



BRILL

*Behaviour* 161 (2024) 311–330

**Behaviour**  
brill.com/beh

# Maternal genetic and non-genetic effects on the development of exploration and anxiety-like behaviours in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*

Misha K. Rowell<sup>a,b,\*</sup> and Tasmin L. Rymer<sup>a,b</sup>

<sup>a</sup> College of Science and Engineering, James Cook University, P. O. Box 6811, Cairns, QLD 4870, Australia

<sup>b</sup> Centre for Tropical Environmental and Sustainability Sciences, James Cook University, P.O. Box 6811, Cairns, QLD 4870, Australia

\*Corresponding author's e-mail address: [misha.rowell@my.jcu.edu.au](mailto:misha.rowell@my.jcu.edu.au)

ORCID iDs: Rowell: 0000-0003-3829-9178; Rymer: 0000-0002-9963-6345

Received 18 April 2023; initial decision 27 July 2023; revised 27 February 2024; accepted 27 February 2024; published online 11 March 2024

---

## Abstract

Personality in non-human animals has been a popular area of research; however, it is still unknown how genetic and non-genetic factors influence the development of personality in many species. Therefore, we investigated how maternal genetic and non-genetic effects influenced adult offspring personality (exploration and anxiety) in the fawn-footed mosaic-tailed rat *Melomys cervinipes*. We first measured the amount of maternal care mothers provided to their offspring. Later, we assessed mothers and adult offspring over two testing sessions for exploratory behaviour using open field and novel object tests, and anxiety behaviour in a light/dark test. We calculated repeatability of behaviours and used parent–offspring regressions to assess heritability of behaviours. No measure of maternal care significantly influenced offspring personality. However, exploration of new spaces was constrained by maternal genetic effects. In contrast, anxiety and exploration of novel objects was more flexible, suggesting these behaviours may be more influenced by an individual's experiences during development.

## Keywords

behavioural repeatability, heritability, indirect genetic effects, personality, phenotypic plasticity.

Published with license by Koninklijke Brill NV | DOI: 10.1163/1568539X-bja10262

© MISHA K. ROWELL AND TASMIN L. RYMER, 2024 | ISSN: 0005-7959 (print) 1568-539X (online)

This is an open access article distributed under the terms of the CC BY 4.0 license.

Downloaded from Brill.com 09/19/2024 12:28:04AM  
via Open Access. This is an open access article distributed under the terms  
of the CC BY 4.0 license.

<https://creativecommons.org/licenses/by/4.0/>

## 1. Introduction

In non-human animals, personality refers to inter-individual differences in behaviour that are consistent over time and across different contexts (Sih et al., 2004). It is a popular area of study, with personality being found in mammals (e.g., chacma baboons *Papio ursinus*; Carter et al., 2014), birds (e.g., red junglefowl *Gallus gallus*; Favati et al., 2016), reptiles (e.g., eastern box turtle *Terrapene carolina*; Carlson & Tetzlaff, 2020), fish (e.g., three-spine stickleback *Gasterosteus aculeatus*; Bell & Sih, 2007), and even invertebrates (e.g., beadlet anemone *Actinia equina*; Briffa & Greenaway, 2011). Despite this recent interest, most work has focused on the ultimate aspects (sensu lato, Tinbergen, 1963) of personality, particularly the adaptive significance. For example, great tit (*Parus major*) parents with extreme personalities (i.e., very exploratory father and very shy mother) had higher reproductive success, producing more offspring than parents with intermediate personalities (Both et al., 2005). Similarly, mud crab *Panopeus herbstii* predator avoidance behaviours (bold vs. shy) and subsequent survival rates were related to specific predators, with bold mud crabs being predated more by blue crabs *Callinectes sapidus*, while shy mud crabs were predated more by toadfish (*Opsanus tau*; Belgrad & Griffen, 2016).

Currently, little is known about the development of personality, or the mechanisms that control its expression (i.e., the proximate aspects, Groothuis & Trillmich, 2011). Some studies have found that personality has a heritable component (e.g., novel object exploration is heritable in Japanese macaques *Macaca fuscata*; Arnaud et al., 2017; fearfulness is heritable in rhesus macaques *Macaca mulatta*; Williamson et al., 2003). However, an individual's personality can also change over its lifetime as it undergoes physiological (e.g., sexual maturation; Cabrera et al., 2021) or social changes (e.g., change in dominance; Briffa et al., 2015), and because of complex genotype–environment interactions (GxE; Han & Dingemanse, 2015). For example, house mouse *Mus musculus* pups raised in enriched environments displayed higher heritability of personality measures than pups raised in standard environments (Matzel et al., 2019). Similarly, both environmental quality and heritability affected exploratory behaviour in a wild population of great tits (Quinn et al., 2009). Furthermore, African striped mouse species (*Rhabdomys* spp.) displayed similar personalities when they occupied similar environments, but not when they occupied different environments (Mackay & Pillay, 2021).

The physical structure of the environment is not the only extrinsic factor that may affect offspring development. In mammals in particular, the maternal environment is important for offspring development, as offspring rely on the mother for food (quality/quantity of milk), as well as care (e.g., grooming, toileting). The level of maternal care has been found to influence neural development (e.g., hippocampus neurons, Bredy et al., 2003) and subsequent behavioural and cognitive expression (Champagne, 2008). Therefore, it is not surprising that maternal effects also influence the development of personality in offspring. For example, non-genetic maternal effects (e.g., differences in maternal stress levels), affected exploratory behaviours in the multimammate mouse *Mastomys natalensis*, with fast-exploring mothers potentially having higher stress levels that resulted in reduced offspring exploration (Vanden Broecke et al., 2021). Similarly, in red squirrel *Sciurus vulgaris* offspring activity was related to maternal effects as estimated using an animal model (Taylor et al., 2012). Furthermore, anxiety behaviours in laboratory rats *Rattus norvegicus* (Caldji et al., 1998) were influenced by maternal care, with offspring that received lower levels of tactile stimulation and nursing being more fearful than offspring that received higher levels of care. However, maternal care does not always significantly affect offspring behaviours (e.g., problem solving in fawn-footed mosaic-tailed rats *Melomys cervinipes*; Rowell & Rymer, 2022), as other extrinsic factors (e.g., predator exposure; Tapocik et al., 2021) may have a larger effect on offspring behavioural development. We therefore do not fully understand the contribution that maternal care has to offspring behavioural development in many species.

In this study, we investigated how maternal genetic and non-genetic effects influenced adult offspring personality (exploration and anxiety) in the fawn-footed mosaic-tailed rat *Melomys cervinipes*. Mosaic-tailed rats are native Australian rodents found in forests along the eastern coast (Moore et al., 2008). They display more of a K-selected reproductive strategy than other similar-sized rodents (Rowell & Rymer, 2020a), with females having up to 4 pups and showing a prolonged period of pre- and post-natal care (Callaway et al., 2018). Previous studies showed that adult mosaic-tailed rats have individual personalities (Turner, 2015; Rowell & Rymer, 2021), suggesting that both intrinsic and extrinsic factors, including developmental effects, could play a role in driving differences in behaviour (Lynn & Brown, 2009). We hypothesised that both maternal genetic and non-genetic effects

would influence offspring personality (Caldji et al., 1998). Specifically, we expected that mosaic-tailed rat pups would have similar personalities to their mothers, as exploration and anxiety often have heritable components in other species (e.g. great tits; Dingemanse et al., 2002). In addition, we predicted that pups born to mothers that provided high levels of care would be more exploratory and less anxious than pups born to mothers that provided less care, indicating a non-genetic maternal effect, as observed in laboratory rats (Champagne, 2008).

## **2. Methods**

### *2.1. Husbandry*

We used 10 adult female mosaic-tailed rats and their offspring ( $N = 19$ ) for the maternal care component of this study (see below). Adult females were either trapped from the Smithfield Conservation Park and James Cook University Nguma-bada campus or originated from a colony ( $N = 2$ ; see details in Rowell & Rymer, 2020b). During this experiment, adult female mosaic-tailed rats and their pups were kept individually in glass tanks ( $44 \times 35 \times 32$  cm) under partially controlled environmental conditions ( $22\text{--}26^\circ\text{C}$ ,  $50\text{--}65\%$  relative humidity) with a window providing natural lighting. Tanks had approximately 5 cm of wood shavings as a base layer and contained a cylindrical plastic nest box ( $11 \times 11 \times 20$  cm) filled with nesting material (a handful of pasture hay and two pieces of paper towel). We also provided animals with cardboard rolls (for chewing) and sticks (for climbing; Rader & Krockenberger, 2006) for behavioural enrichment. While females were with pups, they were fed with up to 10 g of mixed seeds and rodent chow (Vetafarm Origins) and up to 15 g of fruit/vegetable (e.g., apple/sweet potato) daily, depending on the size and age of the pups. Water was available ad libitum. We briefly removed pups from their mothers every second day from 3 days old to measure behavioural and physical development (see Rowell & Rymer, 2020a), returning the pups to their mother immediately after measurements were taken. Pups were weaned from their mothers at 21 days old, at which point mothers were removed from the tanks and housed individually in wireframe cages (see below), while siblings were kept together in the tank until approximately 2 months old (Rowell & Rymer, 2022).

To increase the sample size for the heritability component of this study (see below), we used these same individuals ( $N = 29$ ), and a further six

adult females and their adult offspring ( $N = 13$ ) in the personality component of this study. These additional individuals originated from a captive colony and the offspring were already mature adults at the time of the study, which excluded them from the maternal care experiment. Mosaic-tailed rats were kept individually in wireframe cages ( $34.5 \times 28 \times 38$  cm) with deep plastic bases ( $34.5 \times 28 \times 11$  cm) filled with approximately 10 cm of wood shavings. Nesting and enrichment items (as above) were placed in the cages, as well as a wire shelf to allow for climbing. We gave each individual 5 g of mixed seed and rodent chow, and 5 g vegetable/fruit daily.

## 2.2. General testing procedures

Due to the staggered trapping of adult female mosaic-tailed rats, and the extended period of time juveniles take to reach sexual maturity (5 months; Yom-Tov, 1985), data collection was prolonged, occurring between June 2018 and March 2021. Tests were conducted during the peak activity period of mosaic-tailed rats (1800–2200 h; Wood, 1971) under red light (except for the light/dark test, see below), which does not interfere with mosaic-tailed rat behaviours (Paulling et al., 2019; Rowell & Rymer, 2020b). All behavioural tests were recorded using a Sony HDR-CX405 camcorder. Behavioural data were scored by one observer (MKR) from videos using the video analysis software BORIS (Friard & Gamba, 2016).

### 2.2.1. Maternal care

We recorded maternal care as described in Rowell & Rymer (2022). Briefly, maternal care was measured every second night, for a total of six sessions, from when pups were two days old (Baker et al., 2008; Nel et al., 2015). We briefly moved mothers and pups out of the nest and placed them in an empty plastic box. During this time, we removed excess nesting material from the tank, leaving only the nesting cylinder and some paper towel strips in the tank for the duration of the test (to allow the mother to be easily filmed). We then gently moved the mother and pups to the front of the nest box and recorded the mother's behaviour for 20 min, totalling each behaviour over the six nights (direct care: time spent huddling over the pups, and time spent licking and grooming pups; indirect care: time spent moving the nesting material (paper towel strips) around). The total duration of all three behaviours for each night were also added together to produce a total measure of maternal care. Care measures were divided by the number of pups in each litter to calculate the average amount of care given to each individual pup, as we

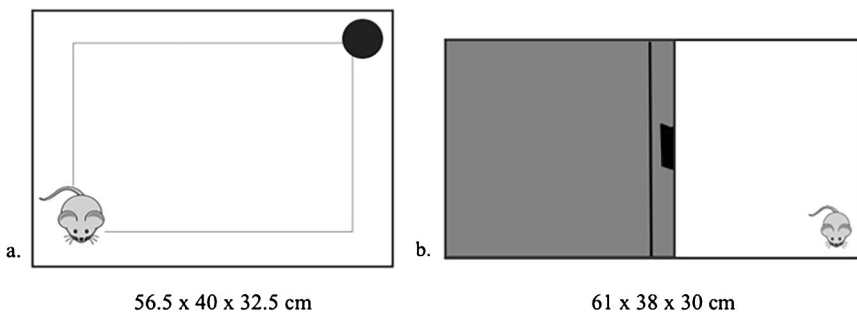
could not always be certain which specific pup was receiving care at any time due to mothers huddling over pups and obscuring the camera.

### 2.2.2. Personality tests

We conducted three personality tests (open field test, novel object test, and light/dark box test) following Rowell & Rymer (2021). All individuals were tested for two replicates (at least four weeks apart) in personality tests as adults (at least 5 months old; Rowell & Rymer, 2021). Tests were presented to animals in a random order, except the novel object test, which was always presented immediately following the open field test. All individuals from the heritability component of this study ( $N = 29$ ) plus additional mothers ( $N = 6$ ) and offspring ( $N = 13$ ) were used for this component. All individuals (both mothers and offspring) were tested as adults after being housed individually for several months.

To measure exploration, we used a coloured plastic storage container ( $56.5 \times 40 \times 32.5$  cm) with a 3.5 cm perimeter (edge) marked for the open field test arena (Figure 1a). The test began when we placed an individual in the centre of the open field, after which it was left in the arena for 10 min. We measured its latency to return to the centre after moving to the edge, the number of crosses made between the centre and edge, the duration of time spent in the centre (irrespective of activity) and the duration of time spent active in the centre by the individual.

Immediately following this period, a novel object (e.g., a pencil eraser) was placed in the container at the opposite end to the subject (Figure 1a). Different objects (e.g., coloured clothes peg, tennis ball) were used for each



**Figure 1.** Testing conditions used to measure personality in fawn-footed mosaic-tailed rats (*Melomys cervinipes*). (a) Container used for open field and novel object tests with novel object placed on the opposite side to the individual's location (dark circle). (b) Light/dark box set up. From Rowell & Rymer (2021).

round of testing to ensure the object was novel to the animals. The same novel objects were used across individuals, thus novel object colour, shape and size was standardised across individuals. Again, we recorded the individual's behaviour for a 10-min period. We measured the latency to approach the novel object, the duration of time spent investigating the novel object (sniffing and/or chewing), the frequency of interactions with the object (i.e., how many times it investigated the object), the frequency of crosses between the centre and periphery of the arena, and the duration of time spent active (i.e., not stationary) in the centre.

To measure anxiety-like behaviour, we used a light/dark box arena. This was constructed from a glass tank ( $61 \times 38 \times 30$  cm) divided in half with a plastic barrier that had a small doorway ( $10 \times 10$  cm) to allow individuals to move freely between sections (Figure 1b). We painted one section black (dark compartment), providing a refuge, while the other section was left transparent (light compartment). The box was covered with a plastic lid that was transparent over the light side and painted black over the dark side. An LED lamp illuminated the light compartment to simulate heightened predation risk via exposure (Hascoët et al., 2001). We started the test by placing a mosaic-tailed rat in the light compartment furthest from the door. We measured the latency to enter the dark compartment from this point. The individual was then allowed to explore for 10 min after it entered the dark compartment. We measured the latency to re-enter the light compartment after entering the dark compartment, the frequency of crosses between compartments, the time spent active in the light compartment and the duration of time spent in each compartment, irrespective of activity. If the individual did not return to the light compartment, it received the maximum score for latency (i.e., 600 s).

### 2.3. Statistics

Statistical analyses were performed using R version 4.0.2 (R Core Team, 2020). The model-level significance was set at  $\alpha = 0.05$ . Data and models were tested for normality (Shapiro–Wilk test). Significant differences in the main effects were identified using Tukey's post hoc tests (emmeans package; Lenth et al., 2020).

#### 2.3.1. Establishing personality measures

We analysed personality following Rowell & Rymer (2021). As personality involves behaviours that are consistent over time (Sih et al., 2004), we ran

repeatability analyses across replicates for each behaviour, (rptR package; Stoffel et al., 2017) and calculated confidence intervals by running 500 bootstrappings on each model. Replicate number was included as a categorical fixed factor, and individual identity (ID) was included as a random factor to account for repeated measures within individuals. For these repeatability analyses, some behavioural data were square-root transformed to allow Gaussian distributions to be used. For each behaviour that was repeatable (Table 1), we calculated the average over the replicates, which was used in later analyses to account for the correlation of repeated measures (Dingemanse & Wright, 2020).

Personality is also comprised of behaviours that are related over different contexts (Sih et al., 2004). We therefore ran two separate principal component analyses (PCAs; corrplot package; Wei et al., 2017) as two personality types (exploration and anxiety-like behaviour) were being studied. PCAs were used to reduce the number of predictor variables (Dingemanse & Wright, 2020). We included the averaged values for each repeatable open field/novel object behaviour in the first PCA, and the averaged values for each repeatable light/dark box behaviour in the second PCA. This generated principal components (PC) of unique values for each individual that described their relative behavioural position in the population. We included PCs in the final analyses only if eigenvalues were above 1, and if the PCs explained close to 70% of the variance (combined or alone). For the open field/novel object PCA, PC 1 (eigenvalue = 6.27; hereafter Exploration PC1) and PC 2 (eigenvalue = 1.55; hereafter Exploration PC2) combined explained 78.3% of the variance and comprised eight behaviours (Table 1). Exploration PC1 mostly included exploration behaviours of novel objects, whereas Exploration PC 2 typically described exploration of novel spaces (Table 2). For the light/dark box PCA, the first PC (eigenvalue = 2.13) explained 71.2% of the variance and was comprised of three behaviours (100% of that variation; Table 1). Finally, to look for relationships between these different personality measures (i.e., behavioural syndromes, Sih et al., 2004), we ran separate regression models, where one PC was the dependent variable (e.g., Exploration PC 1) and another PC was the independent variable (e.g., Exploration PC 2).

### *2.3.2. Maternal care and personality measures*

We used the `descdist` function (`fitdistrplus` package, Delignette-Muller & Dutang, 2015) to assess the best model distribution to use for the data. We



**Table 1.**

Repeatability outputs and principal component loadings of fawn-footed mosaic-tailed rat (*Melomys cervinipes*) behaviours measured in three personality tests (open field test, novel object test and light/dark box).

Behaviour	Test			
	Repeatability output	Mean $\pm$ SE	Confidence intervals	PC loading
<b>Open field (exploration)</b>				
Time active	$R = 0.28, p = 0.027^*$	$377.3 \pm 16.2$	0.02, 0.52	8.49% (1)
Time in centre	$R = 0.43, p = 0.001^*$	$102.3 \pm 11.6$	0.19, 0.63	35.25% (2)
Time active in centre <sup>a</sup>	$R = 0.50, p < 0.001^*$	$62.4 \pm 6.3$	0.25, 0.68	14.44% (2)
Latency to re-enter centre <sup>a</sup>	$R = 0.21, p = 0.070^*$	$68.6 \pm 12.3$	0.00, 0.47	N/A
Crosses	$R = 0.57, p < 0.001^*$	$12.7 \pm 6.3$	0.24, 0.70	11.37% (2)
<b>Novel object (exploration)</b>				
Latency to approach object <sup>a</sup>	$R = 0.59, p < 0.001^*$	$285.3 \pm 26.6$	0.40, 0.75	11.05% (1)
Time interacting with object <sup>a</sup>	$R = 0.58, p < 0.001^*$	$102.1 \pm 12.3$	0.37, 0.75	9.64% (1)
Number of interactions with object	$R = 0.57, p > 0.001^*$	$7.2 \pm 0.8$	0.28, 0.79	12.49% (1)
Time active <sup>a</sup>	$R = 0.49, p < 0.001^*$	$300.6 \pm 20.6$	0.23, 0.68	12.63% (2)
Time active in centre*	$R = 0.16, p = 0.026^*$	$72.9 \pm 8.5$	0.40, 0.77	10.78% (1)
Crosses	$R = 0.57, p < 0.001^*$	$6.6 \pm 0.8$	0.30, 0.78	11.61% (1)
<b>Light/dark box (anxiety)</b>				
Latency to enter dark <sup>a</sup>	$R = 0.04, p = 0.383$	$16.6 \pm 10.3$	0.00, 0.34	N/A
Latency to re-enter light <sup>a</sup>	$R = 0.12, p = 0.214$	$150.7 \pm 19.2$	0.00, 0.40	N/A
Time active in light <sup>a</sup>	$R = 0.42, p = 0.001^*$	$67.7 \pm 7.0$	0.18, 0.63	43.50%
Time in light <sup>a</sup>	$R = 0.57, p < 0.001^*$	$83.2 \pm 10.2$		35.16%
Crosses	$R = 0.49, p < 0.001^*$	$5.6 \pm 0.5$	0.21, 0.69	21.35%

Where two PCs were selected, we have included the PC number after the loading value to indicate which PC the behaviour loaded onto. PC loading is N/A if a behaviour was not included in either PCA.

<sup>a</sup> Behaviours square-root transformed for repeatability analyses.

\* Significant result.

used separate general linear models on square-root transformed data (time spent in the centre during the open field test, time spent active in the light compartment in the light/dark test), and a model with a beta distribution

**Table 2.**

Statistical outputs, power estimates and R-squared values for maternal care models for personality in fawn-footed mosaic-tailed rat *Melomys cervinipes* offspring.

Behaviour variable	Statistical output	Power estimate	Model R-squared
Time in centre of open field			
Direct	$F_{(1,20)} = 2.15, p = 0.162$	1.0	0.37
Indirect	$F_{(1,20)} = 0.82, p = 0.379$	0.99	
Total	$F_{(1,20)} = 1.94, p = 0.182$	1.0	
Sex	$F_{(1,20)} = 2.82, p = 0.113$	0.98	
Interactions with novel object			
Direct	$\chi^2_1 = 1.63, p = 0.202$	1.0	0.12
Indirect	$\chi^2_1 = 1.10, p = 0.294$	0.99	
Total	$\chi^2_1 = 1.40, p = 0.237$	1.0	
Sex	$\chi^2_1 = 0.19, p = 0.664$		0.62
Time active in light compartment			
Direct	$F_{(1,20)} = 0.34, p = 0.566$	1.0	-0.04
Indirect	$F_{(1,20)} = 1.13, p = 0.303$	0.99	
Total	$F_{(1,20)} = 2.19, p = 0.156$	1.0	0.15
Sex	$F_{(1,20)} = 4.65, p = 0.045^*$	0.98	

\* Significant result.

(‘betareg’ package, Cribari-Neto & Zeileis, 2010) for the number of interactions/highest interaction value +1 (to create a value between 0 and 1, as required for a beta-regression model). As only a subset of the mosaic-tailed rat colony had maternal care measured ( $N = 19$ ), we could not use the PC values (which were generated from the relationships of behaviours present in the whole sample size) as a personality measure. Instead, for this subset, we used separate models to investigate how general measures of exploration or anxiety (dependent variables) were influenced by the direct, indirect, and total level of maternal care received, and offspring sex (independent variables included as direct effects). We used the PC weightings to identify behaviours to use in these models (i.e., which behaviours accounted for the most variance in the PC, thus best representing each personality measure). The behaviours we identified as the general measures of exploration and anxiety were time spent in the centre of the open field centre, number of interactions with novel object and time spent active in the light compartment. We used two separate models to investigate the influence of maternal care and sex on the time spent active in the light compartment (model 1 =

total care and offspring sex; model 2 = direct care and indirect care) as a single model including all care measures would not run.

### 2.3.3. Heritability of personality measures

We calculated the heritability of personality following Rowell & Rymer (2022) using parent–offspring regressions to estimate the narrow-sense heritability ( $h^2$ ; Haldane, 1996). As personality is a continuous behavioural measurement, and its heritability is unknown in mosaic-tailed rats, we calculated the narrow-sense heritability of the each personality measure (two Exploration PCs and the Anxiety PC) by regressing the scaled averaged PC value for every litter (the mid-offspring value) on the scaled PC value of the mothers (Keller et al., 2001) using the *lmtest* package (Zeileis & Hothorn, 2002), hereafter referred to as parent–offspring regressions. We used the scale function to standardize each factor based on its mean and standard deviation, thereby allowing the beta coefficient to be calculated for each regression model (Cheng & Wu, 1994). In each model, the average pup PC values were the dependent variables, and the mother PC values were the independent variables.

We used the beta coefficient of the parent–offspring regressions to estimate the maternal genetic contribution to each personality measure. We only focused on maternal contributions as wild-caught females were already pregnant when they were captured; thus, we could not assess the behaviour of their unknown mates. The genetic contribution from parents to offspring may not necessarily be equal (Yang & Wu, 1993). Therefore, we could not assume that the maternal genetic contribution represented only  $\frac{1}{2}h^2$ . As we could not estimate total heritability values of personality, we simply present the maternal  $h^2$  (i.e., the beta coefficient). We calculated the correlation of each parent–offspring aggression using  $\sqrt{\frac{1}{2}h^2}$  (Wray & Visscher, 2008). We assumed that negative heritability estimates were zero (Robinson et al., 1955), but we still present them here, as suggested by Dudley & Moll (1969).

## 3. Results

### 3.1. Personality

All behaviours in the open field test, except for the latency to return to the centre after reaching the edge, and all behaviours in the novel object test, were repeatable over testing sessions. These repeatable behaviours were

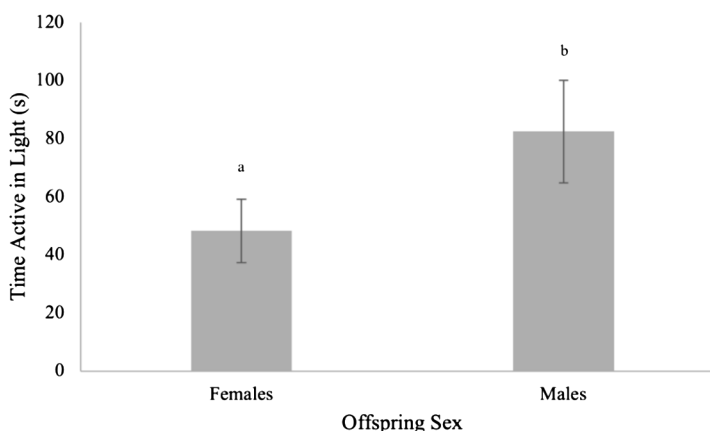
included in the first PCA to generate exploration scores (Table 1). In the light/dark box, the time spent in the light compartment, the time spent active in the light compartment, and the number of crosses made between compartments, were repeatable (Table 1), and were included in the second PCA to generate an anxiety score. None of the PCs from either PCA were significantly correlated with each other (Table A1 in the Appendix). Therefore, they could not be grouped together to generate a single personality score.

### 3.2. Maternal care effects

The time spent active in the light compartment varied significantly between offspring sexes (Table 2), with males spending significantly more time active than females (Figure 2). No other behavioural measure was significantly influenced by any maternal care levels (total, direct or indirect) or offspring sex (Table 2).

### 3.3. Heritability

We found significant heritability for Exploration PC2 (Table 3), and a non-significant positive trend for heritability for Exploration PC1, with offspring from exploratory mothers being more exploratory than offspring from less exploratory mothers (Figure 3). Offspring Anxiety PC was not significantly related to mother Anxiety PC, suggesting that this does not have a heritable



**Figure 2.** The mean time ( $\pm$  SE) spent active (s) in the light compartment of the light/dark box of female and male fawn-footed mosaic tailed rat *Melomys cervinipes* offspring. Different letters indicate significant differences among means.

**Table 3.**

Narrow sense heritability ( $h^2$ ) estimates and statistical outputs of parent–offspring regression models of personality measures in adult fawn-footed mosaic-tailed rats *Melomys cervinipes*.

Personality measure	$h^2 \pm SE$	Statistics	Power	Prop. variation
Exploration PC1	0.33 $\pm$ 0.25	$F_{(1,14)} = 1.75, p = 0.207$	0.99	0.21
Exploration PC2	0.56 $\pm$ 0.22	$F_{(1,14)} = 6.32, p = 0.025^*$	0.54	0.21
Anxiety PC	-0.04 $\pm$ 0.27	$F_{(1,14)} = 0.03, p = 0.875$	0.67	0.21

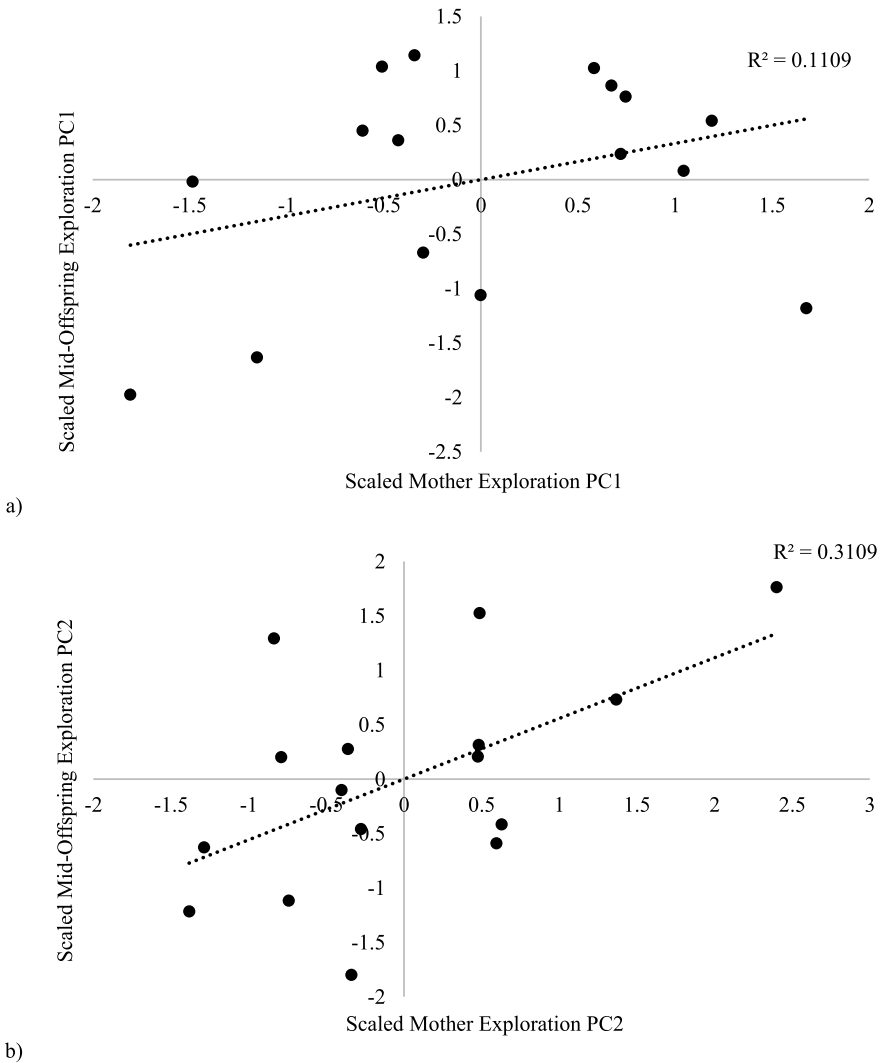
\* Significant result.

component (Table 3). The proportion of variance to the overall variance was approximately 21% for each PC (Table 3).

#### 4. Discussion

In our study, we investigated the genetic and non-genetic maternal effects on adult offspring personality (exploration and anxiety behaviour) in mosaic-tailed rats. We found that the level of maternal care (direct, indirect, or total) received during the early postnatal period did not significantly affect offspring exploration or anxiety behaviour. A previous study also found a lack of maternal care effects on offspring problem solving behaviour in mosaic-tailed rats, possibly because offspring nipple-clinging behaviour results in low variation in maternal care levels between mothers and low variation in the amount of care received between pups (Rowell & Rymer, 2022). A lack of maternal care effects has been found in some rodents that do not nipple-cling. For example, maternal care did not significantly affect offspring behaviour in an activity box or plus maze in laboratory rats (Wöhr & Schwarting, 2008). In this study, we only measured postnatal maternal care; thus, it is possible that offspring behaviour may be affected by prenatal maternal care (Landete-Castillejos et al., 2009) or other factors, such as maternal prenatal diet (e.g., fat content, Johnson et al., 2017) or stress exposure (Enayati et al., 2020), but this remains to be tested. As mosaic-tailed rats experience changes in their exploratory behaviour across development (Rowell & Rymer, 2023), this suggests that these behaviours may be flexible, and less affected by variation in the maternal environment (Cabrera et al., 2021).

As expected, we found that the personality measure Exploration PC 2, which mostly described how individuals explored new spaces, was heritable



**Figure 3.** Parent–offspring regression of (a) Exploration PC1 and (b) Exploration PC2 in fawn-footed mosaic-tailed rats *Melomys cervinipes*.

between mothers and offspring in mosaic-tailed rats. Although, the power estimate for this relationship was only of medium strength, our results are consistent with other studies where exploration behaviour is often found to be heritable, with an average heritability  $h^2$  value of 58% found across studies on various taxa (van Oers et al., 2020). For example, exploration

of a novel environment had an  $h^2$  value of 22–41% in parent–offspring regressions of great tits (Dingemanse et al., 2002). The presence of individual variation (Rowell & Rymer, 2021) in, and heritability of, exploratory behaviour in mosaic-tailed rats suggests that this behaviour may be adaptive and maintained by natural selection (Dingemanse et al., 2002).

However, the other personality scores (Exploration PC 1, how individuals explored novel objects; Anxiety PC, how individuals behaved in a well-lit space) were not significantly heritable, although there was a positive trend in Exploration PC 1. These results suggest that there is limited genetic influence on these behaviours, which has also been found with object exploration in collared flycatchers *Ficedula albicollis* (Morinay et al., 2019). These behaviours are therefore more flexible in mosaic-tailed rats, potentially being influenced by non-genetic developmental effects rather than constrained by direct genetic effects. A previous study found that mosaic-tailed rats changed their exploration of novel objects across their development (Rowell & Rymer, 2023), supporting the behavioural flexibility of exploration in response to novel objects. The flexibility of anxiety-like behaviour has not yet been investigated in mosaic-tailed rats. In other species, behavioural development changes in response to morphology and physiology. For example, lower levels of serotonin during neo-natal development resulted in laboratory rats showing reduced novel object exploration (Rok-Bujko et al., 2012). Furthermore, behaviour can change based on previous experience, as seen with exploration behaviour in a poeciliid fish, *Brachyrhaphis episcopi*, which varied based on previous levels of exposure to predators (Brown et al., 2007). Flexible behaviour may therefore be beneficial to mosaic-tailed rats.

We found that male offspring spent significantly more time active in the light compartment than female offspring, suggesting that male offspring were less anxious. This is not surprising as sex differences in behaviour are relatively common, and other studies have found a relationship between reproductive hormones, particularly testosterone, and the anxiety response. For example, intact male laboratory rats were less anxious (as indicated by a reduced startle response in a light compartment) compared to female rats and castrated males (Toufexis, 2007). A similar relationship between exploratory behaviour and testosterone has previously been found in mosaic-tailed rats, with increased post-stress testosterone concentrations being associated with increased exploration behaviour in males (Turner, 2015). Furthermore, as the sex with the highest parental investment is generally predicted to be more

risk-averse (Palanza, 2001), this could also explain why female mosaic-tailed rats were less active in the light compartment. Future work should investigate the physiological mechanisms underpinning anxiety behaviour in mosaic-tailed rats.

Overall, these results suggest that mothers only have a limited influence on the development of personality in their offspring in mosaic-tailed rats. Postnatal maternal care did not appear to influence personality in mosaic-tailed rat offspring. However, Exploration PC 2 (exploration of new spaces) was constrained to a degree by maternal genetic effects. Anxiety and exploration behaviours in response to novel objects appear to be more flexible than exploration of novel spaces and may be more influenced by an individual's experiences during its lifetime. Mosaic-tailed rats may therefore be able to adjust their behaviour to better exploit novel resources (e.g. new types of food) but may be less flexible in adjusting to variation in spatial environmental conditions.

## Acknowledgements

We would like to thank Skyrail Rainforest Foundation and the Australasian Society for the Study of Animal Behaviour for funding this study. We would also like to thank all the volunteers who assisted in maintaining the captive colony of mosaic-tailed rats. Permission to catch animals was granted by Queensland Parks and Wildlife (permits WISP14530814, WITK14530914, WA0014502 and PTU19-001632). The research adhered to the Australian Code for the Care and Use of Animals for Scientific Purposes (NHMRC 2013). The study was approved by the Animal Ethics Screening Committee of James Cook University (clearance number: A2539).

## References

- Arnaud, C.M., Suzumura, T., Inoue, E., Adams, M.J., Weiss, A. & Inoue-Murayama, M. (2017). Genes, social transmission, but not maternal effects influence responses of wild Japanese macaques (*Macaca fuscata*) to novel-object and novel-food tests. — *Primates* 58: 103-113.
- Baker, S., Chebli, M., Rees, S., LeMarec, N., Godbout, R. & Bielajew, C. (2008). Effects of gestational stress: 1. Evaluation of maternal and juvenile offspring behavior. — *Brain Res.* 1213: 98-110.
- Belgrad, B.A. & Griffen, B.D. (2016). Predator–prey interactions mediated by prey personality and predator hunting mode. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 283: 20160408.



- Bell, A.M. & Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). — Ecol. Lett. 10: 828-834.
- Both, C., Dingemans, N.J., Drent, P.J. & Tinbergen, J.M. (2005). Pairs of extreme avian personalities have highest reproductive success. — J. Anim. Ecol. 74: 667-674.
- Bredy, T.W., Humpartzoomian, R.A., Cain, D.P. & Meaney, M.J. (2003). The influence of maternal care and environmental enrichment on hippocampal development and function in the rat. — Neuroscience 118: 571-576.
- Briffa, M. & Greenaway, J. (2011). High in situ repeatability of behaviour indicates animal personality in the beadlet anemone *Actinia equina* (Cnidaria). — PLOS ONE 6: e21963.
- Briffa, M., Sneddon, L.U. & Wilson, A.J. (2015). Animal personality as a cause and consequence of contest behaviour. — Biol. Lett. 11: 20141007.
- Brown, C., Burgess, F. & Braithwaite, V.A. (2007). Heritable and experiential effects on boldness in a tropical poeciliid. — Behav. Ecol. Sociobiol. 62: 237-243.
- Cabrera, D., Nilsson, J.R. & Griffen, B.D. (2021). The development of animal personality across ontogeny: a cross-species review. — Anim. Behav. 173: 137-144.
- Caldji, C., Tannenbaum, B., Sharma, S., Francis, D., Plotsky, P.M. & Meaney, M.J. (1998). Maternal care during infancy regulates the development of neural systems mediating the expression of fearfulness in the rat. — Proc. Natl Acad. Sci. USA 95: 5335-5340.
- Callaway, W.A., Turner, A.A., Croshaw, O.B., Ferguson, J.A., Julson, Z.J.-N., Volp, T.M., Kerr, S.E. & Rymer, T.L. (2018). *Melomys cervinipes* (Rodentia: Muridae). — Mamm. Species 50: 134-147.
- Carlson, B.E. & Tetzlaff, S.J. (2020). Long-term behavioral repeatability in wild adult and captive juvenile turtles (*Terrapene carolina*): implications for personality development. — Ethology 126: 668-678.
- Carter, A.J., Marshall, H.H., Heinsohn, R. & Cowlshaw, G. (2014). Personality predicts the propensity for social learning in a wild primate. — PeerJ 2: e283.
- Champagne, F.A. (2008). Epigenetic mechanisms and the transgenerational effects of maternal care. — Front. Neuroendocrinol. 29: 386-397.
- Cheng, K.F. & Wu, J.W. (1994). Adjusted least squares estimates for the scaled regression coefficients with censored data. — J. Am. Stat. Ass. 89: 1483-1491.
- Cribari-Neto, F. & Zeileis, A. (2010). Beta regression in R. — J. Stat. Softw. 34: 1-24.
- Delignette-Muller, M.L. & Dutang, C. (2015). *fitdistrplus*: an R package for fitting distributions. — J. Stat. Softw. 64: 1-34.
- Dingemans, N.J. & Wright, J. (2020). Criteria for acceptable studies of animal personality and behavioural syndromes. — Ethology 126: 865-869.
- Dingemans, N.J., Both, C., Drent, P.J., van Oers, K. & van Noordwijk, A.J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. — Anim. Behav. 64: 929-938.
- Dudley, J.W. & Moll, R.H. (1969). Interpretation and use of estimates of heritability and genetic variances in plant breeding 1. — Crop Sci. 9: 257-262.
- Enayati, M., Mosafari, B., Homborg, J.R., Diniz, D.M. & Salari, A.-A. (2020). Prenatal maternal stress alters depression-related symptoms in a strain- and sex-dependent manner in rodent offspring. — Life Sci. 251: 117597.

- Favati, A., Zidar, J., Thorpe, H., Jensen, P. & Løvlie, H. (2016). The ontogeny of personality traits in the red junglefowl, *Gallus gallus*. — *Behav. Ecol.* 27: 484-493.
- Friard, O. & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. — *Methods Ecol. Evol.* 7: 1325-1330.
- Groothuis, T.G.G. & Trillmich, F. (2011). Unfolding personalities: the importance of studying ontogeny. — *Dev. Psychobiol.* 53: 641-655.
- Haldane, J.B.S. (1996). The negative heritability of neonatal jaundice\*. — *Ann. Hum. Genet.* 60: 3-5.
- Han, C.S. & Dingemanse, N.J. (2015). Effect of diet on the structure of animal personality. — *Front. Zool.* 12: S5.
- Hascoët, M., Bourin, M. & Dhonnchadha, B.Á.N. (2001). The mouse light-dark paradigm: a review. — *Prog. Neuropsychopharmacol. Biol. Psychiatr.* 25: 141-166.
- Johnson, S.A., Javurek, A.B., Painter, M.S., Murphy, C.R., Conard, C.M., Gant, K.L., Howald, E.C., Ellersieck, M.R., Wiedmeyer, C.E., Vieira-Potter, V.J. & Rosenfeld, C.S. (2017). Effects of a maternal high-fat diet on offspring behavioral and metabolic parameters in a rodent model. — *J. Dev. Orig. Health Dis.* 8: 75-88.
- Keller, L.F., Grant, P.R., Grant, B.R. & Petren, K. (2001). Heritability of morphological traits in Darwin's finches: misidentified paternity and maternal effects. — *Heredity* 87: 325-336.
- Landete-Castillejos, T., García, A., Carrión, D., Estevez, J.A., Ceacero, F., Gaspar-López, E. & Gallego, L. (2009). Age-related body weight constraints on prenatal and milk provisioning in Iberian red deer (*Cervus elaphus hispanicus*) affect allocation of maternal resources. — *Theriogenology* 71: 400-407.
- Lenth, R., Singmann, H., Love, J., Buerkner, P. & Herve, M. (2020). Package "emmeans". Available online at <https://cran.r-project.org/web/packages/emmeans/index.html>.
- Lynn, D.A. & Brown, G.R. (2009). The ontogeny of exploratory behaviour in male and female adolescent rats (*Rattus norvegicus*). — *Dev. Psychobiol.* 51: 513-520.
- Mackay, M.K. & Pillay, N. (2021). Environmental correlates of exploratory behavior and anxiety in three African striped mouse (*Rhabdomys*) taxa occurring in different habitats and contexts. — *J. Comp. Psychol.* 135: 304.
- Matzel, L.D., Bendorath, S., Herzfeld, M., Crawford, D.W. & Sauce, B. (2019). Mouse twins separated when young: a history of exploration doubles the heritability of boldness and differentially affects the heritability of measures of learning. — *Intelligence* 74: 34-42.
- Moore, L.A., Burnett, S. & van Dyck, S. (2008). Fawn-footed melomys. — In: *The mammals of Australia*, 3rd edn. (van Dyck, S. & Strahan, R., eds). Reed New Holland, Sydney, NSW, p. 671-672.
- Morinay, J., Daniel, G., Gustafsson, L. & Doligez, B. (2019). No evidence for behavioural syndrome and genetic basis for three personality traits in a wild bird population. — *Anim. Behav.* 153: 69-82.
- Nel, K., Rimbach, R. & Pillay, N. (2015). Dietary protein influences the life-history characteristics across generations in the African striped mouse *Rhabdomys*. — *J. Exp. Zool. Part Ecol. Genet. Physiol.* 323: 97-108.
- Palanza, P. (2001). Animal models of anxiety and depression: how are females different? — *Neurosci. Biobehav. Rev.* 25: 219-233.

- Paullig, K., Wilson, D. & Rymer, T.L. (2019). Olfactory recognition of snake cues by fawn-footed mosaic-tailed rats *Melomys cervinipes*. — Behaviour 156: 1235-1253.
- Quinn, J.L., Patrick, S.C., Bouwhuis, S., Wilkin, T.A. & Sheldon, B.C. (2009). Heterogeneous selection on a heritable temperament trait in a variable environment. — J. Anim. Ecol. 78: 1203-1215.
- R Core Team (2020). R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna.
- Rader, R. & Krockenberger, A. (2006). Three-dimensional use of space by a tropical rainforest rodent, *Melomys cervinipes*, and its implications for foraging and home-range size. — Wildl. Res. 33: 577-582.
- Robinson, H.F., Comstock, R.E. & Harvey, P.H. (1955). Genetic variances in open pollinated varieties of corn. — Genetics 40: 45.
- Rok-Bujko, P., Krząścik, P., Szyndler, J., Kostowski, W. & Stefański, R. (2012). The influence of neonatal serotonin depletion on emotional and exploratory behaviours in rats. — Behav. Brain Res. 226: 87-95.
- Rowell, M.K. & Rymer, T.L. (2020a). Growth and behavioural development of the fawn-footed mosaic-tailed rat (*Melomys cervinipes*). — Aust. Mammal. 43: 330-334.
- Rowell, M.K. & Rymer, T.L. (2020b). Innovation in a native Australian rodent, the fawn-footed mosaic-tailed rat (*Melomys cervinipes*). — Anim. Cogn. 23: 301-310.
- Rowell, M.K. & Rymer, T.L. (2021). Exploration influences problem solving in the fawn-footed mosaic-tailed rat (*Melomys cervinipes*). — Ethology 127: 592-604.
- Rowell, M.K. & Rymer, T.L. (2022). Problem solving in fawn-footed mosaic-tailed rats *Melomys cervinipes* is not significantly influenced by maternal care or genetic effects. — J. Exp. Zool. Part Ecol. Integr. Physiol. 337: 802-811.
- Rowell, M.K. & Rymer, T.L. (2023). The consistency of exploration behaviours across life stages in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*. — Behav. Process. 207: 104857.
- Sih, A., Bell, A.M., Johnson, J.C. & Ziemba, R.E. (2004). Behavioral syndromes: an integrative overview. — Q. Rev. Biol. 79: 241-277.
- Stoffel, M.A., Nakagawa, S. & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. — Methods Ecol. Evol. 8: 1639-1644.
- Tapocik, J.D., Schank, J.R., Mitchell, J.R., Damazdic, R., Mayo, C.L., Brady, D., Pincus, A.B., King, C.E., Heilig, M. & Elmer, G.I. (2021). Live predator stress in adolescence results in distinct adult behavioral consequences and dorsal diencephalic brain activation patterns. — Behav. Brain Res. 400: 113028.
- Taylor, R.W., Boon, A.K., Dantzer, B., Réale, D., Humphries, M.M., Boutin, S., Gorrell, J.C., Coltman, D.W. & McAdam, A.G. (2012). Low heritabilities, but genetic and maternal correlations between red squirrel behaviours. — J. Evol. Biol. 25: 614-624.
- Tinbergen, N. (1963). On aims and methods of ethology. — Ethology 20: 410-433.
- Toufexis, D. (2007). Region- and sex-specific modulation of anxiety behaviours in the rat. — J. Neuroendocrinol. 19: 461-473.

- Turner, A.A. (2015). Do *Melomys cervinipes* have personalities? Variations in behaviour and hormones in a tropical rainforest rodent. — Honours thesis, James Cook University.
- van Oers, K., Sepers, B., Sies, W., Gawehns, F., Verhoeven, K.J.F. & Laine, V.N. (2020). Epigenetics of animal personality: DNA methylation cannot explain the heritability of exploratory behavior in a songbird. — *Integr. Comp. Biol.* 60: 1517-1530.
- Vanden Broecke, B., Bongers, A., Mnyone, L., Matthysen, E. & Leirs, H. (2021). Nonlinear maternal effects on personality in a rodent species with fluctuating densities. — *Curr. Zool.* 67: 1-9.
- Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y. & Zemla, J. (2017). Package “corrplot”. — *Statistician* 56: 316-324.
- Williamson, D.E., Coleman, K., Bacanu, S.-A., Devlin, B.J., Rogers, J., Ryan, N.D. & Cameron, J.L. (2003). Heritability of fearful-anxious endophenotypes in infant rhesus macaques: a preliminary report. — *Biol. Psychiatr.* 53: 284-291.
- Wöhr, M. & Schwarting, R.K.W. (2008). Maternal care, isolation-induced infant ultrasonic calling, and their relations to adult anxiety-related behavior in the rat. — *Behav. Neurosci.* 122: 310-330.
- Wood, D.H. (1971). The ecology of *Rattus fuscipes* and *Melomys cervinipes* (Rodentia: Muridae) in a south-east Queensland rain forest. — *Aust. J. Zool.* 19: 371-392.
- Wray, N. & Visscher, P. (2008). Estimating trait heritability. — *Nature Educ.* 1: 29.
- Yang, N. & Wu, C. (1993). Unequal genetic contributions of parents to offsprings and their optimal control. — *Acta Genet. Sin.* 20: 294-299. (in Chinese).
- Yom-Tov, Y. (1985). The reproductive rates of Australian rodents. — *Oecologia* 66: 250-255.
- Zeileis, A. & Hothorn, T. (2002). Diagnostic checking in regression relationships. — *R News* 2: 7-10.

**Table A1.**

The statistical outputs of regressions between principal components (PC) generated from fawn-footed mosaic-tailed rat *Melomys cervinipes* personality principal component analyses (PCAs).

PC	Variable PC	Statistical output
Exploration PC1	Exploration PC2	$F_{(1,20)} < 0.01, p = 0.991$
	Anxiety PC	$F_{(1,20)} = 0.88, p = 0.353$
Exploration PC2	Exploration PC1	$F_{(1,20)} < 0.01, p = 0.991$
	Anxiety PC	$F_{(1,20)} = 0.82, p = 0.370$
Anxiety PC	Exploration PC1	$F_{(1,20)} = 1.12, p = 0.300$
	Exploration PC2	$F_{(1,20)} = 0.36, p = 0.553$