

**Personality and behavioural syndromes in wild-caught Namaqua rock mice  
(*Micaelamys namaquensis*)**

**Running title: Personality in Namaqua rock mice**

Tasha Oosthuizen\*, Heike Lutermann

*Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Pretoria,  
0082, South Africa*

**\*Corresponding author:** Tasha Oosthuizen

Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria,

Private Bag X20, Hatfield 0028, South Africa

Email: [u15004938@tuks.co.za](mailto:u15004938@tuks.co.za)

**Summary**

Rodents from the southern hemisphere are underrepresented in studies of animal personality. In the current study, we assessed personality in 22 wild-caught Namaqua rock mice (*Micaelamys namaquensis*), a species that is widespread throughout southern Africa. We assessed exploration, aggression, and boldness scores and evaluated the effects of intrinsic (i.e., sex) and extrinsic (i.e., captive environment) factors on personality. Rock mice showed personality and behavioural plasticity. While sex alone was not an important factor in the personality of this species, the initial trial differed significantly from subsequent ones, indicative of capture stress and/or subsequent habituation. We found a behavioural syndrome between aggressiveness and exploration, as well as between aggressiveness and boldness scores. Thus, our study extends our knowledge of personality and behavioural syndrome in wild

rodents and suggests a role of sex on habituation. The fitness implications of these findings for the study species merit further study in the future.

**Keywords:** *Aethomys*, Africa, aggressiveness, boldness, exploration, repeatability, rodent

## 1. Introduction

Animal personality, individual behavioural responses that are repeatable over time and/or between contexts, is increasingly recognised to affect an animal's fitness and survival (Réale et al., 2007; Stamps & Groothuis, 2010). Personality describes the variation among individuals that is likely contributing to population dynamics and evolutionary trends of a species including dispersal patterns, reproductive abilities, survival and dominance (Sih et al., 2004; Réale et al., 2007; Smith & Blumstein, 2008; Cole & Quinn, 2014; Vanden Broecke et al., 2021). Although a certain consistency of individual behavioural responses is part of the definition of animal personality, individuals may still differ in their flexibility (also referred to as plasticity) of behaviours, i.e. reversible changes in an individual's behaviour in response to environmental conditions (Réale et al., 2010; Dingemanse & Wolf, 2013). Such flexibility of personality can be affected by the genetic make-up of an individual, previous environmental conditions experienced, or a combination of both (Dingemanse & Wolf, 2013; Vanden Broecke et al., 2021). Exploitation of different ecological niches can be promoted through personality and thus, reduce intra-specific competition. Plasticity allows individuals to adapt to new or changing environments and hence, improve their survival (Nicolaus et al., 2012; Snell-Rood, 2013).

Another aspect of personality concerns behavioural syndromes, which is when behaviours exhibited in one personality trait (e.g. exploration) are correlated with one or more of the others (e.g. boldness) (Dingemanse et al., 2012; Herczeg & Garamszegi, 2012). Correlations between these traits can either constrain evolution (if it is of physiological or genetic origin) or be adaptive (Bell, 2005; Dochtermann & Dingemanse, 2013). Consequently,

studying behavioural syndromes is important to understand the behaviours contributing to the syndrome along with the selection pressures underlying them (Sih et al., 2004; Dochtermann & Dingemanse, 2013). Furthermore, through investigating behavioural syndromes we gain insight into both within- and between-individual variation as both an individual and a population can possess a behavioural syndrome (Sih et al., 2004).

The maintenance and flexibility of distinct personalities within and between populations has been linked to differences in individual states that can be distinguished as intrinsic (e.g. age, sex, or body mass) or extrinsic (e.g. food availability or captivity, Dall et al., 2004; Luttbegg & Sih, 2010; Mathot et al., 2012; Sih et al., 2015). For example, sex differences in aggression and exploration between males and females have been reported for several vertebrate species such as prairie voles (*Microtus ochrogaster*), zebra finches (*Taeniopygia guttata*), and striped mice (*Rhabdomys pumilio*, Bales & Carter, 2003; Schuett & Dall, 2009; Yuen et al., 2015). Similarly, sex differences in behavioural syndromes, such as males being more explorative and aggressive compared to females, have been observed in some species (Goulet et al., 2021 and references therein). However, not all studies have found such sex differences possibly because their effects are likely small (Chock et al., 2017; Yuen et al., 2017; Niemelä & Dingemanse, 2018; Vanden Broecke et al., 2018, 2019).

The small contributions of intrinsic states could suggest that extrinsic states play a more important role in animal personality than intrinsic states (Niemelä & Dingemanse, 2018). In fact, it is reasonable that temporary changes in behaviour in response to new environmental conditions provide significant survival benefits as they allow an individual to cope with the new situation (Dingemanse & Wolf, 2013; Sih et al., 2015). For example, a shy animal can become less shy and a bold animal less bold, however, their personality still remains stable as the shy animals still remain shy compared to the bold animals (Frost et al., 2007; Luttbegg & Sih, 2010). Nevertheless, such environmental changes are often stressful for an individual and, in addition to behavioural changes, physiological adjustments (e.g., increases in corticosteroid levels) can often be observed (Gormally & Romero 2018, Careau et al. 2020).

Repeated or long-term exposure to extrinsic changes can attenuate physiological and behavioural responses, a process termed habituation (Cyr & Romero, 2009). In addition to natural environmental stressors, being submitted to experimentation or being introduced into captivity, such as for trials of personality, can be stressful and result in behavioural changes (Drent et al., 2003; Butler et al., 2006; Beisner & Isbell, 2008). While the repeatability of personality does not necessarily increase with the number of trials (Bell et al., 2009), animals might become habituated to the experimental setup and thus not perform ideally concerning the experiment (Martin & Réale, 2008; Bell et al., 2009; Chock et al., 2017; Carlson & Tetzlaff, 2020). However, while habituation can affect animal behaviour and personality, this is not always the case (Rodríguez-Prieto et al., 2011; Blumstein, 2016; Chock et al., 2017; Vanden Broecke et al., 2019).

Studies of animal behaviour and personality are geographically biased to the northern hemisphere, particularly those focussed on rodents. To date, personality has only been investigated in a limited number of African rodent species including African striped mice (*Rhabdomys* spp.; Yuen et al., 2015, 2016, 2017; Joshi & Pillay, 2016; Silber, Joshi, & Pillay, 2019), multimammate mice (*Mastomys natalensis*; Vanden Broecke et al., 2018) Karoo bush rats (*Myotomys unisulcatus*; Agnani et al., 2020) and naked mole-rats (*Heterocephalus glaber*; Majelantle et al., 2022) despite the much greater diversity of this order on the continent. In the current study, we aimed to provide the first data on personality in an endemic rodent species, the Namaqua rock mouse (*Michaelmas namaquensis*, previously known as *Aethomys namaquensis*). It is a widespread southern African rodent species that is a nocturnal generalist with an omnivorous diet (Skinner & Chimimba, 2005; van der Merwe & Bennett, 2014). Rock mice are polygamous but lack a sexual dimorphism in body size (Fleming & Nicolson, 2004; Skinner & Chimimba, 2005). Although they have been proposed to live communally, females appear to occupy exclusive home ranges with male territories overlapping multiple female ranges during the breeding season (Fleming & Nicolson, 2004).

The objectives of this study were to determine if personality is present in wild-caught rock mice and whether the species exhibits flexibility of personality and/or a behavioural syndrome.

Furthermore, we investigated possible intrinsic (i.e. sex) and extrinsic (i.e. novel environment) effects on animal personality in the study species. Animal personality was evaluated using four trials over approximately six months, roughly corresponding to the average life expectancy in this species (T. Oosthuizen, D.M. Fagir & H. Lutermann, unpublished data). We hypothesised that 1) personality would be present in the study species and also expected between-individual differences in the behavioural changes of personality, similar to the findings in other rodent species. Furthermore, due to the generally low contributions of intrinsic factors on personality, we predicted that 2) there would be no sex differences in personality, as our species do not exhibit sexual dimorphism. Conversely, we hypothesised that 3) personality would be affected by extrinsic factors as a result of habituation to captive conditions. Lastly, we predicted 4) a behavioural syndrome would be present with a correlation between the three axes measured, namely exploration, aggressiveness, and boldness, as these three traits make up the proactive-reactive axis (Koolhaas et al., 1999, 2010).

## **2. Materials and Methods**

### *2.1 Animal trapping procedure*

A total of 24 rock mice (12 of each sex) were caught at Telperion Nature Reserve (S25.70827 E28.93005, Gauteng, South Africa) during the dry autumn season of 2019. This sample size was chosen based on calculations using G\*Power (version 3.1.9.2, Franz Faul, Germany) assuming an effect size of 0.8 and two study plots (Faul et al., 2007, 2009). We selected two study plots approximately 150 m apart and set 150 Sherman live traps on each plot (H. B. Sherman Traps Inc., Tallahassee, Florida). Both plots were dominated by rocky terrain and surrounded by grassland. Traps were placed in three parallel rows with 50 traps each, with any two traps approximately 10 m apart, for four nights. Each trap contained a bait ball made from a mixture of peanut butter and oats. We opened the traps in the afternoon and inspected them the following morning until the required number of animals was captured. We removed all mice caught from the traps and sexed them before we subjected the individuals to the first

personality trial in the field laboratory (for details see personality trial below). For the field laboratory, we used a room in a house located in the reserve where animals could be contained and external disturbances were kept to a minimum. Temperature and lighting conditions equalled those in the field. The test arena and other equipment used for the personality trials were identical to that in subsequent ones (see below). Only non-reproducing mice weighing a minimum of 25 g were included as study animals. The average body mass of non-gravid adults in this study location is 45g (H. Lutermann et al. unpublished data). We transported the animals in their housing cages to the laboratory at the University of Pretoria for further trials. Once processed, we released the animal into a rodent cage (11 x 38 x 28.4 cm).

### *2.2 Animal housing in the laboratory*

In the laboratory, animals were housed individually in cages (22.5 x 37.7 x 34 cm) with wood shavings and paper towels as nesting material. All animal cages were kept in a climate-controlled room with a constant ambient temperature of 24 °C ± 1 °C and a 12 h light/12 h dark light schedule. Each cage contained a rock, a toilet paper roll and an egg carton for enrichment, which we replaced when needed. The animals had *ad libitum* access to water, and we fed them a combination of sweet potato, apple, and carrot pieces daily. In order to prevent excessive mass gain, we provided rodent pellets only once per week. The health of the animals was monitored by weekly weighing of each individual. We cleaned the cages every second week to minimize disruption and stress to the animals.

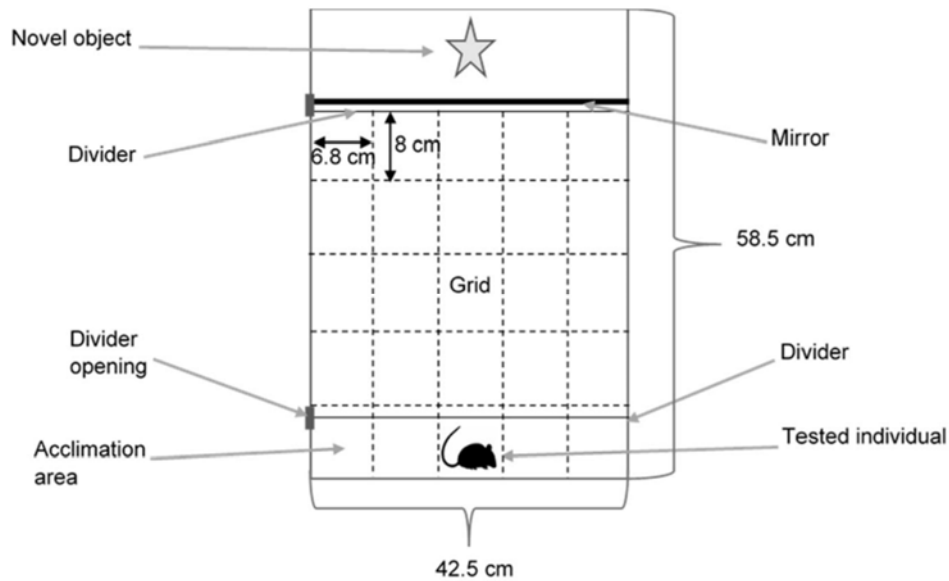
### *2.3 Personality trial*

For the personality trials, we used a three-component behavioural experiment consisting of an exploratory test (ET), an aggressive response test (AT) and a boldness test (BT; Archer, 1973). The personality test apparatus consisted of a customised arena made of an test arena (58.5 x 42.5 x 36 cm) with transparent sides, which we divided into three segments with two cardboard dividers and covered with a wire grid on top to prevent escape and paper on the

sides to minimize disturbances (Figure 1). Animals were subjected to all three tests consecutively to minimize the effect of handling and observer presence (Archer, 1973). The order of these tests remained constant over time, as the test apparatus could not be modified to accommodate a different test order. While a non-randomized test sequence has been suggested to affect the behaviour of the test animals in some instances, this is not always the case (Bell, 2013) and aided to minimize stress, another factor potentially confounding behavioural assessments, for our animals. Animals were taken from their housing cage and placed in the acclimation area within the test arena and were allowed to settle for three minutes. Subsequently, we removed the first divider through a slit on the side of the container and started the observations for the ET. This consisted of an open area with no potential shelters (Figure 1) and trials lasted for the next five minutes; this is also referred to as an open-field test (Piquet et al., 2018). Removing the next divider exposed the animal to a mirror the same size as the dividers to create the illusion of another individual being present in the arena to test their aggressive response (Figure 1). We trust that this test is suitable to test for aggression in our study species as it have been used in previous rodent studies (for example see Baker et al., 2016; Hurtado & Mabry, 2017) and aggressive behaviour has been observed in *M. namaquensis*. Observations of aggression include the regular observation of injuries sustained by individuals of both sexes throughout the year in the field, as well as males killing females they were mated with in the laboratory (D. M. Fagir and H. Lutermann, unpublished data).

After a second five-minute observation period had elapsed, we removed the mirror to reveal a novel object (colourful plastic squeaky toys of differing shapes, a small orange rugby ball and a red dog chew toy, all approximately 12.5 cm in size) at the end of an open area for the BT (Frost et al., 2007) and recorded the individual's behaviour for another five minutes. A different novel object was used in each trial (i.e., 1, 2, 3 and 4) and the same object was used for all animals in the same trial. Gridlines (25 blocks with dimensions 8 x 6.8 cm) were drawn on the bottom of the arena to determine the distance from the divider, mirror, and novel object (Figure 1). As we only had one personality trial for two of the females that died suddenly of

unknown causes, we excluded them from all further analyses. This was done to remove any possible effects of illness on behaviour. However, including their data did not change the results of our analyses (data not included). For a third female, we could not complete the last trial; however, the data for its three trials were included.



**Figure 1.** A visual representation of the personality test arena. The first section (bottom of the figure) is the acclimation area, followed by the exploration area, the mirror used for the aggressive response test, and finally a novel object for the boldness test.

We recorded each trial with a video camera (Sony Handycam, DCR-SX65, 70X zoom) placed on a tripod over the test arena. Animals were returned to their home cage after each trial and the test arena, mirror, and novel object were cleaned with soapy water and 70% ethanol. Animals were subjected to four experimental trials conducted over 144-146 days. The first trial (trial 1, Figure S1) was conducted on the day of capture in the field laboratory. The second trial (trial 2) took place after 19-22 days in captivity (Figure S1). We completed the third trial (trial 3) 47-54 days after the first (Figure S1). The fourth and final trial (trial 4) was completed



144-146 days after the first trial to ensure personality measures over an extended period that corresponded to the average life span of this species in our study area (Figure S1).

All video files were analysed using The Observer XT v10.5 (Noldus Information Technology Inc., Wageningen, The Netherlands). We recorded between six (ET) and eight variables (AT and BT) for each test for further analyses applying the same categories to each individual (Table 1). Separate measurements were collected for each of the trials (ET, AT and BT). In addition, we measured the speed (cm/s) and distance (cm) travelled during the exploration test with EthoVision XT v11.5 (Noldus Information Technology Inc., Wageningen, The Netherlands).

**Table 1.** Variables recorded during the exploratory (ET), aggressive response (AT) and boldness test (BT).

<b>Behaviour</b>	<b>Measure</b>	<b>Description</b>
Latency to move (ET, AT, BT)	Duration	The time elapsed before the animal started moving with more than one paw
Stationary (ET, AT, BT)	Duration	Animal immobile
Sniffing (ET)	Duration	Nose exploring object/surface
Touching divider (ET)	Frequency	Front paw touching divider
Grooming (ET)	Frequency	Licking or scratching any body part
Rearing (ET)	Frequency	Standing upright on hindfeet
Approaching object (AT, BT)	Duration	Moving towards mirror/novel object with more than two paws in the direction of the mirror/object
Retreating from object (AT, BT)	Duration	Moving away from mirror/novel object with more than two paws and back facing away from mirror/object
Time close to object (AT, BT)	Duration	Time spent within half a body's length to the mirror/novel object
Touching object (AT, BT)	Frequency	Making contact with front paws to mirror/novel object
Latency touching (AT, BT)	Duration	Time elapsed before first touching the object with front paws

## 2.4 Data analysis

To reduce the number of variables for each test (ET, AT, and BT) we carried out principal component analyses (PCAs) for each trial for each test separately using SPSS v26 (IBM Corp., New York). Individual principal component (PCs) scores with an eigenvalue larger than one were extracted using the Bartlett method and only PC scores explaining more than 50% of the variance were included in the subsequent analyses. Further analyses were carried out using R v3.6.1 (RStudio Core Team, 2019). We used the extracted PC scores for each individual per test and trial as response variables and tested all of them for normality using the Shapiro-Wilk test and visual inspection of the residuals. In addition, we confirmed the residual pattern of our data using the “DHARMA” package (Hartig, 2021).

The data distributions of the response variables were not parametric ( $p \leq 0.011$ ) and transformations were unsuccessful. Hence, we used two approaches to test for behaviour changes over time of exploration, aggression and boldness scores. These two approaches included generalized linear mixed models (GLMMs) as our data were non-parametric and we further analyzed the data using the rptR package as this fulfills the requirements for best practice (Dingemanse & Wright, 2020). We firstly used separate GLMMs with a Gamma distribution and log-link function for each response variable (package lme4, Bates et al., 2015). We added the trial number (i.e., trial 1 – 4), sex and the interaction between trial and sex as independent variables. Animal ID was included as a random effect to control for the repeated measurement of the same individual. The time elapsed since the first trial was also included in the model. We sequentially removed non-significant terms from the models using the “drop1” function to identify the most parsimonious models (Table S1). Initially, we also included body mass as a co-variate. However, since this variable had no significant effect and was dropped from all models, we only report the more parsimonious models here. For post-hoc comparisons, we used the emmeans package (Lenth et al., 2020).

Since it has been suggested that mixed-effects models are somewhat robust to violations of the assumed data distribution (Dingemanse & Wright, 2020; Schielzeth et al., 2020), we furthermore tested for repeatability of our personality measures by using the rptR

package employing bootstrapping with a 1000 iterations (Stoffel, Nakagawa, & Schielzeth, 2017). Based on the results of the GLMM (see results section) we carried out these analyses for the data from all four trials and repeated it excluding the first trial. In order to assess the influence of individuals on our model, we compared the best fitting random slope models with intercept models excluding either ID or the time since the first trial using the likelihood ratio test, LRT (Dingemanse et al., 2010; Dingemanse & Dochtermann, 2013).

To test for possible relations between the three different tests (i.e., interactions across contexts), we averaged PC scores across trials for each personality test and then used correlations. The mean PC scores for AT and BT were not normally distributed ( $p \leq 0.0003$ ) while the PC score for ET complied with the assumptions of parametric data ( $p = 0.334$ ). Therefore, we used a Spearman's rank correlations test to assess correlations between the averages of the PC scores for all four trials. We repeated this analysis for the means of trials 2 to 4 as we found temporal effects on repeatability (see results section below). As the data distribution for these data was parametric ( $p \geq 0.155$ ), we used Pearson's correlations for these analyses.

### **3. Results**

#### *3.1 Personality indices*

Two PCs exceeded an eigenvalue of one for the ET. PC1 explained more than 50% of the variance observed (Table 2, Figure S2), whilst PC2 explained 17.2%; however, as PC2 did not meet the 50% variance explained threshold, it was not used for subsequent analyses. The PC1 score increased with a decreased duration spent stationary, increased frequency of touching the divider and rearing, as well as speed and distance travelled (Table 2). Thus, individuals with higher ET PC1 score were more explorative.

**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	<b>-0.644</b>	<b>-0.667</b>
Stationary (s)	<b>-0.891</b>	<b>-0.940</b>	<b>-0.900</b>
Sniffing (s)	0.289	-	-
Touching divider/object (frequency)	<b>0.898</b>	<b>0.840</b>	<b>0.783</b>
Grooming (frequency)	0.283	-	-
Rearing (frequency)	<b>0.957</b>	-	-
Approaching object (s)	-	<b>0.946</b>	<b>0.930</b>
Retreating from object (s)	-	<b>0.812</b>	<b>0.762</b>
Time close to object (s)	-	<b>0.708</b>	<b>0.653</b>
Latency touching (s)	-	<b>-0.857</b>	<b>-0.857</b>
Speed (cm/s)	<b>0.888</b>	-	-
Distance (cm)	<b>0.916</b>	-	-
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.

For the AT, a single PC was extracted with an eigenvalue larger than one that explained almost 70% of the variance observed (Table 2, Figure S3). The AT PC score decreased with increasing time spent stationary, latency to touch the mirror and latency to start moving (Table 2). At the same time, the PC score increased with increased time spent retreating, approaching the mirror, frequency touching the mirror and time spent near the mirror (Table 2). This suggests that individuals with high factor loadings of these variables showed higher aggression scores.

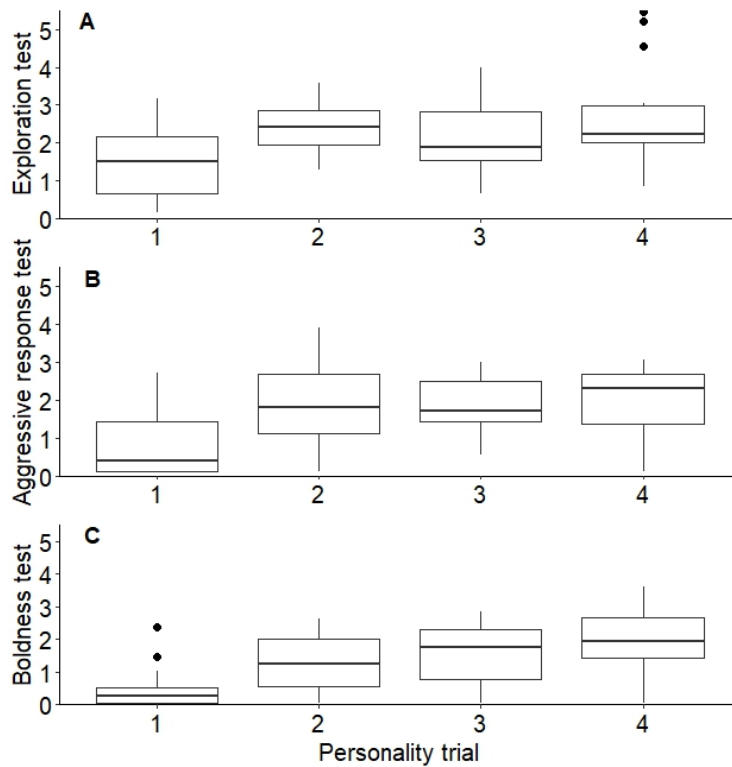
Lastly, one PC exceeding an eigenvalue of one was extracted for the BT (Table 2). This PC explained 63.9% of the observed variation (Table 2, Figure S4) and all variables included in the analysis significantly influenced the BT PC score (Table 2). The PC score decreased with increased time spent stationary, latency to touch the novel object and latency to move (Table 2). At the same time, the PC score increased with increased time spent retreating and approaching the novel object, the frequency the novel object was touched, and the duration of time spent near the novel object (Table 2). Thus, individuals with high BT PC scores were considered bolder.

### 3.2 Temporal repeatability, plasticity and sex effects on personality

Trial number significantly influenced the ET PC score (Table 3, Figure 2A). Post-hoc analyses revealed that the PC score for trial 1 was significantly lower compared to all subsequent trials ( $p \leq 0.005$ , Figure 2A). None of the other pairwise comparisons was significant ( $p \geq 0.543$ ).

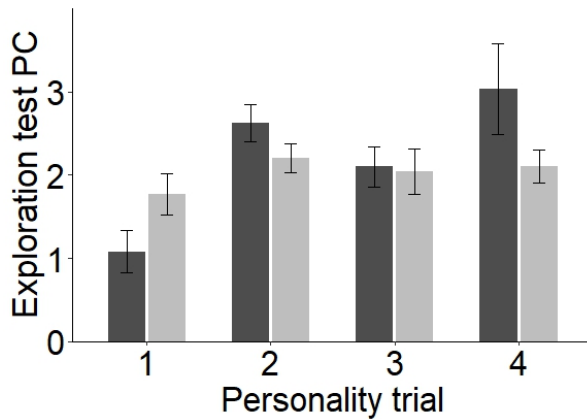
**Table 3:** The best fitting GLMMs for exploration, aggression and boldness PC scores. Significant values are highlighted in bold ( $p < 0.05$ ).

		<i>Trial number</i>	<i>Sex</i>	<i>Trial number*Sex</i>
<b>Exploration PC score</b>	X <sup>2</sup>	21.456	0.051	11.440
	df	3	1	3
	p-value	<b>&lt;0.0001</b>	0.821	<b>0.01</b>
<b>Aggression PC score</b>	X <sup>2</sup>	31.779	1.687	-
	df	3	1	-
	p-value	<b>&lt;0.0001</b>	0.194	-
<b>Boldness PC score</b>	X <sup>2</sup>	67.012	0.141	-
	df	3	1	-
	p-value	<b>&lt;0.0001</b>	0.708	-



**Figure 2.** Effect of personality trial on A – PC score for the exploration test, B – PC score for the aggressive response test and C – PC score for the boldness test.

Sex did not significantly influence the ET PC score (Table 3). However, the interaction between trial and sex was significant (Table 3, Figure 3). The post-hoc analyses showed that females were significantly less exploratory in trial 1 compared to trials 2, and 4 ( $p \leq 0.005$ , Figure 3). Females in trial 1 were also significantly less exploratory compared to males in trials 2 to 4 ( $p \leq 0.050$ , Figure 3). None of the other comparisons was significant ( $p \geq 0.508$ ).



**Figure 3.** The effect of sex (female: dark grey, male: light grey) and trial number on the PC score for the exploration test.

Similarly, the trial number significantly affected the AT PC score (Table 3, Figure 2B). Post-hoc analysis showed that it was significantly lower for trial 1 compared to all subsequent trials ( $p < 0.0001$  for all, Figure 2B). None of the other comparisons between trials was significant ( $p \geq 0.984$ ). Sex did not influence the AT PC score significantly (Table 3) and the interaction between sex and trial was dropped from the most parsimonious model (Table S1).

Trial significantly affected the BT PC score (Table 3, Figure 2C). Post-hoc analyses showed that it was significantly lower for trial 1 compared to all subsequent trials ( $p < 0.0001$  for all, Figure 2C). Additionally, trial 2 was significantly lower than trial 4 ( $p = 0.052$ , Figure 2C), while none of the remaining pairwise comparisons were significant ( $p \geq 0.297$ ). Sex did not significantly influence the BT PC score (Table 3). The interaction between sex and trial was not included in the most parsimonious model.

The repeatability analyses for the four trials showed a low but significant repeatability for the ET PC scores (Repeatability [R2] =  $0.195 \pm 0.113$ , likelihood-ratio test [LRT] = -114.96,  $p = 0.021$ ). Repeatability was low for the AT PC score ( $R = 0.153 \pm 0.105$ , LRT = -110.755,  $p = 0.052$ ). For the BT PC score across the four trials, repeatability was moderate but significant ( $R = 0.335 \pm 0.117$ , LRT:  $\chi^2 = -107.331$ ,  $p = 0.0004$ ). There were no differences in repeatability in the ET PC score (LRT  $\chi^2 = 0.581$ ,  $p = 0.749$ ) and the AT PC

score (LRT  $\chi^2 = 3.794$ ,  $p = 0.1501$ ) between the trials, but time since the first trial did significantly affect the BT PC score (LRT  $\chi^2 = 8.682$ ,  $p = 0.013$ ). Conversely, *M. namaquensis* ID explained a significant proportion of the variance observed for all three personality axes (ET PC score: LRT  $\chi^2 = 8.5694$ ,  $p = 0.014$ ; AT PC score: LRT  $\chi^2 = 6.328$ ,  $p = 0.043$ ; BT ET score: LRT  $\chi^2 = 23.065$ ,  $p < 0.0001$ ).

After excluding the first trial from the analyses the repeatability became moderate for the ET PC score ( $R = 0.324 \pm 0.139$ , LRT = -90.630,  $p = 0.007$ ) as well as the AT PC score which was significant ( $R = 0.356 \pm 0.134$ , LRT = -91.510,  $p = 0.003$ ). Repeatability remained moderate but significant for the BT PC score ( $R = 0.448 \pm 0.133$ , LRT = -89.035,  $p = 0.0003$ ). Time elapsed since the first trial explained a significant proportion of the variance observed in the ET PC score (LRT  $\chi^2 = 16.248$ ,  $p = 0.0003$ ) but not for the AT PC score (LRT  $\chi^2 = 2.479$ ,  $p = 0.290$ ) or the BT PC score (LRT  $\chi^2 = 5.271$ ,  $p = 0.072$ ). In contrast, the ID of an individual explained a significant proportion of the observed variance for the ET PC score (LRT  $\chi^2 = 23.834$ ,  $p < 0.0001$ ) and the BT PC score (LRT  $\chi^2 = 12.098$ ,  $p = 0.002$ ) but not the AT PC score (LRT  $\chi^2 = 4.780$ ,  $p = 0.092$ ).

### 3.3 Behavioural syndromes

The mean AT PC score was significantly correlated with both the mean ET PC score ( $R_S = 0.640$ ,  $p = 0.0013$ ) and the mean BT PC score ( $R_S = 0.555$ ,  $p = 0.007$ ). There was however, no significant correlation between mean ET PC and mean BT PC scores ( $R_S = 0.236$ ,  $p = 0.291$ ).

Results were similar when only mean PC scores for trials 2 to 4 were considered; the mean AT PC score was significantly correlated with the mean ET PC score ( $R_P = 0.554$ ,  $t = 2.975$ ,  $df = 20$ ,  $p = 0.0075$ , Figure S5) as well as the mean BT PC score ( $R_P = 0.569$ ,  $t = 3.095$ ,  $df = 20$ ,  $p = 0.006$ , Figure S6). Conversely, there was no significant correlation between mean ET PC score and mean BT PC score ( $R_P = 0.282$ ,  $t = 1.314$ ,  $df = 20$ ,  $p = 0.200$ , Figure S7).



#### 4. Discussion

Namaqua rock mice exhibited animal personality (Careau et al., 2015; Yuen et al., 2015; Chock et al., 2017; Vanden Broecke et al., 2018; Agnani et al., 2020). Similar to what has been reported for other rodents, we did not find support for an effect of sex on personality (Chock et al., 2017; Schuster et al., 2017; Yuen et al., 2017; Vanden Broecke et al., 2018). For example, Yuen et al. (2017) found that sex did not have an influence on the traits they assessed in striped mice. However, Yuen et al. (2015) reported that sexual selection was important in maintaining personality in the same species. Multimammate mice also showed no sex influence on their personality (Vanden Broecke et al., 2018). While some authors have attributed this to a lack of sexual dimorphism, also observed in the study species (Chock et al., 2017), others have stressed that the sexes experience divergent forces of sexual selection in polygynous species with sexual dimorphism (Gosling, 1998; Schuett et al., 2010). While *M. namaquensis* does display sexual dimorphism in habituation rates for example, it does not display sexual dimorphism in body size (Skinner & Chimimba, 2005). Thus, it is possible that the factors influencing the personality of our study species are not as driven by such differences. However, the absence of an effect is not necessarily proof that it does not exist and we cannot exclude the possibility that the lack of sex effects may be due to our limited sample size. In addition, our study was conducted during the non-breeding season when such forces might be limited (Fraser et al., 2001; Garamszegi et al., 2012; Chock et al., 2017). Alternatively, but not mutually exclusive, the communal lifestyle reported for the study species may negate sex-specific trajectories (Skinner & Chimimba, 2005) and this warrants further investigation. When more rodents with different mating systems are studied, it could become possible to predict when and when not sex specific personalities are to be expected (Schuster et al., 2017).

Changes in the environment had significant effects on the expression of behavioural responses and we observed increases in repeatability for later trials of personality compared to the initial one. This was confirmed by both approaches taken and while the GLMMs

indicated that the number of the trial was a significant factor, the exclusion of the first trial from the repeatability analyses resulted in increased repeatability for exploration and aggression but not boldness scores. The capture of animals and subsequent transfer to a captive setting is likely to be a major stressor (Martin & Réale, 2008; Cyr & Romero, 2009; Dingemanse et al., 2012; Gormally & Romero, 2018). Behavioural habituation experienced after capture was observed in several other African rodents and can also influence the results of personality trials (Yuen et al., 2016; Vanden Broecke et al., 2019; Agnani et al., 2020). Our study protocol differs from those of other African rodents in that animals in other studies were familiar with the trapping procedures and frequently handled. Furthermore, the time spent in the traps before the first trial was likely more variable for our animals. In addition, rodents in other studies were kept in captivity only for a brief period of several hours (Yuen et al., 2016; Vanden Broecke et al., 2019; Agnani et al., 2020). This could account for a significant reduction in repeatability for the first compared to subsequent trials in our study species (Garamszegi et al., 2012). However, compared to some other studies repeatability in our study animals was high; a study on multimammate mice found their exploration repeatability to be 0.22 for example (Vanden Broecke et al., 2019), particularly after excluding the initial trial from the analyses. This was despite our repeated trials being carried out over a longer period, equating to the average life span of *M. namaquensis*. This suggests that personality remains consistent in adults as reported for striped and multimammate mice (Yuen et al., 2016; Vanden Broecke et al., 2019) as well as the Australian fawn-footed mosaic-tailed rat (*Melomys cervinipes*, Rowell & Rymer, 2021).

We observed sex differences in habituation and female exploration scores, but not aggressiveness or boldness scores. Additionally, the scores for the first trial were significantly lower than those for all subsequent trials for both sexes. Several studies reported sex differences with regard to habituation, with males habituating faster and exploring more than females (Ensminger & Westneat, 2012; Vanden Broecke et al., 2019). Females of polygynous rodents tend to be more territorial than males that regularly undertake forays into unfamiliar spaces when searching for mates (Vanden Broecke et al., 2019). Thus, sex-specific

differences in fitness pay-offs for exploring unfamiliar environments could account for the observed differences in apparent habituation between the sexes. This could be indicative of an interaction between intrinsic and extrinsic states that modulate exploration in the study species.

Rock mice exhibited a behavioural syndrome between aggressiveness and boldness scores. More aggressive individuals were also bolder. However, the assumption that a bold individual will be highly explorative as well as aggressive, did not hold in the study species. While many rodent studies have tested for correlations between personality axes, they differ widely in the axes measured as well as the trials used (Montiglio et al., 2012; Schoepf & Schradin, 2012; Petelle et al., 2013; Careau et al., 2015; Yuen et al., 2016; Chock et al., 2017; Vanden Broecke et al., 2018, 2019; Agnani et al., 2020). Aggressiveness and boldness have been measured in a number of these studies, however, they have not necessarily found a similar syndrome as observed in our study species (Martin & Réale, 2008; Schoepf & Schradin, 2012; Yuen et al., 2016). Conversely, several rodent studies assessing at least two of the three axes measured in the current study have reported behavioural syndromes between exploration (or activity) and boldness or aggressiveness (Boon et al., 2008; Martin & Réale, 2008; Montiglio et al., 2012; Yuen et al., 2016; Chock et al., 2017; Agnani et al., 2020). It remains unclear whether this diversity in the prevalence of behavioural syndromes is a reflection of the diversity of behavioural or experimental trials or may indicate that such syndromes are species-specific (Dingemanse et al., 2010). In addition, the ambiguity in definitions for the different axes and tests measuring the same axis or a single test to measure a range of axes likely adds further variance.

In conclusion, our study showed that while sex had little effect on the expression of the three personality axes measured, this was not the case for the extrinsic factor, namely the habituation to the experimental design. Whereas personality traits were stable during prolonged captivity, repeatability was significantly lower for the trial immediately after capture either due to the stress experienced in response to capture or due to the more stable environmental conditions in captivity, with females habituating at a slower pace. Rock mice

also exhibited a behavioural syndrome between aggressiveness and boldness scores. Thus, our study provides evidence for differences in personality, plasticity and behavioural syndromes in the study species.

## **Acknowledgements**

We are indebted to the staff and management of Telperion Nature Reserve, particularly Elsabe Bosch and Duncan MacFadyen for allowing us to capture our study animals on their property. In addition, we are thankful to the volunteers helping with capture and animal maintenance. This study was approved by University of Pretoria ethics committee (Protocol number: NAS065/2019). We are grateful to the National Research Foundation for providing funding for this study and the Gauteng Department of Nature Conservation for issuing the permits (CPB1 0631, CPB4 000382). This manuscript was greatly improved by the feedback from two anonymous reviewers.

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