is always solitary with home ranges of males overlapping that of multiple females and association between males and females restricted to breeding (Schradin & Pillay, 2005). Home range size differs between the species with home ranges of female *R. d. chakae* being six times that of *R. pumilio* females and home ranges of male *R. d. chakae* being 10 times the size of *R. pumilio* males (Schradin & Pillay, 2005). Rymer and Pillay (2012) reported taxon-level differences in personality, where *R. pumilio* was more exploratory, bolder, and less anxious than *R. d. chakae* (see Mackay & Pillay, 2021).

Since learning and memory carry neural metabolic costs as well as fitness costs (Dunlap & Stephens, 2009), it is expected that individuals of closely related taxa that differ in environmental complexity and social organizations, would have developed different levels

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of cognition that might affect their learning ability because of the different demands their respective environments place on them (Mettke-Hofmann, 2014). We investigated the variation in cognition in two populations each of *R. dilectus chakae* and *R. pumilio* to understand differences in learning and memory between populations from different environments. Given the differences in social and environmental complexity between the species, we tested the following two alternative predictions. (1) *R. dilectus chakae* will have greater learning ability than *R. pumilio* if complex habitats shape learning because the mesic grassland in which *R. d. chakae* occurs is visually more complex than the semi-desert in which *R. pumilio* occurs. (2) If learning and sociality are coupled in a broad sense (i.e., all learning is shaped by the ability to have greater general memory), *R. pumilio* will have a greater learning ability than *R. d. chakae*. In addition, if personality influences learning and memory in *Rhabdomys*, we predicted that the bolder *R. pumilio* would engage quicker with learning tasks than *R. d. chakae*.

2 | MATERIALS AND METHODS

2.1 | Subjects

We used two populations each of *R. d. chakae*, Suikerbosrand Nature Reserve (26°29′1″ S, 28°13′45″ E) in Gauteng Province and Willem Pretorius (28°18′26″ S, 27°13′56″ E) in the Free State Province and *R. pumilo*, from Goegap Nature Reserve in the Northern Cape Province (29°40′53″ S, 17°58′9″ E) and Jonkershoek Nature Reserve in the Western Cape (33°55′51″ S, 18°51′16″ E). The populations of *R. d. chakae* (Suikerbosrand NR and Willem Pretorius NR) and populations of *R. pumilio* (Goegap NR and Jonkershoek NR) were located >350 km apart. The populations differ in their general ecology (Supplementary Material).

Wild-caught individuals from each population were bred at the Milner Park Animal Unit at the University of the Witwatersrand. We used a total of 10 males and 10 females from the F2 and F3 generation from each population to investigate individual learning and memory. Females were confirmed to be anoestrous from vaginal smears prior to undertaking experiments. Experiments were approved by the University of the Witwatersrand Animal Ethics Screening Committee (2015/15/2A).

2.2 | Husbandry

The striped mice used in this study were all adults and were housed under partially controlled environmental conditions, with lights on at 05 h00, a 14:10 h L:D cycle, at 22–24°C temperature and relative humidity of 30%–50%. Subjects were housed individually in clear standard lab-o-tec cages (15 × 42 × 15 cm) after weaning. Group or individual housing does not stress either species (confirmed using corticosterone by Rimbach et al., 2022). Tanks contained a paper-towel-filled plastic nesting box (10 × 10 × 10 cm), wood-shavings on the floor, a wooden chew block, dry grass and a cardboard roll for enrichment. Mice were given water and Epol™ mouse cubes ad libitum, 5 g of fresh vegetables, and one teaspoon of millet per day.

2.3 | Experimental procedure

All individuals were used in two experiments, first, when they were ~80 days old and secondly when they were ~110 days old. All experiments took place between 08 h00 and 12 h00, the peak activity period of *Rhabdomys* (Rymer & Pillay, 2012; Schradin, 2004). All data were scored by two observers blind to animal ID and treatment to reduce observer bias.

2.4 | Experiment 1: Novel object recognition

Individual memory was tested by means of a novel object recognition test following the protocol outlined by Akkerman et al. (2012) and validated for striped mice by Pillay et al. (2016). The novel object recognition task is commonly used as a personality measure as it takes advantage of the natural inclination of rodents toward novelty (Van Goethem et al., 2012). The experiment was conducted in three sessions: the habituation session, the training session, and the retention session with an inter-session interval of 24 h. The 24-h inter-session interval has previously been successful in detecting object recognition differences in the genus (Pillay et al., 2016).

We used a glass tank (45 × 30 × 30 cm, l × b × h), lined with a thin layer of wood shavings in this experiment. In the habituation session, test mice were allowed to explore the tank for 10 min before being returned to their home cages. In the training session, two small wells, 5 cm apart, were created in the wood shavings along one of the short ends of the tanks. Two identical plastic objects were attached to the bottom of the tank with doubled-sided tape, one in each well. The test mouse was placed in the centre of the tank and was allowed to explore both objects. The session was terminated after 10 min, and the test subject was returned to its home cage.

During the retention session, one of the objects was replaced with a novel plastic object, of a different shape but similar in size from the first object and individuals were allowed to explore the objects for 10 min. The exploration behaviour (i.e., sniffing, pawing, biting) of the individual was video-recorded and scored later. After the testing session ended, the test subject was returned to its home cage and the testing apparatus and plastic objects were thoroughly washed to remove all olfactory cues as well as to remove the double-sided tape.

We scored the duration of investigation of each of the objects by test mice in both the training and retention sessions. Shorter investigation of objects is indicative of faster habituation. We assessed five variables as outlined by Akkerman et al. (2012) and recorded by Pillay et al. (2016) in another study: (1) the additive time (O1 + O2) spent investigating identical objects in the training session; (2) the additive time spent (O + N) investigating one familiar and one novel

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object in the retention session; (3) the absolute difference between the time (N – O) spent investigating the novel object and the familiar object in the retention session; (4) the time [(N – O)/(N + O)] spent investigating the novel object relative to the total time spent investigating in the retention session; and (5) the proportion of time [N/(N + O)] spent investigating the novel object in the retention session. We also assessed a sixth variable where we compared the investigation of the identical objects (O1 + O2) in the training trial and the familiar and novel objects (O + N) in the retention trial. These variables were used to assess whether the test mice could identify and hence learn about a novel object.

2.5 | Experiment 2: Associative learning test

In this experiment, individuals were required to learn to associate one of two neutral scents (neutrality tests in Supplementary Material) with food incentives. Associative learning trials consisted of two phases: (1) the learning phase where test subjects learned to associate a scent with a food incentive over the course of 20 trials and (2) the retention trial where the scent-reward association was tested without a food incentive and we tested whether test subjects remembered the association through conditional learning (i.e., the scent was the conditioned stimulus). We used a scent association as a stimulus cue instead of a visual cue because rodents use odour cues as a primary sensory cue and because differences in the visual processing of our study species is not well studied.

Tests were run in a glass tank (45 × 30 × 30 cm, l × b × h), lined with a thin layer of wood shavings with a similar setup to the NOR experiment. We ran two sets of experiments in sequential order based on the choice of scent and food incentives. (A) Lavender scent paired with one sunflower seed incentive versus tea tree scent paired with no seeds; our lab has shown striped mice prefer sunflower seeds. (B) Lavender scent paired with one sunflower seed incentive versus menthol scent paired with five seeds. The scents were essential oils in an inert grapeseed carrier oil in a 1:3 (essential oil: grapeseed oil) ratio. Prior to both experiments, the subjects were tested for their latency to respond to the scents to assess scent preference; neither species showed a preference for lavender, tea tree or menthol scents. We also report successful/unsuccessful responses in the Supplementary Material. Analyses of the latency to approach the lavender and tea tree scents in experiment (A) and the lavender and menthol scents in experiment (B) indicated the subjects responded equally to both scents (results for these analyses are included in Table S2). Individuals used in experiment A were the same as those used in the NOR task. To avoid carry over effects from the NOR task, the experiments were conducted a month apart. Different subjects were used in experiment A and experiment B to avoid any influence of prior learning. By using two different food incentives (one seed versus five seeds), we could assess whether the strength of the association was based on the quantity of the incentive.

Each experiment started with a learning phase, in which an individual underwent 20 learning trials, i.e., two 5-min trials per day over the course of 10 days, with an inter-trial interval of 15 min. In experiment (A), for the learning trials, we introduced a ~2 cm cotton wool ball scented with either 0.05 mL lavender or 0.05 mL tea tree oil in 0.15 mL of carrier oil (experiment 1) along with a food incentive of one seed with the lavender scent or no seeds with the tea tree scent. The cotton wool balls, and food incentive (for the lavender scent) were placed on the bottom of one short side of the tank, located at least 5 cm apart. The placement of the lavender and tea tree scented cotton wool was randomized between trials and was equally presented on the left and right side of the tank. A test mouse was introduced individually in the tank on the opposite side to the cotton wool/seed. The scent/reward was alternated per mouse for the daily/learning trials (lavender scent/1 seed on Day 1, tea tree scent/0 seed on Day 2, and so on). After each trial, the test subject was returned to its home tank and the experimental tank was thoroughly washed.

Two days after the learning phase ended, individuals were tested in retention trials in a single 5-min session. In this trial, two cotton wool balls with either lavender or tea tree were placed 5 cm apart along the one short side of the tank; the position of the cotton wool balls was randomised. A test mouse was introduced individually in the tank on the opposite side to the cotton wool balls. All learning and retention trials were video recorded and analysed later. The latency to approach each stimulus in the retention trial only was recorded. A test mouse was considered to have approached the scented cotton wool ball when its nose touched the cotton wool ball. We also recorded the duration spent with the scent balls but >80% of test mice spent less than 2 s in total with the scent balls. Thus, duration was not included in the analyses.

Learning and retention trials for lavender scent versus menthol scent in experiment (B) were run a month after experiment (A). Experiment (B) was run and scored in a similar way as experiment (A). In the learning trials for menthol scent, the 5 sunflower seeds were clumped together. In all learning trials in experiments (A) and (B), striped mice consumed all the sunflower seeds in the training trials.

2.6 | Data analysis

Behaviours were scored by two observers who were naïve to the experimental treatment. We found high inter-observer reliability (novel object: $0.86 < rs < 0.97$; associative learning: $0.84 < rs < 0.98$; Spearman rank order correlation). All data analyses were run using *RStudio* (R version 3.6.1 and RStudio version 1.2.1335, RStudio Team, 2018). We used Shapiro–Wilk normality tests to confirm normality. Homogeneity of variance was confirmed for all variables using Levene's test for homogeneity of variance ('car' package; Fox & Weisberg, 2019). All tests were two-tailed, and alpha was set at 0.05.

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Models run with both species and population included as either fixed or random effects failed to converge and/or produced singular fits. Because linear models (NOR) and linear mixed-effects models (associative learning) run with population (in Supplementary Material) but without species as a fixed effect revealed no within-species variation, we report models aggregated by population per species that is included as a fixed factor. All data are presented as untransformed mean ± SE. Significant statistical results were analysed using the 'emmeans' package (Lenth, 2019) and a Tukey adjustment for multiple comparisons to assess specific differences between levels of the fixed factors.

2.7 | Experiment 1. Novel object recognition

Normality tests indicated exploration in the training trial, the additive time spent investigating identical objects in the training session (O1 + O2) and the absolute difference between the time spent investigating the novel object and the familiar object in the retention session (N − O) were normally distributed. All other variables were not normally distributed. Using the 'bestNormalize' package (Peterson & Cavanaugh, 2019), the exploration in the retention trial, the relative difference in the retention trial and the proportion of investigation in the retention trial were transformed using the order-norm function while the total time spent investigating between the test and retention trials was log transformed.

We used separate restricted maximum likelihood linear models to analyse the NOR variables using the 'lme4' package (Bates et al., 2015) and obtained *p*-values with the 'lmerTest' package (Kuznetsova et al., 2017). Species effects were analysed separately using type III two-way analysis of variance (ANOVA) models with NOR measures included as the dependent variables, and species and sex included as fixed factors. The total time spent investigating the objects between the two trials included species, sex and trial as fixed effects and identity as a repeated measure in repeated measures ANOVA models.

2.8 | Experiment 2. Associative learning

Latencies in the retention trials for both experimental groups were non-normally distributed and could not achieve a normal distribution through transformations. We used generalised linear mixed-effects models with a repeated measures design ('lme4' package; Bates et al., 2015 and 'lmerTest' package; Kuznetsova et al., 2017) to test for differences in learning. We used a 'gamma' family with a 'log' link function and a 'poisson' family with a 'log' link function for the glm models for experiment 2A and 2B, respectively. We analysed the latency to approach each scented cotton wool ball in the retention trial for experiment (A) and (B) in two separate models. We included latency as the response variable, species, scent and sex as fixed factors, and individual as the repeated measure (Pillay et al., 2016).

2.9 | Personality and learning and memory

To assess the relationship between personality and learning, in separate models we regressed the relative proportion of time spent exploring the novel object relative to the total exploration in the retention trial and the latencies to approach the previously incentivised scents (lavender in experiment 2A and menthol in experiment 2B). We log-transformed the NOR response variable to achieve a normal distribution, confirmed with a Shapiro-Wilks test. We conducted linear, quadratic and polynomial (with k-fold cross-validation and degree determined by the lowest mean squared error) multiple regressions on the relative proportion of time spent exploring the novel object relative to the total exploration (log-transformed for normality) with latency for scents as predictive variables in two separate models. Because the polynomial models produced the lowest AIC scores, we report the results for the first-degree and third-degree polynomial regression for the incentivised scent in experiment 2A and 2B, respectively.

3 | RESULTS

3.1 | Experiment 1. Novel object recognition

3.1.1 | Exploration in training trial

Here, we calculated the additive time test mice spent investigating identical objects in the training session (O1 + O2). Species ($F_{1,76} = 6.47$, $p = 0.013$) alone was a significant predictor of the time individuals of *Rhabdomys* spent investigating when presented with similarly shaped objects. Post hoc analysis indicated that individuals of *R. d. chakae* investigated two similar objects for longer durations than individuals of *R. pumilio* (Figure 1).

3.1.2 | Exploration in retention trial

We calculated the additive time test mice spent investigating one familiar and one novel object in the retention session (O + N). Species, sex, and the species*sex interaction (Table S5) were not significant predictors of the exploration of individuals of either species in the retention trial when presented with one familiar and one novel object.

3.1.3 | Absolute difference in retention trial

We calculated the absolute difference as the difference between the time test mice spent exploring the novel object and the familiar object during the retention session (N − O).

Species ($F_{1,76} = 4.54$, $p = 0.036$), but not sex or the interaction (Table S5), significantly predicted the absolute difference in exploration by the two taxa between novel and familiar objects. Individuals

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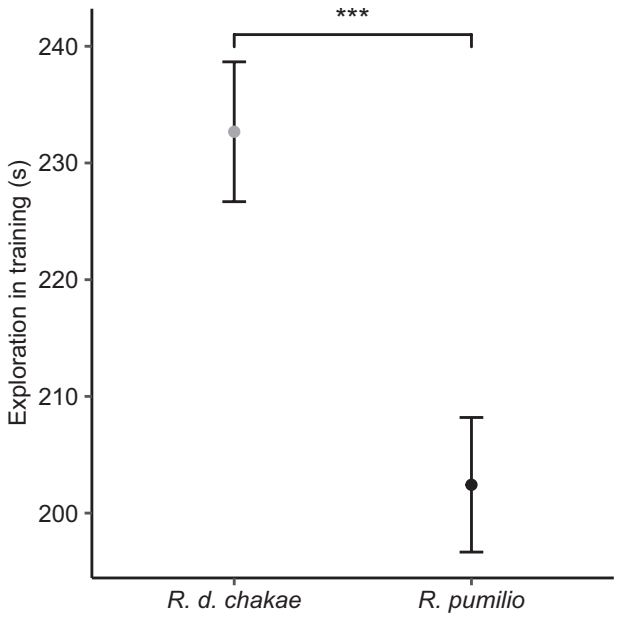


FIGURE 1 Mean ± SE duration of exploration of two identical objects in a training trial by *R. d. chakae* ($N = 40$) and *R. pumilio* ($N = 40$). Significant differences between factors are indicated by ***($p < 0.001$).

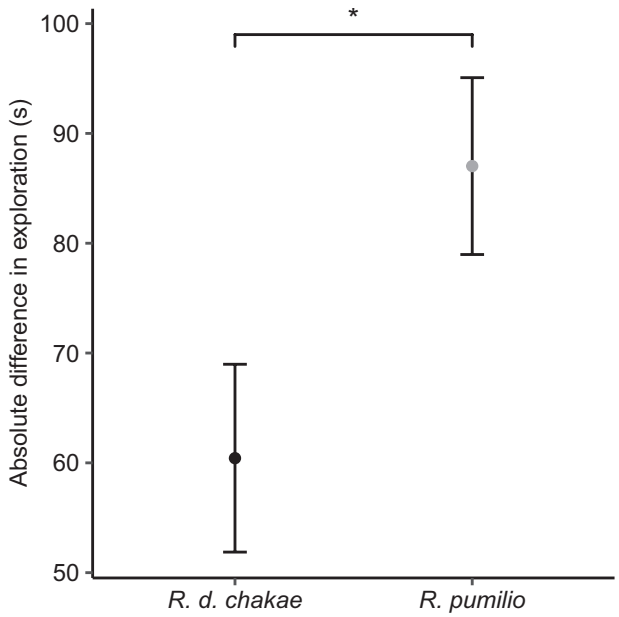


FIGURE 2 Mean ± SE absolute difference in the exploration of a novel and a familiar object in a retention trial by individuals of *R. d. chakae* ($N = 40$) and *R. pumilio* ($N = 40$). Significant differences between factors are indicated by *($p < 0.05$).

of *R. pumilio* investigated the novel object longer than individuals of *R. d. chakae* (Figure 2).

3.1.4 | Relative time spent exploring the novel object during the retention trial

We calculated the relative time spent exploring the novel object as the difference in exploration of the novel and familiar objects by test mice relative to the total time spent exploring in the retention session [(N-O)/(N + O)]. Species, sex, and species*sex were not significant predictors of the relative time spent exploring the novel object by the two species (Table S5).

3.1.5 | Proportion time spent with novel object during the retention trial

We calculated the proportion of time spent investigating the novel object relative to the total time spent exploring novel and familiar objects in the session [N/(N + O)]. Species, sex, and species*sex were not significant predictors of the proportion of time spent by the two species with the novel object in the retention trial (Table S5).

3.1.6 | Total time spent investigating objects in the test and retention trial

Finally, we compared the additive time spent investigating identical objects (O1 + O2) in the training trial and time spent investigating one familiar and one novel object (N + O) in the retention trial. Species, sex, session and all second and third level interactions were not significant predictors of the difference in exploration in the training and retention trials (Table S5).

3.2 | Experiment 2. Associative learning

3.2.1 | Experiment (A) lavender versus tea tree

In this experiment, striped mice were trained with lavender and one sunflower seed versus tea tree oil with no seeds. They were tested with these scents without seeds in the retention trials. Individuals of both taxa approached the lavender scent faster than the tea tree scent, indicating that both taxa associated the lavender scent with a previous food incentive. Species ($F_{1,152} = 12.85$, $p < 0.001$), scent ($F_{1,152} = 317.43$, $p < 0.001$) and species*scent ($F_{1,152} = 13.67$, $p < 0.001$) were the only significant predictors of latency to approach the stimulus. *R. pumilio* approached the lavender scent significantly faster than *R. d. chakae* but both species approached the lavender scent faster than the tea tree scent (Figure 3).

3.2.2 | Experiment (B) lavender versus menthol

In this experiment, striped mice were trained with lavender and one sunflower seed versus menthol with five sunflower seeds. They were tested with these scents without seeds in a retention trial. Sex ($\chi^2_{1,76} = 10.27$, $p = 0.002$), species*sex ($\chi^2_{1,76} = 10.80$, $p = 0.001$), species*scent ($\chi^2_{1,76} = 8.26$, $p = 0.004$), sex*scent ($\chi^2_{1,76} = 4.07$,

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$p=0.044$), and species*sex*scent ($\chi^2_{1,76}=5.58$, $p=0.018$) were significant predictors of latency to approach the scent balls. Post hoc analyses showed that only *R. pumilio* females and *R. d. chakae* males approached the menthol scent significantly faster than the lavender scent. *R. pumilio* males approached both scents significantly faster than *R. d. chakae* males. Similarly, *R. pumilio* females approached the menthol scent significantly faster than *R. d. chakae* females, but females did not significantly differ from each other in their approach of the lavender scent. Within species comparisons between the sexes indicated that female *R. d. chakae* approached the lavender scent faster than male conspecifics (Figure 4). Species and scent were not significant predictors of the latency to approach the scent balls (Table S5).

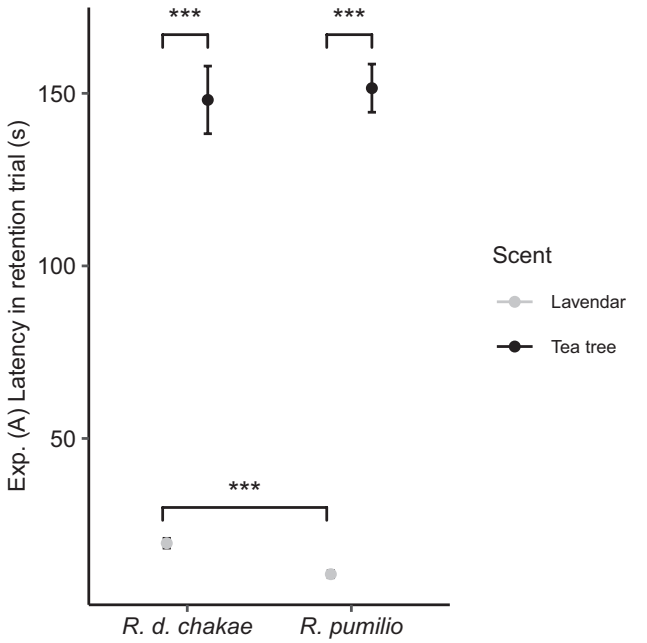


FIGURE 3 Mean ± SE latency to approach lavender or tea tree scent balls in the retention trial of an associative learning experiment (*R. d. chakae*, $N=40$; *R. pumilio*, $N=40$). Significant differences between factors are indicated by ***($p<0.001$).

3.3 | Relationship between personality and learning

Using a first-order polynomial regression, exploration of the novel object relative to the total exploration was significantly related to the latency to approach the lavender scent in the retention trial of experiment 2A ($F_{1,46}=5.35$, $p=0.025$, $R^2=0.10$) (Figure 5a). While the relationship was weak, mice that were showed greater exploration of the novel object were quicker to approach the lavender scent (Figure 5a).

The best fit model testing the relationship between the exploration of the novel object relative to the total exploration and the latency to approach the incentivised menthol odour in experiment 2B was a third-degree polynomial regression. We found a significant, positive relationship ($F_{5,42}=5.71$, $p=0.006$, multiple $R^2=0.31$) between exploration and the latency to approach the menthol scent at lower latencies and exploration but a negative relationship at greater exploration and latencies ($t=2.46$, $p=0.018$; Figure 5b).

4 | DISCUSSION

We investigated learning and memory in populations of two sister taxa, *R. dilectus chakae* and *R. pumilio*, originating from four different populations. Based on the differences in social organisation, taxon-level personality, and environmental complexity we expected that species would differ in learning and memory. We did not find evidence to support our prediction of a difference in learning in both species. In the novel object recognition experiments, *R. pumilio* investigated the similar objects less than *R. d. chakae* in the training

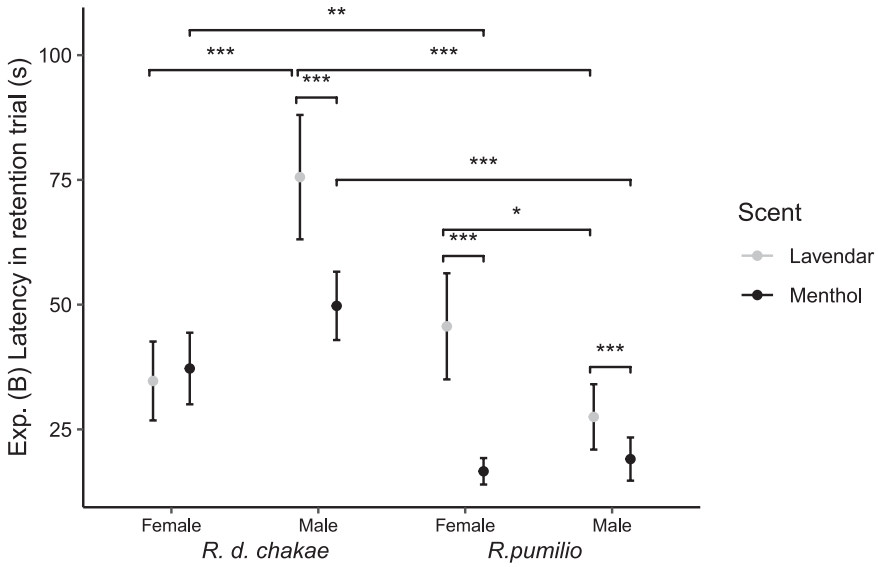


FIGURE 4 Mean ± SE latency to approach the lavender and menthol scent balls in the retention trial of an associative learning experiment by male and female *R. d. chakae* ($N=40$) and *R. pumilio* ($N=40$). Significant differences between factors are indicated by *($p<0.05$), **($p<0.01$) and ***($p<0.001$).

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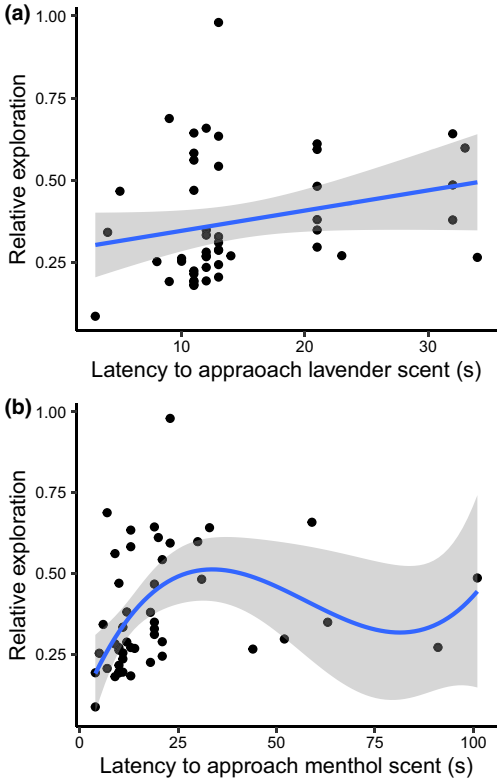


FIGURE 5 Scatterplot of the relationship between the relative time spent exploring the novel object and the latency to approach a previously incentivized scent for (a) experiment 2A where the lavender scent was previously incentivized by a single seed ($y = -1.398 + 0.025x$), and (b) experiment where the menthol scent was previously incentivized by five seeds ($y = -2.14 + 0.092x - 0.002x^2 + 0.0001x^3$).

phase, but there were no differences between the taxa in their recognition of novel objects and memory of the familiar object in the retention trial. However, *R. pumilio* spent longer exploring the novel object than the familiar object indicated by higher absolute differences in exploration (N – O).

In two associative learning experiments, individuals of *R. pumilio* approached both stimuli faster than individuals of *R. d. chakae*. Mice of both taxa associated the scent with its previous incentive in the lavender versus tree tea experiment, preferring the lavender scent in the retention trial. Similarly, both taxa preferred the menthol scent over the lavender, indicating memory of the greater incentive associated with menthol in the training phase. This indicates that the strength of the association (one seed versus five seeds) is as important as the presence (one seed versus no seeds) for striped mice. The species showed similar responses, despite occurring in different environments. These results show the general patterns of learning and memory do not differ between the species since both species learned the association, but that any apparent differences are likely linked to personality supporting our third prediction of a personality influence on task engagement.

Animals from environments that are more variable/complex frequently show better learning and memory (Mettke-Hofmann, 2014; Shumway et al., 2006; Spence et al., 2011). For example, bats that forage in more complex and cluttered environments (*Myotis myotis* and *Myotis emarginatus*) were faster and more flexible learners in a maze task than *Myotis capaccinii*, which forages in an open environment (Clarin et al., 2013). In contrast, in some species, the differences in learning and memory between taxa from different environments are present in spatial, but not non-spatial, learning and memory-related tasks (Pravosudov & Clayton, 2002). For instance, black-capped chickadees from Alaska (where food availability is more temporally variable) made fewer errors in a food-locating task than conspecifics from Colorado (where food availability is not as temporally variable) without spatial cues but not when spatial cues were present (Pravosudov & Clayton, 2002). Our study supports a similarity in non-spatial learning and memory in taxa from differentially complex environments, despite previous findings of better spatial memory in *R. pumilio* than *R. dilectus* (Neves & Pillay, 2022).

Phylogenetic constraints may result in behavioural similarity among closely related taxa primarily through constraining anatomical structure and function (Price & Lanyon, 2002). For instance, seven species of deer mice *Peromyscus* all build dome-shaped nests, although the latency taken to do so is variable by species (Lewarch & Hoekstra, 2018). When the selection pressures animals experience are similar in different environments, there may be convergence in cognition (Mettke-Hofmann, 2014). For example, populations of Bishop toothcarp *Brachyrhaphis episcopi* from low-predation environments made fewer errors in a spatial maze than conspecifics from high-predation environments (Brown & Braithwaite, 2005). Yet, whether this similarity in non-spatial memory in our study species is a result of phylogenetic or developmental constraints or convergence due to similar selection pressures between environments requires further investigation.

Despite the similarity in cognitive ability, species-level personality differences appear to modulate the speed of response in *Rhabdomys*. The shorter investigation time of *R. pumilio* to similar objects, increased exploration when novelty is introduced and its faster approach to scents than *R. d. chakae* suggests taxon-level personality differences may play a role in learning and memory in striped mouse taxa. Personality has been linked to learning in a variety of taxa, typically influencing the rate of success in a task (Guenther et al., 2014; Guillette et al., 2009). Boldness and activity (i.e., two personality metrics) influence how quickly an individual obtains information about a novel situation and thus may affect how quickly a novel task is learned (Sih & Bell, 2008). Personality types can also vary at both the population and taxon level. For example, individuals from high-risk environments are frequently bolder, less anxious, and more exploratory than individuals from low-risk environments (Harris et al., 2010; Kozlovsky et al., 2014; Mazza et al., 2018). Our laboratory has established that taxon-level differences in personality exist within *Rhabdomys*, specifically that *R. pumilio* is bolder, more exploratory, and less anxious than *R. d. chakae* (Mackay & Pillay, 2021; Rymer & Pillay, 2012).

Our results provide support for this taxon-level personality difference since we found a significant difference in exploration

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between taxa in the novel object recognition training when individuals were presented with similar objects, as well as in the exploration of the novel object in the retention trial. However, there were no differences in any other measures in the novel object recognition test. Thus, *R. pumilio* showed a greater preference for novelty than *R. d. chakae* as indicated by increased exploration of the novel object. This does not, however, result in better learning or memory in the object recognition and memory tests since the populations otherwise performed similarly. In addition, in the associative learning tasks, *R. pumilio* approached the scents faster than *R. d. chakae* but both taxa were able to learn the association and showed a preference for the previously incentivised scent. Our results also indicated a broad relationship between personality and learning because more exploratory mice also tended to approach the incentivised scent faster, while mice that took longer to approach the scent also tended to be less exploratory. Taken together, it appears that the speed of responses in tests is not a predictor of the ability to recognize and remember the novel object or distinguish between scents, contrary to the conclusions reached in other studies about personality and learning (Mazza et al., 2018; Trompf & Brown, 2014). Yet in a study of spatial learning and memory, *R. pumilio* was able to learn to navigate a Barnes maze faster, and with fewer errors, than *R. dilectus* (Neves & Pillay, 2022). It may thus be that general learning and memory are phylogenetically conserved, while spatial learning and memory are modulated by the environment of occurrence in taxa of striped mice.

The strength of the association appears to be related to the value of the incentive within populations of both taxa of striped mice. Striped mice of both species were able to differentiate and retain the memory of a greater reward (5 seeds) associated with one scent when an incentive of lesser value (1 seed) was associated with a second scent. However, *R pumilio* approach the correct scent faster. Similarly, individuals of *R. pumilio* approach a previously incentivised scent faster than individuals of *R. d. chakae*, but both learned the associations between the incentivised and non-incentivised stimuli. Memories encoded under positive emotional valence alongside the presentation of an incentive, result in improved memory consolidation (Wittmann et al., 2008). Faster approaches to the scent associated with the higher quantity of seeds may be an indication of a stronger encoding of the initial memory in the training trials based on higher positive emotional valence associated with the greater incentive (Smith & Torregrossa, 2021), which would aid in locating food faster. Food is more limited in the semi-desert than in the grasslands, and when present in any relative abundance is likely to be more clumped in the environment (Schradin, 2005). While *R. pumilio* lives in small close-kin groups, it is a solitary forager in their shared group territory (Schradin & Pillay, 2004). Thus, while it would be important for mice from the semi-desert to know where to locate food generally, of greater value would be the ability to better remember locations where there is more food. So, while personality may influence the greater speed with which *R. pumilio* were able to approach the incentivised scent, we cannot exclude the selective pressures of the environment from which they originate as a modulating influence.

Previous studies in various taxa have shown males are more frequently the bolder and more exploratory sex (Brown et al., 2007; Jolles et al., 2015; Starling et al., 2013). For example, male cardinals (*Brachyrhaphis roseni*) were bolder than females which have been hypothesized to be a result of divergent mating strategies between the sexes (Ingley et al., 2014). *Rattus norvegicus* males were more exploratory and bolder in novel environments and environments with predator scent cues than females (Jolles et al., 2015). However, the same study found that female rats explored more than males when the predator scent was removed and suggested that female rats might be more responsive to changes in their environment (Jolles et al., 2015). Generally, females are more reactive, slower learners but retain associative memories better than male conspecifics, whereas male performance is better in fear-conditioned learning experiments (reviewed by Dalla & Shors, 2009). Whether these characteristics also explain responses of female and male *Rhabdomys* in our study requires further testing.

In conclusion, we found that two sister taxa of *Rhabdomys* showed differences in their learning and memory, although to a limited degree, in two sets of experiments that tested novel object recognition and conditioned learning. The arid, group-living *R. pumilio* from two populations with different ecologies approached stimuli faster than two *R. d. chakae* populations. These results suggest a personality influence on learning and memory. The similarity in responses suggests similar learning and memory capacities (at least in the experiments conducted) in *Rhabdomys* taxa. Moreover, our results suggest that personality and/or habitat may modulate the strength of cognitive abilities associated with learning and memory in *Rhabdomys* of different taxa occurring in different habitats. Future studies should explore other forms of learning, such as problem-solving, to test the extent to which the similarities in learning and memory revealed in our study extend to other cognitive domains, and which might be under different selection pressures.

AUTHOR CONTRIBUTIONS

Candice N. Neves: Conceptualization; data curation; investigation; writing – original draft; project administration; visualization; funding acquisition; methodology; formal analysis. **Neville Pillay:** Supervision; resources; writing – review and editing; funding acquisition; formal analysis.

ACKNOWLEDGEMENTS

The authors wish to thank the National Research Foundation (grant number 117920) and the University of the Witwatersrand for funding this study.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

The data and code used in this study are available on 'figshare' [doi: 10.6084/m9.figshare.25469914].

SIGNIFICANCE STATEMENT

Learning and memory is hypothesised to differ between populations occurring in environments with different complexities. We tested this hypothesis by studying memory and non-spatial learning between two species of striped mouse from different environments (grassland vs. semi-desert). We showed that all striped mice distinguished between a novel and familiar object and learned an incentivized association. Striped mice from the semi-desert were more active and completed the tasks faster, although this species difference disappeared when the incentive was greater. We did not find full support for our initial hypothesis, suggesting that memory is phylogenetically constrained in *Rhabdomys*; yet personality modulates speed of response in the species.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Neves, C. N., & Pillay, N. (2024). Personality may modulate learning and memory differences in two taxa of the African striped mouse genus *Rhabdomys*. *Ethology*, *130*, e13509. https://doi.org/10.1111/eth.13509

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