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# Habitat and sex effects on behaviour in fawn-footed mosaic-tailed rats (*Melomys cervinipes*)

Habitat complexity and *M. cervinipes* behaviour

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**Abstract.** Habitat complexity reflects resource availability and predation pressure, factors that influence behaviour. We investigated whether exploratory behaviour and activity varied in fawn-footed mosaic-tailed rats (*Melomys cervinipes*) from two habitats that were categorised differently based on vegetation. We conducted vegetation surveys to determine structural complexity and vegetation cover, confirming that an abandoned hoop-pine (*Araucaria cunninghami*) plantation forest was structurally less complex, with lower vegetation cover, than a variable secondary rainforest. We then tested mosaic-tailed rats from both sites in four behavioural tests designed to assess exploratory and activity behaviours (open field, novel object, light-dark box, acoustic startle), predicting that rats from the less structurally complex habitat would be less exploratory, and show lower activity. Our results provide some evidence for a context-specific trade-off between exploratory behaviour and predation risk in rats from the abandoned hoop pine plantation, as rats were less active, and showed a freezing strategy in the light-dark box. We also found context-specific sex differences in behaviour in response to a novel object and sound. Our results suggest that small-scale variation in habitat structure and complexity, as well as sex differences, are associated with variation in behaviour, most likely through effects on resource availability and/or predation risk.

**Additional keywords:** activity, exploratory behaviour, habitat complexity, native rodent, vegetation cover

## Introduction

Habitat complexity refers to the level of variance in vegetation structure and cover over spatial and temporal scales (Wiens 2000). Environments with low complexity are more homogeneous, with resources being evenly distributed and constant over space and/or time, while environments with high complexity are more heterogeneous, with resources varying spatially and/or temporally (Rymer *et al.* 2013). In less complex environments, perceived predation risk is often higher due to lower vegetation cover (Sutherland and Dickman 1999), although this may be species-specific. Given this variability in habitats of differing complexity, differences in resource distribution and levels of predation risk will drive selection for differences in exploratory behaviour and activity (Marín *et al.* 2003).

Exploratory behaviour involves gathering information about an environment (Mettke-Hofmann *et al.* 2002). During exploration, information is collected about the distribution and abundance of profitable feeding sites, refuges and escape routes, and potential mates (Boon *et al.* 2008). In less complex, more homogenous habitats, individuals must trade off the need to gain access to resources against the risk of predation (Marín *et al.* 2003). Individuals from these habitats tend to move faster and more directly between resource patches, and are less exploratory, minimising time exposed to predators (Schultz *et al.* 2012). However, resources may be less abundant, promoting competition, with higher fitness generally achieved by larger, more aggressive individuals (Glazier and Eckert 2002). In complex environments, resources may be unpredictably distributed spatially and temporally, while higher vegetation cover mitigates perceived predation risk (Rader and Krockenberger 2006).

While ecological factors may affect exploratory behaviour, they may also affect activity. When animals are directly exposed to predators, they may respond in a number of ways. Initially, they might avoid detection by remaining still (freezing; Edut and Eilam 2003), relying on camouflage (e.g. lesser Egyptian jerboa (*Jaculus jaculus*), Hendrie *et al.* 1998). Alternatively, they might choose to flee (flight; Edut and Eilam 2003), relying on speed to access a refuge (e.g. spiny mice (*Acomys cahirinus*), Ilany and Eilam 2008). Finally, if they are unable to avoid or evade a predator, they might be forced to defend themselves (fight; Edut and Eilam 2003). The decision regarding which behaviour should be used depends on a variety of factors, such as the availability of cover and distance to a refuge. Cover provides protection from predation during foraging (Lagos *et a*l. 1995; Orrock *et al.* 2004), and a place of refuge during times of inactivity (Cassini and Galante 1992). However, cover can also impede movement and obstruct locomotory ability (Schooley *et al.* 1996). Consequently, in less complex, homogeneous environments, with lower cover and higher perceived predation risk (Sutherland and Dickman 1999), an animal may be more likely to freeze in response to perceived predation risk because they would likely would have to forage away from cover (Edut and Eilam 2003). In addition, animals from these environments might be less active overall to reduce exposure to predators. Animals from complex, heterogeneous habitats with more cover may consequently be more willing to flee because cover is readily available, and they might be more active overall in these environments due to lower perceived predation risk (Wilson and Godin 2009).

While the environment and an individual's experiences influence behaviour, behaviour can also be affected by an individual's sex. Males are often more active and exploratory than females (e.g. zebra finches (*Taenipygia guttata*), Schuett and Dall 2009; three-spined sticklebacks (*Gasterosteus aculeatus*), King *et al.* 2013; Middle East blind mole rats (*Spalax ehrenbergi*), Heth *et al.* 1987). Similarly, males may respond differently to perceived threats. For example, male and female fawn-footed mosaic-tailed rats (*Melomys cervinipes*) respond differently to predator odour cues, with males being less neophobic (fear of novelty; Barnett 1958) than females (Paulling *et al.* 2019). These differences could be modulated by sex-specific differences in gonadal hormone expression (Beatty 1979), or could be a consequence of the individual's development. For example, female spiny mouse (*Acomys cahirinus*) pups were more exploratory than males, most likely because mothers directed more parental care towards sons, and physically inhibited sons from exploring, indicating maternal effects on the development of exploratory behaviour (Birke and Sadler 1991).

We investigated whether behaviours associated with exploratory behaviour and activity varied in fawn-footed mosaic-tailed rats from two habitats. Mosaic-tailed rats are medium-sized (72.9 ± 12 g; Callaway *et al.* 2018) murid rodents (Wood 1971) endemic to forest habitats along the eastern coast of Australia (Callaway *et al.* 2018). They also occur in disturbed forest edges (Laurance 1994) and open environments, such as open shrubland (Woodall 1989). They are nocturnal, with some variations in activity depending on moonlight and time of year (Wood 1971), and use olfactory cues to identify and avoid predators (Hayes *et al.* 2006; Paulling *et al.* 2019). Natural predators include feral cats (*Felis catus*), dingos (*Canis lupus dingo*), spotted tail (*Dasyurus maculatus*) and northern quolls (*D. hallucatus*), sooty (*Tyto tenebricosa*) and lesser sooty owls (*T. multipunctata*), southern boobooks (*Ninox boobook*), Amethystine (*Morelia amethistina*), carpet (*M. spilota variegata*) and spotted pythons (*Antaresia maculosa*) and red-bellied black snakes (*Pseudechis porphyriacus*; Callaway *et al.* 2018).

Mosaic-tailed rats are scansorial (Watts and Aslin 1981), favouring trees with attached vegetation that aids climbing (Wood 1971). Much of the night is spent actively foraging, and mosaic-tailed rats use the arboreal environment extensively for this purpose, although they also forage on the ground (Rader and Krockenberger 2006). They are generalists, feeding primarily on foliage and vegetation, but will eat fruits, nuts, seeds, fungi and flowers, and may eat insects if necessary (Callaway *et al.* 2018). Interestingly, mosaic-tailed rats can also innovate, solving novel problems to access resources (Rowell and Rymer 2020).

We selected two habitats that were located in close spatial proximity (Smithfield, Cairns) but were classified differently based on vegetation composition and underlying geological structure (WTMA 2009), and appeared to differ in complexity. We first conducted vegetation surveys to confirm structural complexity differences. We then predicted that mosaic-tailed rats from the less structurally complex habitat would be less exploratory, and show lower activity, due to higher perceived predation risk (Sinclair 1979), and a need to trade off foraging against predation risk (Brown 1999). We made no *a priori* predictions of sex differences in behaviour because other studies suggest that strain/species differences may occur (Küçük and Gölgeli 2007).

## Materials and methods

### *Study Sites*

The mosaic-tailed rats originated from two sites on the James Cook University (JCU) Cairns Campus, Australia, and surrounds. The first site (16° 49' S, 145° 40' E) was a *complex notophyll vine forest on moist foothills and uplands on metamorphics and granites* (7c; WTMA 2009), designated HP. At this site, we focused habitat surveys and mosaic-tailed rat collection in an abandoned hoop pine (*Araucaria cunninghamii*) plantation undergoing natural revegetation. The second site (16° 49' S, 145° 41' E) was a *variable rainforest secondary successional forest complex on alluvium* (61a; WTMA 2009), designated RF. At this site, we focused habitat surveys and mosaic-tailed rat collection along a small creek (Atika Creek).

*Habitat Complexity*

Habitat complexity was assessed at each site based on Coops and Catling (2000) and Cousin and Phillips (2008). We also included other elements (presence of vines and different substrates) that contribute to the complexity of forest environments.

Five 10 x 10m quadrats were randomly located in each habitat. For each quadrat, we recorded structural complexity in five vertically defined strata: 1) ground level; 2) 0–2 m above ground level; 3) 2–10 m; 4) 10–30 m; and 5) > 30 m. At ground level, we counted the number of substrate types (e.g. rocks, grass; Table S1). We divided the number of substrates within a quadrat by the total number of substrates detected across all quadrats to give a relative measure of substrate diversity (from 0 to 1). For each vertical stratum above ground level, we recorded number of trees (abundance), number of tree species (diversity), number of vines, and number of vine species (Table S1). Each of the four measurements within each quadrat was then divided by the maximum value detected across all quadrats surveyed (assuming that this was representative of the full potential structural diversity available in this site) for that measure, giving four relative abundance or diversity scores. We then calculated the average scores for all five strata combined to get a single measure of stratum complexity (from 0 to 1, where 0 = lowest complexity and 1 = greatest complexity). Finally, to assess the relative level of cover available to an animal foraging on the forest floor (0–2 m), we summed the number of trees and vines measured for each habitat, and then divided by the total area measured for each habitat.

*Subjects*

40 mosaic-tailed rats (HP: males: n = 11 males; females: n = 9; RF: males: n = 11; females: n = 9) were live trapped between April and September 2014 using Elliot traps baited with balls of peanut butter, vanilla essence, honey and oats. Only adult males and adult, obviously non-pregnant and non-lactating females were used to reduce potential hormonal effects on behaviour (Picazo and Fernández-Guasti 1993; Chen *et al.* 2009). Although we were systematic in our placement of traps (one week in the RF

site, followed by the next trapping week in the HP site), we were more successful in the RF site during the first three months. In order to balance the sample sizes between sites and sexes, we increased trapping effort in the HP site during the last three months. Consequently, variations in the abiotic environment could also contribute to any differences in behaviour observed. Therefore, we obtained the minimum and maximum temperatures, humidity and rainfall from the Bureau of Meteorology website (www.bom.gov.au), cloud cover from the Weather Underground website (https://www.wunderground.com) and moon phase from the Universe Today website (https://www.universetoday.com) for each individual for each day kept in captivity.

We transferred individuals from the site of capture in cotton bags to glass holding tanks (61 x 38 x 30 cm) in the Animal Behaviour Laboratory on the JCU Cairns campus. Individuals were housed alone under partially controlled environmental conditions (22-26 °C; 50-65% relative humidity; natural ambient lighting). The floor of each tank was covered with a layer of coarse wood shavings (approx. 2 cm deep) for bedding. A cylindrical plastic nest tube (10 x 21 cm), a piece of paper towel and a handful of leaves collected from the capture site were provided for nesting. A cardboard roll was provided for enrichment. Each individual received ± 4 g of sunflower seeds and ± 5 g of apple daily. Seeds were sprinkled around the cage to stimulate natural foraging behaviour. Water was available *ad libitum*.

Individuals remained in their home tanks for four days to acclimate to captivity before behavioural tests began (see below). After behavioural tests were complete, a small patch of fur was cut from above the left hind leg to enable identification of recaptured animals, and individuals were released at the site of capture at dusk.

### *Behavioural Tests*

As mosaic-tailed rats are nocturnal (Wood 1971), behavioural tests were video-recorded in the absence of observers using a Panasonic HC v 110 camera from above, under red light (which does not influence mosaic-tailed rat behaviour; Paulling *et al.* 2019) and during the peak activity period between 22h00 – 00h00 (Callaway *et al.* 2018). Testing arenas were washed with warm soapy water, wiped with ethanol and left to air-dry following individual testing.

We used four tests, frequently used for other rodent species (e.g. Rymer and Pillay 2012), to assess exploratory behaviour and activity in mosaic-tailed rats. Mosaic-tailed rats experienced the open field test first, followed immediately by the novel object test.

Individuals were then returned to their home tanks after testing, and rested for 24 hours before the next test. The following night, individuals experienced the light-dark box test, which was followed immediately by the acoustic startle test. Individuals were then returned to their home tanks after testing, and released the following day at dusk.

### Open field

The open field test exploits the natural aversion of rodents to open areas (Carola *et al.* 2002) and can be used to assess general locomotor activity and willingness to explore an environment (Gould *et al.* 2009). The open field arena consisted of a glass tank (61 x 38 x 30 cm) with a ± 2 cm deep layer of coarse wood shavings. We placed an individual in the centre of the tank and allowed it to acclimate for five minutes (as per Rymer and Pillay 2012). Behaviour was then recorded for 10 minutes. We measured several behaviours that were mutually exclusive (i.e. an animal could not be exploring and inactive at the same time): the duration of time spent exploring (moving into the centre of the open field), time spent thigmotactic (wall-hugging), time spent rearing on the hind legs (freely or against the sides) and time spent inactive (sitting, without obvious movement, in a fixed position). We could not distinguish between active vigilance when inactive and general non-activity without vigilance when animals were inactive due to the red light and the distance from which recording occurred.

### Novel object

The novel object test assesses an individual’s response to novelty (neophobia or neophilia; Ennaceur *et al.* 2009). This test occurred immediately after the open field test, in the same arena. A novel object (purple rubber Smiggle© horse; base 4.2 cm, height 5 cm) was placed in the centre of the arena, and behaviour was video-recorded for a further 10 minutes. In addition to the behaviours measured in the open field, we also measured the latency to approach the novel object (measured from the start of the novel object test to the time the individual approached within 1 cm of the novel object) and duration of time sniffing the object. A longer latency to approach the object, and less time spent sniffing the object, are indicators of neophobia (Ennaceur *et al.* 2009). All behaviours, barring latency to approach the object, are mutually exclusive.

### Light-dark box

The light-dark box test is based on a rodent's innate aversion to brightly lit areas (Bourin and Hascoët 2003). The light-dark box consisted of a glass tank (61 x 38 x 30 cm), separated into two equal compartments with a plastic barrier, with an opening (10 x 10 cm) that allowed the animal to move between the compartments. One half of the tank, and the divider, was painted black (dark compartment), while the other half remained clear (light compartment). A rat was placed in the light compartment, facing away from the opening. Behaviour was video-recorded for five minutes, as pilot tests of 10 minutes showed that individuals either moved into the dark compartment and stayed there or stopped moving in the light compartment within 5 minutes. We did not use white light to illuminate the light compartment, but used the light entering from the laboratory window to maintain a more natural setting. For nocturnal rodents, greater illumination of an environment by moonlight increases relative predation risk (Bengsen *et al.* 2010). Consequently, we are mindful that there could have been some variation in natural illumination due to cloud cover and moon phase, which we controlled for statistically (see below). We measured the latency to enter the dark compartment, the latency to return to the light compartment, the number of transitions between compartments (frequency, which is discrete, rather than continuous), the duration of time spent in the dark compartment, and the time spent inactive, exploring and engaged in thigmotaxis in the light compartment only. We did not record rearing behaviour because it was very rare in this test (< 1% of behaviours), most likely because the dark compartment represented a refuge. All behaviours, barring latencies and frequency of transitions, are mutually exclusive.

### Acoustic startle response

The acoustic startle response test is used to assess an individual's response to a novel acoustic stress, which could indicate a predator in the environment (Valsamis and Schmid 2011). After the light-dark box test, we waited a maximum of five minutes for the individual to re-enter the light compartment if it was in the dark. We did not forcibly remove individuals from the dark compartment to minimise stress and to maintain ecological validity. Once it had moved into the light, or if the individual was already in the light compartment, we played the 'alarm' sound on an iPhone 5 beside the tank (volume full; duration for three 'rings'). We recorded behaviours described previously for the light-dark box test following the startle. If the individual did not return to the light compartment after the light-dark box test, it was marked as a non-participant and returned to its home tank.

*Statistical analyses*

Statistical analyses were conducted using RStudio (version 1.0.153; https://www.rproject.org; R version 3.5.0, https://cran.rstudio.com). The model-level significance was set at α = 0.05. Data were tested for normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test) prior to analyses. Data were transformed where necessary (Table 1). Data for one RF male from the novel object test, and a different RF male from the light-dark box test, were excluded due to camera failure. Only 22 individuals (5 RF; 17 HP) re-entered the light compartment to participate in the acoustic startle test.

For the different abiotic factors, in order to reduce the number of predictors, we ran a principal components analysis (PCA; corrplot package, Wei *et al.* 2017) including the continuous variables of average minimum and maximum temperatures, humidity and rainfall (calculated over the testing period of each individual). We only included a principal component (PC) in the final analyses if the eigen value was above 1, and we only included principle components that explained at least 70% of the variance (alone or combined).

We used t-tests to first assess whether the two sites differed in complexity and cover. We also used t-tests to assess whether body mass differed between sites and sexes, as preliminary data suggested this might be the case. In order to generate a single behavioural score for each individual within each test, we ran separate PCAs including all behaviours within each test. We first log-transformed number of transitions in the light-dark box and acoustic startle tests as PCAs are designed to compute continuous variables (Kolenikov and Angeles 2004). Again, for each test, we only included a PC in the final analyses if the eigen value was above 1, and we only included PCs that explained at least 70% of the variance (alone or combined).

We then ran separate linear or general models (lmerTest package, Kuznetsova *et al.* 2020) to assess whether PC behavioural scores within each test were first influenced by sex and site (fixed factors), and body mass (continuous predictor). We also included the interactions between site, sex and body mass because t-tests indicated differences between sites and sexes (see Results). We then ran a second set of models to assess whether the abiotic factors (PC weather scores as continuous predictors, and cloud cover and moon phase as categorical predictors) affected behaviour. Because negative binomial models are unable to deal with negative values (which arise from the PCA), to transform PC variables, we scaled the variables as necessary (Table 1).

*Ethical note*

Mosaic-tailed rats were observed daily, and weighed on capture and before release to assess health. Individuals were held for a maximum of one week before being released at their site of capture. All animals gained weight in captivity. Experimental procedures had no noticeable effects on the welfare of mosaic-tailed rats. The study complied with the Australian Code for the Care and Use of Animals for Scientific Purposes (NHMRC). Permission to catch and release animals was granted by Queensland Parks and Wildlife (permit numbers WITK14530914 and WISP14530814). The study was approved by the Animal Ethics Screening Committee of James Cook University (clearance number: A2020).

## Results

The RF site was significantly more complex (t-test: $t_{7.79} = -5.36$, $P < 0.001$; Fig. 1a), and had greater cover ($t_{4.21} = -3.02$, $P = 0.037$; Fig. 1b) than the HP site. Individuals from the RF site weighed significantly less than individuals from the HP site ($t_{33.82} = 4.91$, $P < 0.001$), weighting 15.1 g less on average. In addition, males were significantly heavier than females ($t_{33.82} = -3.20$, $P = 0.003$), regardless of site, weighing 10.8 g more on average.

For the abiotic factors, the first and second principal components (PCs) collectively explained 87% of the variance (Table S2). For PC1 (hereafter PC_Moisture), humidity contributed 38% to the variance, the minimum temperature contributed 32% and rainfall contributed 28% (collectively 98%). All were positively correlated (i.e. the colder it was, the drier and less humid; Table S3). Because the maximum temperature contributed 90% to the variance of PC2, we elected to treat this abiotic factor independently.

### Open field

In the open field test, site, the first two PCs collectively explained 79% of the variance (Table S2). For PC1 (hereafter PC_Active), thigmotaxis and rearing collectively contributed 48% to the variance, and inactivity also contributed 48% (collectively 95%). There was a positive correlation between duration of thigmotaxis and rearing, and a negative correlation between duration of inactivity and both thigmotaxis and rearing (Table S3). Individuals that spent more time engaged in thigmotaxis and rearing were also more active. While site, mass, sex, and the interactions between site * sex, mass * sex and site * mass * sex did not affect PC_Active scores (Table 1), there was a significant interaction between mass and site (Table 1). Rats from the HP site that were heavier on average, and rats from the RF site that were lighter on average, were more active than heavier rats from the RF site (Fig. 2). None of the abiotic factors affected PC_Active scores (Table 1). Because duration of exploration contributed 81% to the variance of PC2, we elected to treat this behaviour independently. There were no effects of any factors on exploratory behaviour (Table 1).

### Novel object

In the novel object test, the first PC (hereafter PC_Active) explained 76% of the variance (Table S2). Inactivity contributed 22% to the variance, latency to approach the novel object contributed 21%, thigmotaxis contributed 19% and rearing contributed 18% (collectively 80%). There was a positive correlation between duration of inactivity and latency to approach the novel object, with individuals that were more active approaching the novel object faster (Table S3). There was also a positive correlation between thigmotaxis and rearing, with individuals that engaged in more thigmotaxis also rearing more (Table S3). Inactivity/latency was also negatively correlated with thigmotaxis/rearing (Table S3). Site, mass, sex and their interactions, and the measured abiotic factors did not affect PC_Active scores (Table 1). Because duration of sniffing the novel object contributed 75% to the variance of PC2, we elected to treat this behaviour independently. Sex had a significant effect on duration of sniffing of the novel object (Table 1), with females sniffing the object 2.7x more than males (Fig. 3). No other factors affected duration of sniffing of the novel object (Table 1).

### Light-dark box

In the light-dark box test, the first three PCs collectively explained 92% of the variance (Table S2). For PC1 (hereafter PC_Active), inactivity and latency to enter the dark compartment collectively contributed 50% to the variance, while the number of transitions contributed 20% (collectively 70%). There was a positive correlation between duration of inactivity and latency to enter the dark compartment, with rats that were more active entering the dark compartment faster than rats that were less active (Table S3). There was also a negative correlation between inactivity/latency and the number of transitions, with rats that were less active or who took longer to enter the dark compartment making fewer transitions (Table S3). Site had a significant effect on both PC_Active scores (Table 1). Rats from the HP site were less active, took longer to enter the dark compartment, and made fewer transitions than rats from the RF site, which tended to flee and spend more time in the dark compartment (Fig. 4). No other factors affected PC_Active scores (Table 1).

For PC2 (hereafter PC_Shy), duration of time spent in the dark compartment contributed 31% to the variance, latency to re-enter the light compartment contributed 26% and duration of thigmotaxis contributed 22% (collectively 78%).The duration of time spent in the dark compartment was positively correlated with the latency to re-enter the light compartment (Table S3). Rats that spent more time in the dark took longer to re-enter the light compartment. In contrast, the latency to re-enter the light compartment was negatively correlated with the duration of thigmotaxis (Table S3). Rats that took longer to re-enter the light compartment were also less thigmotactic. The duration of time spent in the dark compartment was not correlated with the duration of thigmotaxis (Table S3), and pulled in opposite directions in the PCA. Site was a near significant predictor of PC_Shy scores (Table 1), as rats from the RF site spent 2.05 x more time in the dark compartment, and were 3.86 x less thigmotactic than rats from the HP site. No other factors or their interactions affected PC_Shy scores (Table 1).

For PC3 (hereafter PC_Explore), the duration of exploration contributed 58% to the variance, while the duration of thigmotaxis contributed 37% (collectively 95%). These behaviours were not correlated (Table S3) and could not be performed at the same time, hence they pulled in opposite directions in the PCA. Site had a significant effect on PC_Explore scores (Table 1). When in the light compartment, rats from the HP site were more thigmotactic than rats from the RF site, which spent more time exploring (Fig. 5). Interestingly, the maximum temperature also affected PC_Explore scores, with maximum temperatures cooler than 27 °C associated with lower exploration and higher thigmotactic behaviour (Table 1). No other factors or their interactions affected PC_Explore scores (Table 1).

Acoustic startle response

In the acoustic startle test, the first three PCs collectively explained 96% of the variance (Table S2). For PC1 (hereafter PC_Active), duration of inactivity and latency to enter the dark compartment each contributed 21% to the variance, the number of transitions contributed 19% and the latency to re-enter the light compartment contributed 17% (collectively 77%). Duration of inactivity was positively correlated with the latency to enter the dark compartment and latency to re-enter the light compartment, and these were all negatively correlated with the number of transitions (Table S3). Rats that were more inactive took longer to enter the dark compartment, took longer to re-enter the light and made fewer transitions. Sex, and the interaction between sex and mass, both had a significant effect on PC_Active scores (Table 1). Females were significantly more active than males, and tended to flee in response to the startle, entering the dark compartment sooner than the males (Fig. 6). Females, however, also returned to the light compartment faster after the startle, and made more transitions than males (Fig. 6). Males tended to freeze in response to the startle. Females that were lighter on average, were more active, entered the dark compartment faster, returned to the light compartment faster and made more transitions than heavier females or males in general (Fig. 6). No other factors or their interactions affected PC_Active scores (Table 1).

For PC2 (hereafter PC_Explore), the duration of exploration contributed 52% to the variance, while the duration of thigmotaxis contributed 47% (collectively 99%). These behaviours were not correlated (Table S3) and could not be performed at the same time, hence they pulled in opposite directions in the PCA. No factors or their interactions affected PC_Explore scores (Table 1).

For PC3 (hereafter PC_Shy), duration of time spent in the dark compartment contributed 40% to the variance, latency to re-enter the light compartment contributed 15% and duration of thigmotaxis contributed 17% (collectively 72%). Both time spent in the dark compartment and duration of thigmotaxis were negatively correlated with latency to re-enter the light (Table S3). Rats that took longer to re-enter the light compartment spent more time in the dark and were less thigmotactic than rats that entered the light compartment faster. Interestingly, rats that spent more time in the dark tended to be more thigmotactic (a non-significant positive relationship; Table S3). Site, and the interaction between sex and site, had a significant effect on PC_Shy scores (Table 1). Rats from the RF site spent more time in the dark, but were less thigmotactic and were faster to return to the light compartment than rats from the HP site (Fig. 7). In addition, female rats from the RF site were more “shy” than males and animals from the HP site, spending more time in the dark. However, as a consequence, they were also less thigmotactic, and returned to the light faster after the startle (Fig. 7). No other factors or their interactions affected PC_Shy scores  (Table 1).

## Discussion

In this study, we assessed whether behaviours commonly associated with exploration and activity in fawn-footed mosaic-tailed rats were influenced by the structure and complexity of the habitat in which they occurred, as suggested by Wiens (2000) and Marín *et al.* (2003). We confirmed that the HP site was less complex, and had a lower percentage of cover, than the RF site. Reduced structural complexity and less cover are considered characteristics of a more homogeneous habitat, and homogeneous habitats are often characterised by spatial and/or temporal stability of resources (Rymer *et al.* 2013).

We predicted that mosaic-tailed rats from the less structurally complex habitat would be less exploratory and less active, as individuals would have to trade off foraging against higher perceived predation risk (Sinclair 1979; Brown 1999). Our results provide some evidence for this trade-off; however, this appears to be context-dependent. We acknowledge that we have no replication at the site level, and our interpretation of behavioural differences may also be related to a much broader suite of non-specified differences between the habitats, rather than structural complexity on its own, although we have attempted to control for variation in abiotic factors statistically.

There was no effect of site on exploratory behaviour or activity in either the open field or novel object tests. However, under heightened predation risk (light-dark box and acoustic startle tests), mosaic-tailed rats from the HP site were less active and exploratory than rats from the RF site. This seems to be linked to a site-specific anti-predator strategy, with rats from the HP site adopting a freezing strategy in response to a startle, whereas rats from the RF site were more likely to flee to the dark compartment. Interestingly, while Edut and Eilam (2003) suggested species-specific variation in anti-predator strategy based on species-specific ecology, Blanchard and Blanchard (1989) showed that distance to shelter, or availability of shelter, can also influence anti-predator behaviour. Laboratory Long-Evans rats (*Rattus norvegicus domestica*) readily fled to a shelter when it was available, but froze when none was available (Blanchard and Blanchard 1989). Vegetation cover can help mitigate perceived predation risk (Sutherland and Dickman 1999), allowing individuals to continue exploring even in the presence of a predator. As the HP site had a lower percentage of cover than the RF site, this could explain why mosaic-tailed rats from the HP site were less exploratory and active in general, and froze when exposed to a novel noise when in the light compartment.

Interestingly, we also found an effect of maximum temperature on PC_Explore scores in the light-dark box test, but not for any other behavioural scores or tests. Changes in temperature affect behaviour in other species. For example, increased temperature results in increased exploration and more time in the light compartment by zebrafish (*Danio rerio*, Angiulli *et al.* 2020), whereas decreased water temperature resulted in increased thigmotaxis in the laboratory mouse strain Ts65Dn in the Morris water maze (Stasko and Costa 2004). In these cases, temperature variations were 8 °C and 5 °C, respectively, compared to only an average 2 °C difference in the present study. More testing is required to ascertain what effect temperature has on behaviour in mosaic-tailed rats in general.

In the acoustic start test, the sample sizes were not balanced because RF animals tended to remain in the dark at the end of the light-dark box test, and did not return to the light. Consequently, our results could be biased, although the patterns of individual variation observed here are important to note. The acoustic startle test requires that individuals to be in the light compartment for the test to commence, and we can make no assumptions about how an individual may or may not have responded if it did not return to the light. However, the patterns of behaviour in this test were largely consistent with those seen in the light-dark box test. In the light-dark box test, rats from the RF site were more active and exploratory in the light compartment, and made more transitions, than rats from the HP site, and this pattern was consistent in the acoustic startle test.

Individuals from the HP site were heavier, in general, than individuals from the RF site, which suggests that the two habitats likely differ in the relative abundance and/or quality of food resources (Pulliam 1988), although this requires testing. Interestingly, we found a mass * site effect on PC_Active scores in the open field test. Lima (1986) suggested that increased mass increases the risk of predation as larger fat reserves may affect an individual's ability to escape a predator. This could explain why heavier rats were less active in the RF site. Alternatively, as body mass tends to increase with age in numerous species (rats, Brunelli *et al.* 2006; red foxes (*Vulpes vulpes*), Forbes-Harper *et al.* 2017), and older animals tend to be less active in general than younger ones (Oosthuizen and Bennett 2015), heavier rats in the RF site might simply have been older. However, these explanations do not explain why heavier rats in the HP site were more active. One intriguing hypothesis, that would require considerable testing, relates to owl predation. Trejo and Guthman (2003) found that Magellanic horned owls (*Bubo magellanicus*) actively avoided heavier prey, preferentially selecting smaller individuals. If the lower cover in the HP site exposes rats to higher potential risk from owls, and owls prefer smaller rats, we would expect heavier rats to be more active in this site than lighter ones.

Interestingly, regardless of site, males were heavier than females, indicating sexual dimorphism. This is consistent with Leung (1999) for the Cape York mosaic-tailed rat (*Melomys capensis*), suggesting a general pattern for the genus. However, we also found sex differences in behaviour and activity, which is consistent with Johnston and File (1991) and Golcu *et al.* (2014). Females were more curious than males in the novel object test, spending more time sniffing it than males, which is consistent with laboratory Brattleboro (Schatz *et al.* 2018) and Long-Evans rats (Cost *et al.* 2014). However, this contrasts previous findings in mosaic-tailed rats, where males were less neophobic towards a predator odour than females (Paulling *et al.* 2019), suggesting that the type of novel cue may elicit differential responses from the sexes. Interestingly, sex also had a significant effect on behaviour and activity scores in the acoustic startle test. Females were more active, were faster to enter the dark compartment and made more transitions than males. While Schuett and Dall (2009), King *et al.* (2013) and Heth *et al.* (1987) observed males to be more active than females, other studies have shown that female rodents tend to be more active than males in these types of laboratory tests (e.g. Cavigelli *et al.* 2011; Simpson *et al.* 2012). However, PC_Active scores were also impacted by the interaction between sex and mass, as females that were lighter on average were more active than either heavier females or males, possibly because these lighter females were younger, as suggested above. In addition, PC_Shy scores were also impacted by the interaction between sex and site in the acoustic startle test, with females from the RF site spending more time in the dark after the startle. We are mindful that the sample sizes were small, with only three females and two males from the RF site. Therefore, we recommend additional testing to determine whether this pattern is consistent over a larger sample size, or whether this is specific for these individuals tested, particularly as some studies have found individual variation in the flight or freeze response within the same species (e.g. Gunther's voles (*Microtus socialis guntheri*), Edut and Eilam 2003). That individuals show considerable variation in their behaviour is also of interest here, and warrants future study.

Little is known about the behaviour of fawn-footed mosaic-tailed rats. Our results suggest that even small differences in habitat complexity may lead to variation in behaviour. However, this variation appears to be context-specific, being related specifically to predation risk. Our results also suggest that sex differences in behaviour are present in mosaic-tailed rats, although this may also be context-specific. Small-scale variation in habitat complexity likely affects resource availability and ultimately body state of animals, which may consequently influence behaviours associated with predator avoidance.

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## Conflicts of interest

The authors declare no conflicts of interest.

## References

Angiulli, E., Pagliara, V., Cioni, C., Frabetti, F., Pizzetti, F., Alleva, E., and Toni, M. (2020). Increase in environmental temperature affects exploratory behaviour, anxiety and social preference in *Danio rerio*. *Scientific reports*, **10**, 5385. doi:10.1038/s41598-020-62331-1

Barnett, S. A. (1958). Experiments on 'neophobia' in wild and laboratory rats. *British Journal of Psychology* **49**, 195–201. doi:10.1111/j.2044-8295.1958.tb00657.x

Beatty, W. W. (1979). Gonadal hormones and sex differences in nonreproductive behaviors in rodents: organizational and activational influences. *Hormones and Behavior* **12**, 112–163. doi:10.1016/0018-506X(79)90017-5

Bengsen, A.J., Leung, L.K.P., Lapidge, S.J., and Gordon, I.J. (2010). Artificial illumination reduces bait-take by small rainforest mammals. *Applied Animal Behaviour Science* **127**, 66–72. doi:10.1016/j.applanim.2010.08.006

Birke, L. I., and Sadler, D. (1991). Maternal discrimination and the development of sex differences in exploratory behaviour in infant spiny mice (*Acomys cahirinus*). *The Quarterly Journal of Experimental Psychology B*, **43**, 403–430. doi:10.1080/14640749108401277

Blanchard, R. J., and Blanchard, D. C. (1989). Antipredator defensive behaviors in a visible burrow system. *Journal of Comparative Psychology* **103**, 70–82. doi 10.1037/0735-7036.103.1.70

Boon, A. K., Réale, D., and Boutin, S. (2008). Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos* **117**, 1321–1328. doi:10.1111/j.0030-1299.2008.16567.x

Bourin, M., and Hascoët, M. (2003). The mouse light/dark box test. *European Journal of Pharmacology* **463**, 55–65. doi:10.1016/S0014-2999(03)01274-3

Brown, J. S. (1999). Vigilance, patch use and habitat selection: Foraging under predation risk. *Evolutionary Ecology Research* **1**, 49–71.

Brunelli, S. A., Nie, R., Whipple, C., Winiger, V., Hofer, M. A., and Zimmerberg, B. (2006). The effects of selective breeding for infant ultrasonic vocalizations on play behavior in juvenile rats. *Physiology & Behavior* **87**, 527–536. doi:10.1016/j.physbeh.2005.11.020

Callaway, W. A., Turner, A. A., Croshaw, O. B., Ferguson, J. A., Julson, Z. J.-N., Volp, T. M., Kerr, S. E., and Rymer, T. L. (2018). *Melomys cervinipes* (Rodentia: Muridae). *Mammalian Species* **50**, 134–147. doi:10.1093/mspecies/sey015

Carola, V., D'Olimpio, F., Brunamonti, E., Mangia, F., and Renzi, P. (2002). Evaluation of the elevated plus-maze and open-field tests for the assessment of anxiety-related behaviour in inbred mice. *Behavioural Brain Research* **134**, 49–57. doi:10.1016/S0166-4328(01)00452-1

Cassini, M. H., and Galante, M. L. (1992). Foraging under predation risk in the wild guinea pig: the effect of vegetation height on habitat utilization. *Annales Zoologici Fennici* **29**, 285–290.

Cavigelli, S. A., Michael, K. C., West, S. G., and Klein, L. C. (2011). Behavioral responses to physical vs. social novelty in male and female laboratory rats. *Behavioural Processes* **88**, 56–59. doi:10.1016/j.beproc.2011.06.006

Chen, W., Shields, J., Huang, W., and King, J. A. (2009). Female fear: Influence of estrus cycle on behavioral response and neuronal activation. *Behavioural Brain Research* **201**, 8–13. doi:10.1016/j.bbr.2009.01.019

Coops, N. C., and Catling, P. C. (2000). Estimating forest habitat complexity in relation to time since fire. *Austral Ecology* **25**, 344–351. doi:10.1046/j.1442-9993.2000.01045.x

Cost, K. T., Lobell, T. D., Williams-Yee, Z. N., Henderson, S., and Dohanich, G. (2014). The effects of pregnancy, lactation, and primiparity on object-in-place memory of female rats. *Hormones and Behavior* **65**, 32–39. doi:10.1016/j.yhbeh.2013.10.012

Cousin, J. A., and Phillips, R. D. (2008). Habitat complexity explains species-specific occupancy but not species richness in a Western Australian woodland. *Australian Journal of Zoology* **56**, 95–102. doi:10.1071/ZO07065

Edut, S., and Eilam, D. (2003). Rodents in open space adjust their behavioral response to the different risk levels during barn-owl attack. *BMC Ecology* **3**, 10. doi:10.1186/1472-6785-3-10

Ennaceur, A., Michalikova, S., and Chazot, P. L. (2009). Do rats really express neophobia towards novel objects? Experimental evidence from exposure to novelty and to an object recognition task in an open space and an enclosed space. *Behavioural Brain Research* **197**, 417–434. doi:10.1016/j.bbr.2008.10.007

Forbes-Harper, J. L., Crawford, H. M., Dundas, S. J., Warburton, N. M., Adams, P. J., Bateman, P. W., Calver, M. C. and Fleming, P. A. (2017). Diet and bite force in red foxes: ontogenetic and sex differences in an invasive carnivore. *Journal of Zoology* **303**, 54–63. doi:10.1111/jzo.12463

Glazier, D. S., and Eckert, S. E. (2002). Competitive ability, body size and geographical range size in small mammals. *Journal of Biogeography* **29**, 81–92. doi:10.1046/j.1365-2699.2002.00646.x

Golcu, D., Gebre, R. Z., and Sapolsky, R. M. (2014). *Toxoplasma gondii* influences aversive behaviors of female rats in an estrus cycle dependent manner. *Physiology and Behavior* **135**, 98–103. doi:10.1016/j.physbeh.2014.05.036

Gould, T. D., Dao, D. T., and Kovacsics, C. E. (2009). The open field test. In ‘Mood and anxiety related phenotypes in mice’. (Ed D. Gould) pp. 1–20. )Humana Press: Totowa, NJ.)

Hayes, R. A., Nahrung, H. F., and Wilson, J. C. (2006). The response of native Australian rodents to predator odours varies seasonally: a by-product of life history variation? *Animal Behaviour* **71**, 1307–1314. doi:10.1016/j.anbehav.2005.08.017

Hendrie, C. A., Weiss, S. M., and Eilam, D. (1998). Behavioural response of wild rodents to the calls of an owl: a comparative study. *Journal of Zoology London* **245**, 439–446. doi:10.1017/S0952836998008073

Heth, G., Nevo, E., and Beiles, A. (1987). Adaptive exploratory behaviour: differential patterns in species and sexes of subterranean mole rats. *Mammalia* **51**, 27–38. doi:10.1515/mamm.1987.51.1.27

Ilany, A., and Eilam, D. (2008). Wait before running for your life: defensive tactics of spiny mice (*Acomys cahirinus*) in evading barn owl (*Tyto alba*) attack. *Behavioral Ecology & Sociobiology* **62**, 923–933. doi:10.1007/s00265-007-0516-x

Johnston, A. L., and File, S. E. (1991). Sex differences in animal tests of anxiety. *Physiology & Behavior* **49**, 245–250. doi:10.1016/0031-9384(91)90039-Q

King, A. J., Fürtbauer, I., Mamuneas, D., James, C., and Manica, A. (2013). Sex-differences and temporal consistency in stickleback fish boldness. *PLoS One* **8**, e e81116. doi:10.1371/journal.pone.0081116

Kolenikov, S., and Angeles, G. (2004). *The use of discrete data in PCA: theory, simulations, and applications to socioeconomic indices*. Chapel Hill, NC: Carolina Population Center, University of North Carolina.

Küçük, A., and Gölgeli, A. (2007). Effects of age and sex differences on conditioned and unconditioned fear in anxiety developed animals. *Erciyes Medical Journal* **29**, 13–17.

Kuznetsova, A., Brockhoff, P. B., Christensen, R. H. B., and Jensen, S. P. (2020). Package ‘lmerTest’, https://cran.uib.no/web/packages/lmerTest/lmerTest.pdf.

Lagos, V. O., Contreras, L. C., Meserve, P. L., Gutiérrez, J. R., and Jaksic, F. M. (1995). Effects of predation risk on space use by small mammals: a field experiment with a Neotropical rodent. *Oikos* **74**, 259–264. doi:10.2307/3545655

Laurance, W. F. (1994). Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. *Biological Conservation* **69**, 23–32. doi:10.1016/0006-3207(94)90325-5

Leung, L. K.-P. (1999). Ecology of Australian tropical rainforest mammals. II. The Cape York melomys, *Melomys capensis* (Muridae: Rodentia). *Wildlife Research* **26**, 307–316. doi:10.1071/WR96043

Lima, S. L. (1986). Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* **67**, 377–385. doi:10.2307/1938580

Marín, A. I., Hernández, L., and Laundré, J. W. (2003). Predation risk and food quantity in the selection of habitat by black-tailed jackrabbit (*Lepus californicus*): an optimal foraging approach. *Journal of Arid Environments* **55**, 101–110. doi:10.1016/S0140-1963(02)00264-1

Mettke-Hofmann, C., Winkler, H., and Leisler, B. (2002). The significance of ecological factors for exploration and neophobia in parrots. *Ethology* **108**, 249–272. doi:10.1046/j.1439-0310.2002.00773.x

Oosthuizen, M. K., and Bennett, N. C. (2015). The effect of ambient temperature on locomotor activity patterns in reproductive and non-reproductive female Damaraland mole-rats. *Journal of Zoology* **297**, 1–8. doi:10.1111/jzo.12254

Orrock, J. L., Danielson, B. J., and Brinkerhoff, R. J. (2004). Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behavioral Ecology* **15**, 433–437. doi:10.1093/beheco/arh031

Paulling, K., Wilson, D., and Rymer, T. L. (2019). Olfactory recognition of snake cues by fawn-footed mosaic-tailed rats *Melomys cervinipes*. *Behaviour* **156**, 1235–1253. doi:10.1163/1568539X-00003563

Picazo, O., and Fernández-Guasti, A. (1993). Changes in experimental anxiety during pregnancy and lactation. *Physiology & Behavior* **54**, 295–299. doi:10.1016/0031-9384(93)90114-U

Pulliam, H. R. (1988). Sources, sinks, and population regulation. *Americal Naturalist* **132**, 652–661. doi:10.1086/284880

Rader, R., and Krockenberger, A. (2006). Does resource availability govern vertical stratification of small mammals in an Australian lowland tropical rainforest? *Wildlife Research* **33**, 571–576. doi:10.1071/WR04108

Rowell, M. K., and Rymer, T. L. (2020). Innovation in a native Australian rodent, the fawn-footed mosaic-tailed rat (*Melomys cervinipes*). *Animal Cognition* **23**, 301–310. doi:10.1007/s10071-019-01334-6

Rymer, T. L., and Pillay, N. (2012). The development of exploratory behaviour in the African striped mouse *Rhabdomys* reflects a gene x environment compromise. *Behavior Genetics* **42**, 845–856. doi:10.1007/s10519-012-9555-9

Rymer, T. L., Pillay, N., and Schradin, C. (2013). Extinction or survival? Behavioral flexibility in response to environmental change in the African striped mouse *Rhabdomys*. *Sustainability* **5**, 163–186. doi:10.3390/su5010163

Schatz, K. C., Kyne, R. F., Parmeter, S. L., and Paul, M. J. (2018). Investigation of social, affective, and locomotor behavior of adolescent Brattleboro rats reveals a link between vasopressin's actions on arousal and social behavior. *Hormones and Behavior* **106**, 1–9. doi:10.1016/j.yhbeh.2018.08.015

Schuett, W., and Dall, S. R. (2009). Sex differences, social context and personality in zebra finches, Taeniopygia guttata. *Animal Behaviour* **77**, 1041–1050. doi: 10.1016/j.anbehav.2008.12.024

Schultz, C. B., Franco, A. M. A., and Crone, E. E. (2012). Response of butterflies to structural and resource boundaries. J*ournal of Animal Ecology* **81**, 724–734. doi: 10.1111/j.1365-2656.2011.01947.x

Schooley, R. L., Sharpe, P. B., and Horne, B. V. (1996). Can shrub cover increase predation risk for a desert rodent?. *Canadian Journal of Zoology* **74**, 157–163. doi: 10.1139/z96-020

Simpson, J., Ryan, C., Curley, A., Mulcaire, J., and Kelly, J. P. (2012). Sex differences in baseline and drug-induced behavioural responses in classical behavioural tests. *Progress in Neuro-Psychopharmacology and Biological Psychiatry* **37**, 227–236. doi:10.1016/j.pnpbp.2012.02.004

Sinclair, A. R. E. (1979). Dynamics of the Serengeti ecosystem. In: ‘Serengeti: Dynamics of an Ecosystem’. (Eds A. R. E. Sinclair, and M. Norton-Griffiths.) pp. 1–30 (University of Chicago Press: Chicago.)

Stasko, M. R., and Costa, A. C. (2004). Experimental parameters affecting the Morris water maze performance of a mouse model of Down syndrome. *Behavioural Brain Research* **154**, 1–17. doi:10.1016/j.bbr.2004.01.012

Sutherland, E. F., and Dickman, C. R. (1999). Mechanisms of recovery after fire by rodents in the Australian environment: a review. *Wildlife Research* **26**, 405–419. doi:10.1071/WR97045

Trejo, A., and Guthmann, N. (2003). Owl selection on size and sex classes of rodents: activity and microhabitat use of prey. *Journal of Mammalogy* **84**, 652–658. doi:10.1644/1545-1542(2003)084<0652:OSOSAS>2.0.CO;2

Valsamis, B., and Schmid, S. (2011). Habituation and prepulse inhibition of acoustic startle in rodents. *Journal of Visualized Experiments* **55**, e3446. doi:10.3791/3446

Watts, C. H. S., and Aslin, H. J. (1981). The rodents of Australia. (Angus and Robertson: Sydney, Australia.)

Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., and Zemla, J. (2017). Package 'corrplot'. https://cran.r-project.org/web/packages/corrplot/index.html.

Wet Tropics Management Authority. (2009). SERIES WTMA veg SHEET 8064-3 Edition 1. 1:50,000. Vegetation of the Wet Tropics of Queensland. Wet Tropics Management Authority. Cairns.

Wiens, J. A. (2000). Ecological heterogeneity: an ontogeny of concepts and approaches. In 'The ecological consequences of heterogeneity'. (Eds M. J. Hutchings, E. A. John and A. J. A. Stewart.) pp. 9–31. (Blackwell Science: Oxford, UK.)

Wilson, A. D. M., and Godin, J. G. J. (2009). Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. *Behavioral Ecology* **20**, 231–237. doi:10.1093/beheco/arp018

Wood, D. H. (1971). The ecology of *Rattus fuscipes* and *Melomys cervinipes* (Rodentia: Muridae) in a South-East Queensland rain forest. *Australian Journal of Zoology* **19,** 371–392. doi:10.1071/ZO9710371

Woodall, P. (1989). Habitat of *Melomys cervinipes* (Rodentia: Muridae) on Carlisle Island, Central Queensland. *Australian Mammalogy* **12**, 31–32.

**Table 1.** Statistical data for linear model analyses of principle components generated from the behaviour of fawn-footed mosaic-tailed rats (*Melomys cervinipes*) in four different behavioural tests (open field, novel object, light-dark box, acoustic startle). Significant differences are indicated in bold.

| | | **Test** | | | |
|---|---|---|---|---|---|
| **Predictor** | **Response** | **Open Field** | **Novel Object** | **Light-Dark Box** | **Acoustic Startle** |
| Site | PC_Active | $F_{1,32} = 0.96$; $P = 0.335$ | $F_{1,31} = 0.01$; $P = 0.927$ | **$\chi^2_1 = 4.01$; $P = 0.045$** | $\chi^2_1 = 0.13$; $P = 0.720$ |
| | Duration of exploration | $F_{1,32} = 0.52$; $P = 0.478$ | - | - | - |
| | Duration of sniffing | - | $\chi^2_1 = 0.05$; $P = 0.830$ | - | - |
| | PC_Shy | - | - | $\chi^2_1 = 3.59$; $P = 0.058$ | **$\chi^2_1 = 7.99$; $P = 0.005$** |
| | PC_Explore | - | - | **$\chi^2_1 = 5.84$; $P = 0.016$** | $F_{1,14} = 0.31$; $P = 0.586$ |
| Mass | PC_Active | $F_{1,32} = 0.42$; $P = 0.524$ | $F_{1,31} = 0.62$; $P = 0.437$ | $\chi^2_1 = 0.03$; $P = 0.864$ | $\chi^2_1 = 0.03$; $P = 0.858$ |
| | Duration of exploration | $F_{1,32} = 0.03$; $P = 0.872$ | - | - | - |
| | Duration of sniffing | - | $\chi^2_1 = 0.03$; $P = 0.859$ | - | - |
| | PC_Shy | - | - | $\chi^2_1 = 3.23$; $P = 0.072$ | $\chi^2_1 = 0.26$; $P = 0.610$ |
| | PC_Explore | - | - | $\chi^2_1 = 0.54$; $P = 0.464$ | $F_{1,14} = 0.04$; $P = 0.847$ |
| Sex | PC_Active | $F_{1,32} = 0.23$; $P = 0.637$ | $F_{1,31} = 1.91$; $P = 0.177$ | $\chi^2_1 = 0.03$; $P = 0.863$ | **$\chi^2_1 = 6.89$; $P = 0.009$** |
| | Duration of exploration | $F_{1,32} = 1.61$; $P = 0.214$ | - | - | - |
| | Duration of sniffing | - | **$\chi^2_1 = 6.10$; $P = 0.014$** | - | - |
| | PC_Shy | - | - | $\chi^2_1 = 1.65$; $P = 0.198$ | $\chi^2_1 = 0.78$; $P = 0.376$ |
| | PC_Explore | - | - | $\chi^2_1 = 0.04$; $P = 0.839$ | $F_{1,14} = 1.25$; $P = 0.283$ |

| | | | | | |
|---|---|---|---|---|---|
| Site * Mass | PC_Active | **$F_{1,32} = 7.42$; $P = 0.010$** | $F_{1,31} = 1.45$; $P = 0.238$ | $\chi^2_1 = 0.02$; $P = 0.895$ | $\chi^2_1 = 1.89$; $P = 0.170$ |
| | Duration of exploration | $F_{1,32} = 0.87$; $P = 0.358$ | - | - | - |
| | Duration of sniffing | - | $\chi^2_1 = 0.83$; $P = 0.362$ | - | - |
| | PC_Shy | - | - | $\chi^2_1 = 0.41$; $P = 0.524$ | $\chi^2_1 = 0.17$; $P = 0.681$ |
| | PC_Explore | - | - | $\chi^2_1 = 0.09$; $P = 0.760$ | $F_{1,14} = 1.96$; $P = 0.710$ |
| Site * Sex | PC_Active | $F_{1,32} = 1.33$; $P = 0.258$ | $F_{1,31} = 0.39$; $P = 0.538$ | $\chi^2_1 = 0.19$; $P = 0.662$ | $\chi^2_1 = 0.35$; $P = 0.556$ |
| | Duration of exploration | $F_{1,32} = 0.92$; $P = 0.345$ | - | - | - |
| | Duration of sniffing | - | $\chi^2_1 = 0.00$; $P = 0.963$ | - | - |
| | PC_Shy | - | - | $\chi^2_1 = 0.90$; $P = 0.344$ | **$\chi^2_1 = 4.58$; $P = 0.032$** |
| | PC_Explore | - | - | $\chi^2_1 = 1.92$; $P = 0.166$ | $F_{1,14} = 0.00$; $P = 0.986$ |
| Mass * Sex | PC_Active | $F_{1,32} = 0.01$; $P = 0.909$ | $F_{1,31} = 2.29$; $P = 0.140$ | $\chi^2_1 = 0.36$; $P = 0.550$ | **$\chi^2_1 = 4.88$; $P = 0.027$** |
| | Duration of exploration | $F_{1,32} = 1.24$; $P = 0.274$ | - | - | - |
| | Duration of sniffing | - | $\chi^2_1 = 0.18$; $P = 0.699$ | - | - |
| | PC_Shy | - | - | $\chi^2_1 = 0.96$; $P = 0.328$ | $\chi^2_1 = 1.53$; $P = 0.216$ |
| | PC_Explore | - | - | $\chi^2_1 = 2.36$; $P = 0.125$ | $F_{1,14} = 0.36$; $P = 0.558$ |
| Site * Mass * Sex | PC_Active | $F_{1,32} = 0.03$; $P = 0.856$ | $F_{1,31} = 1.31$; $P = 0.261$ | $\chi^2_1 = 0.48$; $P = 0.488$ | $\chi^2_1 = 0.57$; $P = 0.450$ |
| | Duration of exploration | $F_{1,32} = 0.32$; $P = 0.573$ | - | - | - |
| | Duration of sniffing | - | $\chi^2_1 = 2.78$; $P = 0.096$ | - | - |
| | PC_Shy | - | - | $\chi^2_1 = 2.08$; $P = 0.149$ | $\chi^2_1 = 0.07$; $P = 0.793$ |
| | PC_Explore | - | - | $\chi^2_1 = 1.33$; $P = 0.250$ | $F_{1,14} = 1.03$; $P = 0.328$ |

| | | | | | |
|---|---|---|---|---|---|
| PC_Moisture | PC_Active | $F_{1,35} = 2.83$; $P = 0.101$ | $F_{1,34} = 2.30$; $P = 0.139$ | $\chi^2_1 = 3.02$; $P = 0.082$ | $\chi^2_1 = 0.25$; $P = 0.615$ |
| | Duration of exploration | $F_{1,35} = 0.67$; $P = 0.418$ | - | - | - |
| | Duration of sniffing | - | $\chi^2_1 = 2.61$; $P = 0.106$ | - | - |
| | PC_Shy | - | - | $\chi^2_1 = 0.23$; $P = 0.629$ | $\chi^2_1 = 0.91$; $P = 0.340$ |
| | PC_Explore | - | - | $\chi^2_1 = 2.23$; $P = 0.136$ | $F_{1,17} = 0.47$; $P = 0.502$ |
| Maximum Temperature | PC_Active | $F_{1,35} = 0.09$; $P = 0.763$ | $F_{1,34} = 0.26$; $P = 0.612$ | $\chi^2_1 = 1.70$; $P = 0.192$ | $\chi^2_1 = 0.11$; $P = 0.743$ |
| | Duration of exploration | $F_{1,35} = 0.00$; $P = 0.999$ | - | - | - |
| | Duration of sniffing | - | $\chi^2_1 = 0.16$; $P = 0.694$ | - | - |
| | PC_Shy | - | - | $\chi^2_1 = 1.48$; $P = 0.630$ | $\chi^2_1 = 0.00$; $P = 0.996$ |
| | PC_Explore | - | - | **$\chi^2_1 = 9.59$; $P = 0.002$** | $F_{1,17} = 0.35$; $P = 0.562$ |
| Cloud Cover | PC_Active | $F_{1,35} = 0.36$; $P = 0.555$ | $F_{1,34} = 1.77$; $P = 0.193$ | $\chi^2_1 = 0.02$; $P = 0.895$ | $\chi^2_1 = 0.30$; $P = 0.581$ |
| | Duration of exploration | $F_{1,35} = 0.16$; $P = 0.695$ | - | - | - |
| | Duration of sniffing | - | $\chi^2_1 = 0.54$; $P = 0.464$ | - | - |
| | PC_Shy | - | - | $\chi^2_1 = 0.45$; $P = 0.505$ | $\chi^2_1 = 0.00$; $P = 0.981$ |
| | PC_Explore | - | - | $\chi^2_1 = 0.31$; $P = 0.575$ | $F_{1,17} = 0.74$; $P = 0.402$ |
| Moon Phase | PC_Active | $F_{1,35} = 0.06$; $P = 0.803$ | $F_{1,34} = 0.47$; $P = 0.496$ | $\chi^2_1 = 0.04$; $P = 0.844$ | $\chi^2_1 = 0.17$; $P = 0.681$ |
| | Duration of exploration | $F_{1,35} = 0.18$; $P = 0.673$ | - | - | - |
| | Duration of sniffing | - | $\chi^2_1 = 0.25$; $P = 0.616$ | - | - |
| | PC_Shy | - | - | $\chi^2_1 = 0.02$; $P = 0.885$ | $\chi^2_1 = 0.01$; $P = 0.922$ |
| | PC_Explore | - | - | $\chi^2_1 = 0.70$; $P = 0.401$ | $F_{1,17} = 0.16$; $P = 0.693$ |

PC_Active in the Open Field was scaled up by 400 and square root transformed. Duration of exploration was square root transformed for the Open Field test. PC_Active in the Novel Object was scaled up by 200 and either square root transformed (biological factors) or log transformed (abiotic factors). We used a general linear model with negative binomial distribution and log-link function for duration of sniffing in the Novel Object test. In the Light-Dark Box, PC_Active was scaled up by 400, PC_Shy was scaled up by 300, PC_Explore was scaled up by 100, and we used general linear models with negative binomial distribution and log-link function. In the Acoustic Startle, PC_Active was scaled up by 300, PC_Explore was scaled up by 200 and PC_Shy was scaled up by 100. We used general linear models with negative binomial distribution and log-link function for PC_Active and PC_Shy, and we square-root transformed PC_Explore scores.

## List of Figures

**Figure 1.** Mean ± SE (a) complexity score and (b) vegetation cover (%) in an abandoned hoop pine (*Araucaria cunninghamii*) plantation (HP) undergoing natural revegetation and a variable secondary rainforest (RF) in Cairns, Australia. Number of * indicate strength of significant differences.

**Figure 2.** Mean PC_Active scores in the open field in relation to mean body mass (g) of fawn-footed mosaic-tailed rats (*Melomys cervinipes*) from two sites: an abandoned hoop pine (*Araucaria cunninghamii*) plantation (HP) undergoing natural revegetation and a variable secondary rainforest (RF) in Cairns, Australia. Number of * indicate strength of significant differences.

**Figure 3.** Mean ± SE duration of time spent sniffing (s) a novel object by male and female fawn-footed mosaic-tailed rats (*Melomys cervinipes*) in a novel object test. Number of * indicate strength of significant differences.

**Figure 4.** Mean ± SE PC_Active scores in a light-dark box test by fawn-footed mosaic-tailed rats (*Melomys cervinipes*) from two sites: an abandoned hoop pine (*Araucaria cunninghamii*) plantation (HP) undergoing natural revegetation and a variable secondary rainforest (RF) in Cairns, Australia. Number of * indicate strength of significant differences.

**Figure 5.** Mean ± SE PC_ Explore scores in a light-dark box test by fawn-footed mosaic-tailed rats (*Melomys cervinipes*) from two sites: an abandoned hoop pine (*Araucaria cunninghamii*) plantation (HP) undergoing natural revegetation and a variable secondary rainforest (RF) in Cairns, Australia. Number of * indicate strength of significant differences.

**Figure 6.** Mean ± SE PC_Active scores by body mass (g) for male (n = 11) and female (n = 11) fawn-footed mosaic-tailed rats (*Melomys cervinipes*) in an acoustic startle test in Cairns, Australia. “Combined” indicates the sexes combined. “Light” indicates individuals lighter than the average mass and “Heavy” indicates individuals heavier than the average mass. Number of * indicate strength of significant differences.

**Figure 7.** Mean ± SE PC_Shy scores in an acoustic startle test fawn-footed mosaic-tailed rats (*Melomys cervinipes*) from two sites: an abandoned hoop pine (*Araucaria cunninghamii*) plantation (HP) undergoing natural revegetation and a variable secondary rainforest (RF) in Cairns, Australia. “Combined” indicates sexes combined (HP: n = 17; RF: n = 5). Females (HP: n = 8, RF: n = 3). Males (HP: n = 9; RF: n = 2). Number of * indicate strength of significant differences.