**Rowell, Misha Kyla (2022)** ***Ontogeny of problem solving in a native Australian rodent, the fawn-footed mosaic-tailed rat Melomys cervinipes.*** **PhD Thesis, James Cook University.**

# Ontogeny of problem solving in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*

**Misha Kyla Rowell**

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## Copyright and collaboration

To the best of my knowledge, this thesis does not contain material previously published by any other person, except where acknowledgements have been made. Permission from external copyright holders and collaborators has been obtained when necessary.

## Ethics and approvals

All trapping activities were conducted within the conditions imposed by the Department of Environment and Science (permit number: WA0014502) and Department of National Parks and Resources (permit number: PTU19-001632).

The research presented in this thesis complied with the ABS/ASAB guidelines for the ethical treatment of animals (Bee et al., 2020) and the Australian Care and Use of Animals for Scientific Purposes (National Health and Medical Research Council, 2013). This study was approved by the Animal Ethics Screening Committee of James Cook University (clearance number: A2539).

## Publications arising from this thesis

**Rowell, M.K**., Pillay, N., & Rymer, T.L. (2021). Problem Solving in Animals: Proposal for an Ontogenetic Perspective. *Animals, 11*, 866. https://doi.org/10.3390/ani11030866 **(Chapter 2)**

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**Rowell, M.K**., & Rymer, T.L. (2021). Exploration influences problem solving in the fawn-footed mosaic-tailed rat (*Melomys cervinipes*). *Ethology, 127*, 592-604. https://doi.org/10.1111/eth.13166 **(Chapter 7)**

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# Abstract

Problem solving, the act of overcoming an obstacle or barrier to gain a reward, has been studied in a wide variety of taxa, and there are large variations in problem solving abilities between species, populations, and even individuals. Individual variation could arise due to developmental differences, including intrinsic (genetic, neuroendocrine, and aging), and extrinsic (environmental) factors. However, experimental studies investigating the ontogeny of problem solving are scarce, and our understanding of the relative importance of these factors on the development of problem solving is lacking. To address some of these gaps in knowledge, I maintained a captive colony of fawn-footed mosaic-tailed rats *Melomys cervinipes*, a native Australian rodent, and tracked individuals over their lifetimes. This allowed me to record problem solving ability across multiple tasks and life stages for each individual. I presented six novel problems increasing in complexity (pillar, cylinder, matchbox, obstruction test, tile, and lever) to all adult animals. After finding that all individuals were capable of solving at least the simplest innovative problem, and that there were individual differences in solving ability, I then investigated how early life factors, namely genetic (heritability) and non-genetic (maternal care) effects, influenced problem solving ability, and how this ability changed as juveniles aged and gained experience.

I first monitored mothers and their offspring from the day of birth, measuring direct (time spent grooming and time spent huddling), indirect (time spent nesting), and total amount of maternal care received every second day across early development (postnatal days 1-12). I then used an innovative experimental design to untangle the effects of age and experience on the development of problem solving. I separated juveniles into two age groups (Group 1: tested earlier in development, Group 2: tested later in development) and then measured problem solving in juveniles using the matchbox task (scaled to body size) three times, each separated by 10 days. Group 1 individuals were tested on days 16, 26 and 36 after birth, while Group 2 individuals were tested on days 36, 46 and 56. I then tested all individuals as adults in the six problem solving tasks (pillar, cylinder, matchbox, obstruction test, tile, and lever). I calculated the narrow-sense heritability of problem solving using parent-offspring regressions, and used linear models to assess the effects of maternal care on problem solving. I compared 36-day old juveniles from Groups 1 and 2 to assess the effects of experience, while keeping age constant, and compared 16-day old juveniles from Group 1 to 36-day old juveniles from Group 2 to assess the effects of age,

while keeping experience constant. I found weak evidence of a heritable component to problem solving in some tasks. This suggests that there might only be weak genetic constraints on problem solving, although this could simply be a consequence of heritability for other traits (e.g. personality) involved with problem solving. Total, direct, and indirect maternal care did not influence solving ability in offspring, either as juveniles or adults, further suggesting that the maternal environment is not a major factor in the development of problem solving ability. I also found that the problem solving ability of juveniles improved with experience, but not with age, although adults were more successful solvers than juveniles. This is most likely due to increased experience with handling and manipulating objects in general.

The remainder of my study focussed on what factors could contribute to the individual variation in the problem solving abilities of adults, namely physiology, personality, and cognitive ability. I collected faecal samples during routine husbandry and extracted corticosterone (as a measure of adrenocortical activity) using enzyme-linked immunosorbent assays. I found that corticosterone metabolite concentration did not affect how quickly problems were solved, or how much time the rats spent interacting with the problems, which suggests that other intrinsic factors, such as personality, may be more important for successful solving than adrenocortical activity. I then measured personality across two contexts, namely exploration in an open field and a novel object test, and anxiety under simulated predation risk in a light/dark box. I found that mosaic-tailed rats showed consistent individual differences in behaviour (indicative of personality), and that exploration behaviours, but not anxiety behaviours, affected problem solving, as more exploratory individuals were more successful, and solved problems faster, than less exploratory individuals. However, less exploratory individuals still persist in the population, possibly because other factors, such as cognitive ability, may help them overcome challenges. Finally, I measured cognition across different domains (memory in an odour learning association task, recognition in a novel object recognition task, size discrimination using different sizes of food, and learning across multiple presentations of a food-baited activity board). I found that individuals that successfully completed more tasks, and individuals that were able to remember an association and learn the tile task, solved the problems faster than individuals that completed fewer tasks or individuals that could not learn or remember. This suggests that problem solving ability relies on some forms of cognition.

This study highlights the importance of considering both inter-individual and intra-individual differences in solving ability. During early life, offspring undergo neurological, physiological, and anatomical development. This could be involved in the organisation of developmental pathways necessary for successful problem solving later in life. However, problem solving is also constrained by the development of other individual components, including personality (particularly exploration) and cognition (particularly learning and memory). Overall, my findings suggest that problem solving is not fixed during the early life, allowing mosaic-tailed rats to change their solving responses while they explore their environment, and learn and remember new information or experiences throughout their lifetimes.

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# Chapter 1: General introduction

## Introduction

Problem solving is defined as an animal's ability to access a reward by manipulating itself or an object to overcome a barrier (Chow et al., 2017). This ability relies on an animal's mechanical skill to perform the task (Krasheninnikova et al., 2013), and a series of physiological (Griffin & Guez, 2014), behavioural (van Horik & Madden, 2016), and cognitive (Amici et al., 2019) processes that follow on from the detection of the problem. Problem solving could be important for an animal's survival, as it is thought to be a flexible response to environmental conditions (Kozlovsky et al., 2015). As a result, problem solving may allow animals to rapidly adjust to new conditions or cope with harsh conditions (Sol et al., 2002), and could therefore increase fitness through acquisition of new resources (Cole et al., 2012).

Due to the possible importance of problem solving for fitness and survival, much of the current literature on this topic has focused on the ultimate aspects of problem solving (evolutionary history and adaptive significance, Tinbergen, 1963). In contrast, we do not yet have a comprehensive understanding of the proximate aspects of problem solving, which include its ontogeny, and the mechanisms underlying it (Tinbergen, 1963). These proximate aspects are complementary, and not mutually exclusive, to the ultimate drivers of problem solving. Integrating these approaches will allow us to properly understand problem solving ability (Nesse, 2013), and will ensure that we have a correct and complete understanding of problem solving (Ryan, 2005).

Tinbergen (1963) defined ontogeny as the changes in a behaviour's machinery during development. These changes can last for any duration (e.g. short-term or permanent) and can be reversible, speaking to the flexibility of behavioural traits (Stamps, 2003). Importantly, based on this definition, an animal's maturation is not considered the end point of ontogeny, with development occurring throughout an animal's lifetime (Stamps, 2003). This can, therefore, become quite complicated, as a behaviour can occur during different life stages, could have different functions at different life stages, and could be affected by different developmental factors at different life stages (Stamps, 2003). The ontogeny of a behaviour could also be influenced by both intrinsic (e.g. physiological) and extrinsic (e.g. environmental) factors (Chapter 2; Rowell et al., 2021). Furthermore, these influences on the ontogeny of behaviour could be direct, with the factor influencing the behaviour itself, or indirect, with the factor influencing another aspects of the individual (e.g. physiology), which then goes on to influence the behaviour (Chapter 2; Rowell et al., 2021).

## Motivation for the Thesis

Since an animal's physiology (Forrest et al., 1991), behaviour (Brown & Kraemer, 1997), brain structure (Fischer et al., 2007), and cognition (Lynn & Brown, 2009) changes as it ages and gains experience, its problem solving ability could also change throughout its lifetime, which could affect how it copes with environmental stressors throughout its development (Sol et al., 2002). By understanding how problem solving changes with age, and what factors affect its development, we can more accurately investigate the causes of variation in solving ability within a population (Cussen, 2017), which, in turn, has important fitness consequences.

The primary objective of this thesis was to investigate the development of problem solving in fawn-footed mosaic-tailed rats, *Melomys cervinipes*, over the course of their lifetimes. The first aim was to investigate how genetic and non-genetic factors influence the development of problem solving by teasing apart the direct (maternal genetic) and indirect (maternal care) factors, as well as to untangle the effects of age and experience on problem solving. The second aim was to investigate the factors that could indirectly impact the expression of problem solving, including physiology, personality, and cognition.

## Study Species

The fawn-footed mosaic-tailed rat is a medium-sized (79.2 ± 12 g, Callaway et al., 2018) murid rodent native to the forests along the eastern coast of Australia (Moore et al., 2008), although is also often found thriving in disturbed forest fragments and along habitat edges (Goosem & Marsh, 1997). Mosaic-tailed rats are semi-arboreal, moving up to 16 m into the canopy to forage on fruits, nuts, leaves, and insects (Rader & Krockenberger, 2006). Both males and females occupy solitary territories of approximately 50 $m^2$ (Rader & Krockenberger, 2006), and are capable of breeding year round (Breed, 1979).

Mosaic-tailed rats exhibit a prolonged period of prenatal investment in offspring (Watts & Aslin, 1981). After a gestation of approximately 37 days (Breed, 1979), females have litters of up to four pups, typically with a 50:50 sex ratio (Wood, 1971). Pups nipple cling on the mother initially, and then begin exploring their surroundings once their eyes open at approximately 9 days old (Rowell & Rymer, 2020a). At this stage, pups are capable of eating solid foods (Rowell & Rymer, 2020a). Pups are then weaned at approximately 20 days old (Watts & Aslin, 1981).

Mosaic-tailed rats are easy to keep in captivity, and are long-lived, surviving for more than 3 years in captive conditions (Jackson, 2003). Mosaic-tailed rats were housed individually in wire-frame cages with wood shavings as bedding material. A nest box, nesting material, climbing sticks, and chewing objects were provided for enrichment. Water was available *ad libitum*, and food (fruit/vegetables, mixed seed, and rodent chow) was provided daily. Individuals were visually inspected daily and were weighed every fortnight to monitor health conditions. Due to their housing conditions and longevity, I was able to track and monitor individuals over their lifetimes, and could test the same individuals across multiple behavioural and cognitive experiments. However, due to their long gestation, small litter sizes, and delayed sexual maturity (Rowell & Rymer, 2020a), it was difficult to obtain a large sample size for the juvenile components of the study.

## Chapter Layout

I first reviewed the literature, outlining which developmental factors could influence problem solving (Chapter 2). This provided the broad context for the thesis. I then investigated whether mosaic-tailed rats were capable of innovative problem solving (Chapter 3), which demonstrated the feasibility of the methodology used. I then focused on my first aim, investigating the genetic and non-genetic factors affecting the development of problem solving. I first considered the early life factors that could influence problem solving, namely heritability and maternal effects (Chapter 4). I then considered how age and experience during the early developmental period and over the weaning and dispersal stages affected problem solving (Chapter 5). Thereafter, I focused on my second aim, exploring other developmental factors that could affect the expression of problem solving. As outlined in the literature review, I explored how problem solving in adult mosaic-tailed rats is affected by physiology (Chapter 6), personality (Chapter 7), and cognition (Chapter 8).

## Thesis outline

This thesis comprises the general introductory chapter (Chapter 1), a literature review (Chapter 2), six experimental chapters (Chapter 3-8) as the main body of the thesis, and a general discussion (Chapter 9). The main body chapters are written as separate manuscripts for publication. Chapter 2 (Problem solving in animals: proposal for an ontogenetic perspective) has been published in the journal *Animals* (vol. 11, p. 866). Chapter 3 (Innovation in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*) has been published in the journal *Animal Cognition* (vol. 23, p. 301-310). Chapter 5 (Experience is more important than age for successful problem solving in juvenile fawn-footed mosaic-tailed rats *Melomys cervinipes*) is currently in review with the journal *Behaviour*. Chapter 6 (Corticosterone concentration is not related to problem solving in the fawn-footed mosaic-tailed rat *Melomys cervinipes*) has been published in the journal *Animals* (vol. 12, p. 82). Chapter 7 (Exploration influences problem solving in the fawn-footed mosaic-tailed rat *Melomys cervinipes*) has been published in the journal *Ethology* (vol. 127, p. 592-604). Chapter 8 (Memory enhances problem solving in the fawn-footed mosaic-tailed rat *Melomys cervinipes*) has been published in the journal *Animal Cognition* (In press). As these manuscripts have been published separately, they may contain repetition in background information and methodology. Tables and figures are numbered separately for each chapter. Pages are numbered sequentially throughout the thesis. References for each chapter have been combined into a single reference list at the end of the thesis.

# Chapter 2: Problem Solving in Animals: Proposal for an Ontogenetic Perspective

**Manuscript published in *Animals*** (Rowell, M.K., Pillay, N., & Rymer, T.L. (2021). Problem solving in animals: proposal for an ontogenetic perspective. *Animals, 11*, 866. https://doi.org/10.3390/ani11030866)

animals

MDPI

*Review*

Problem Solving in Animals: Proposal for an Ontogenetic Perspective

Misha K. Rowell [1,2,*], Neville Pillay [3] and Tasmin L. Rymer [1,2,3]

## Abstract

Problem solving, the act of overcoming an obstacle to obtain an incentive, has been studied in a wide variety of taxa, and is often based on simple strategies such as trial-and-error learning, instead of higher-order cognitive processes, such as insight. There are large variations in problem solving abilities between species, populations and individuals, and this variation could arise due to differences in development, and other intrinsic (genetic, neuroendocrine and aging) and extrinsic (environmental) factors. However, experimental studies investigating the ontogeny of problem solving are lacking. Here, I provide a comprehensive review of problem solving from an ontogenetic perspective. The focus is to highlight aspects of problem solving that have been overlooked in the current literature, and highlight why developmental influences of problem-solving ability are particularly important avenues for future investigation. I argue that the ultimate outcome of solving a problem is underpinned by interacting cognitive, physiological, and behavioural components, all of which are affected by ontogenetic factors. I emphasise that, due to the large number of confounding ontogenetic influences, an individual-centric approach is important for a full understanding of the development of problem solving.

## Introduction

Increasing concerns over human-induced rapid environmental change has led to a corresponding increase in interest in understanding how animals will cope with these challenges. Rapid and unpredictable changes may have significant effects on survival and coping ability (Rymer et al., 2013). In order to survive, animals need to gain information about the environment (e.g. relative predation risk and food availability). While this might sometimes be easily attained, such as directly observing fruit on a tree, obtaining resources or avoiding predation may require an ability to solve a problem, such as obtaining fruit that is out of reach.

Problem solving has been documented in all major vertebrate taxa, including mammals (e.g. food-baited puzzles in various mammalian carnivores, Benson-Amram et al., 2016), birds (e.g. food baited puzzles given to multiple parrot and corvid species, Lambert et al., 2019; Taylor, 2014), reptiles (e.g. multiple species of monitor lizards *Varanus* spp. are capable of solving food-baited puzzle boxes, Szabo et al., 2021), amphibians (e.g. detour task, where the animal had to move around an obstacle in brilliant thighed poison frogs *Allobates femoralis*, Munteanu et al., 2016), fishes (e.g. foraging innovation in guppies *Poecilia reticulata*, Laland & Reader, 1999), and some invertebrates (e.g. overcoming a physical barrier in leaf cutting ants *Atta colombica*, Dussutour et al., 2009).

Currently, there is no universally accepted definition of problem solving (Table 1). From my literature search (see below), most definitions consider mechanical (i.e., movements required to solve problems), morphological (i.e., physical structure to manipulate objects to solve a problem) and/or cognitive (i.e., assessing, learning, storing information about problem) components as part of problem-solving ability. I consider problem solving to be the ability of an individual to integrate the information it has gained (knowledge or behaviour) to move itself, or manipulate an object, to overcome a barrier, negative state or agent, and access a desired goal or incentive, such as a resource (Cauchard et al., 2013; Keagy et al., 2009). Most reports of problem solving are based on experimental evidence where animals are presented with a feeding motivation task (e.g. a puzzle box or detour task), in which an animal manipulates an object, or moves itself around the object, to access the food. Occasionally, animals are experimentally presented with an obstacle blocking access to a location, and the animal needs to move the obstacle to access a refuge or their nest. These solutions can be achieved by innovation (the use of a new behaviour, or existing behaviour in a new context, Reader & Laland, 2003) and/or by refining behaviour over repeated sessions with the stimulus (e.g. trial-and-error learning). My literature search has also demonstrated that problem solving is sometimes assessed simply as a dichotomous skill, in which an animal either can or cannot solve a problem, but other studies have focused on how animals vary in the way they solve problems, and how efficiently they solve problems. My definition encompasses all of these aspects.

**Table 2.1**. Definitions of problem solving and innovation quoted from the literature and associated references. I highlight the drivers (i.e., whether the ability to problem solve is linked to internal (e.g. physiology, cognition) or external (e.g. environmental) factors and the properties of the animal (mechanical/morphological abilities or cognitive abilities) that authors attribute to problem solving.

| Terminology | Drivers | Animal Properties | Definition | Reference |
|---|---|---|---|---|
| Innovation | Internal and External | Mechanical/ Morphology and Cognitive | A new or modified learned behaviour not previously found in the population | Kummer & Goodall, 1985 |
| Innovation | Internal and External | Mechanical/ Morphology and Cognitive | The ability to invent new behaviours, or to use existing behaviours in new contexts<br>A new or modified learned behaviour not previously found in the population<br>A process that results in new or modified learned behaviour and that introduces novel behavioural variants into a population's repertoire | Reader & Laland, 2003 |
| Innovation | Internal and External | Mechanical/ Morphology and Cognitive | The devising of new solutions | Dean et al., 2011 |
| Innovation | Internal and External | Cognitive | An animal's ability to apply previous knowledge to a novel problem or apply novel techniques to an old problem | Daniels et al., 2019 |
| Novel behaviour | Internal | Cognitive | The result of an orderly and dynamic competition among previously established behaviours, during which old behaviours blend or become interconnected in new ways | Epstein, 1999 |
| Physical problem solving | External | Mechanical/ Morphology | Use of novel means to reach a goal when direct means are unavailable | Seed & Call, 2010 |
| Problem solving | Internal | Cognitive | Overcoming an obstacle that is preventing animals from achieving their goal immediately | Duncker & Lees, 1945 |
| Problem solving | External | Mechanical/ Morphology and Cognitive | A problem exists when the goal that is sought is not directly attainable by the performance of a simple act available in the animal's repertoire; the solution calls for either a novel action or a new integration of available actions | Scheerer, 1963 |
| Problem solving | Internal | Cognitive | Any goal-directed sequence of cognitive operations | Anderson, 1980 |
| Problem solving | Internal and External | Mechanical/ Morphology and Cognitive | A goal-directed sequence of cognitive and affective operations as well as behavioural responses for the purpose of adapting to internal or external demands or challenges | Heppner & Krauskopf, 1987 |
| Problem solving | Internal | Cognitive | An analysis of means–end relationships | Hauser et al., 1999 |

| | | | | |
|---|---|---|---|---|
| Problem solving | External | Mechanical/ Morphology and Cognitive | A subset of instrumental responses that appear when an animal cannot achieve a goal using a direct action; the subject needs to perform a novel action or an innovative integration of available responses in order to solve the problem | Shimabukuro et al., 2015 |
| Problem solving | Internal | Mechanical/ Morphology | The ability to overcome obstacles and achieve a goal | Chow et al., 2017 |

Successful problem solving has been theorised to be important for survival, as it allows animals to adjust to changing environmental conditions (Sol et al., 2005) and even invade new environments (e.g. bird species introduced to New Zealand, Sol & Lefebvre, 2000), or to cope with harsh or extreme conditions (Kozlovsky et al., 2015). However, the ability of animals to solve problems (Thornton & Samson, 2012), and the specific strategy/manoeuvre that they use to solve problems (Heinrich & Bugnyar, 2005), is highly variable, and this variation can be observed at all taxonomic levels, including between families (e.g. Columbida vs. Icteridae, Webster & Lefebvre, 2001), genera (e.g. *Molothrus* vs. *Quiscalus*, Sol & Lefebvre, 2000), and species (jaguar *Panthera onca* vs. Amur tiger *P. tigris*, Benson-Amram et al., 2016). It is even possible that problem solving is phylogenetically conserved, with some groups having a greater potential to solve problems than others (MacLean et al., 2012). However, variation in problem-solving ability also occurs within species, including between populations (e.g. house finches *Haemorhous mexicanus* given extractive foraging tasks, Cook et al., 2017), and individuals (e.g. meerkats *Suricata suricatta* given food-baited puzzle boxes, Thornton & Samson, 2012). Likely causes of this variation are the conditions that arise during an individual's development. This variation could then allow problem-solving ability to be acted upon by natural selection (Benson-Amram et al., 2016), possibly impacting individual fitness. Therefore, understanding the influence of developmental factors on problem-solving ability is important.

An individual's behaviour, physiology and morphology may change as it grows and ages due to developmental changes in life history traits (Ryan & Wilczynski, 2011; Stamps, 2003). Furthermore, interactions and experiences with other individuals and the immediate environment further feedback into these systems (Groothuis & Trillmich, 2011). These intrinsic and extrinsic factors, either independently or synergistically, influence the individual's ability to cope with, and respond to, environmental challenges (Fraser & Gilliam, 1987), although their outcomes are likely difficult to predict because of myriad interacting factors.

Although aspects of behaviour, physiology and cognition have been studied in an ontogenetic context (Guenther et al., 2014; Rymer & Pillay, 2018) little is currently known about how problem-solving abilities develop and change as individuals grow and age. Developmental differences between individuals could fine tune or modulate the ability to solve problems, causing individual variation in this ability. Importantly, this inter-individual variation in problem solving could have fitness consequences by influencing survival and/or reproductive success. However, untangling the relative influence of intrinsic (genetic, neuroendocrine and aging) and extrinsic (environmental) factors on the development of problem solving is challenging (Cole et al., 2011; Rowe & Healy, 2014). I propose that an integrated approach, focusing on the development of problem solving, is needed to fully appreciate the ability and propensity of animals to solve novel problems. My aim was to review the literature on problem solving to document and then construct the links between intrinsic and extrinsic factors that influence the development of problem-solving.

I therefore conducted a literature search using Google Scholar and the Web of Science database. I included the general search terms “problem solving” “innovation” and “animal” in all searches and excluded all articles with the word “human”. This produced 6100 hits. I further refined the search by including the following as specific terms in individual searches: “development”, “ontogeny”, “heritability”, “personality”, “cognition”, “learning”, “experience”, “age”, “hormone”, “brain”, and “environment”. Articles that were repeated in subsequent searches were ignored. Articles were excluded if: (1) the researchers trained the animals to solve the problem before testing (and, therefore, tested memory rather than natural problem-solving ability); (2) the authors referred to a type of problem solving that did not meet my definition (e.g. relational problems where animals needed to extract and transfer rules between tests); and/or (3) development of problem solving was not investigated. If two papers found similar results (e.g. neophobia hinders problem solving in a bird species), I only reported on one study to avoid repetition and to reduce the overall number of citations.

Numerous studies have shown that animals can problem solve (Kaplan, 2015), and several studies have explored the fitness consequences of problem solving in animals (e.g. Cauchard et al., 2013). However, how problem solving develops is an area that has been little explored. In this paper, I first discuss how intrinsic and extrinsic factors influencing the ontogeny of individuals could affect the development of problem-solving ability. I focus on genetic (direct and indirect), neuroendocrine, and environmental (physical and social) factors, as well as age, learning and experience. Given the relative paucity of empirical studies investigating the development of problem solving in general (42 publications found of seven developmental factors), I demonstrate first how these factors impact other traits in order to create a conceptual framework for addressing problem solving. I acknowledge that limited information currently makes it challenging to separate developmental factors underlying problem-solving ability from other causal mechanisms (e.g. hormones, genetic effects). I then explore how interactions between intrinsic and extrinsic factors during an individual's development could influence problem solving indirectly. Specifically, I focus on how personality (individual differences in behaviour) and behavioural flexibility (ability to change behaviour in response to environmental cues) contribute to differences in problem-solving ability. Finally, I briefly discuss aspects that have been overlooked in studies investigating the development of problem solving, providing hypotheses for future testing. Throughout this paper, I advocate for an individual-centric approach to study the ontogeny of problem solving, where individual variation in solving ability is considered, rather than only using simple population-level averages. Future studies should be tailored to focus on individual differences within and between tests, as well as consider a longitudinal approach to track how individuals change over their lifetimes. Analyses of these experiments should then include individual data points as a measure of individual ability and variation, and should not exclude outliers because these account for the species or population-level variation.

## Factors Affecting the Development of Problem Solving

Problem solving is influenced by direct (Elliot & Scott, 1965) and indirect (epigenetic and transgenerational) genetic (Miller & Sweatt, 2007), and neuroendocrine (Bókony et al., 2014) factors (Figure 2.1). Furthermore, extrinsic factors, including both the physical and social environments, can also affect the development of problem solving (Figure 2.1). However, the development, and ultimately expression, of problem solving is more likely impacted by complex interactions between these intrinsic and extrinsic factors (Figure 2.1), and is also likely to change as the animal ages and experiences (i.e., learns) new situations (e.g. ravens *Corvus corax,* Heinrich & Bugnyar, 2005; North Island robins *Petroica longipes*, Shaw, 2017). Untangling these effects is likely to be challenging.

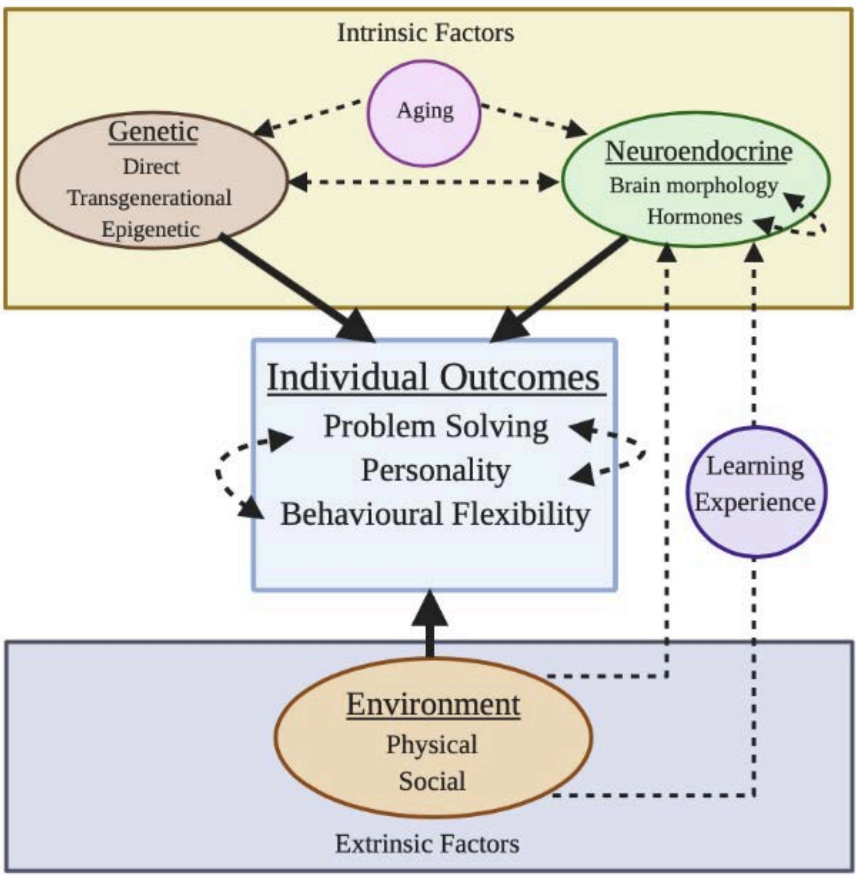

**Figure 2.1.** Intrinsic (genetic, neuroendocrine, and aging), extrinsic (environment) and acquired (learning and experience) factors influencing an individual's development directly (solid arrows) or indirectly (dashed arrows). Arrow heads indicate direction of influence.

## *Intrinsic Factors*

### *Direct Genetic Effects*

Heritable genetic effects influence the development of phenotypic traits. For example, physiological stress (barn swallows *Hirudo rustica*, Jenkins et al., 2014), parental care (African striped mice *Rhabdomys pumilio,* Rymer & Pillay, 2011), exploratory behaviour (great tits *Parus major,* Dingemanse et al., 2002), multiple aspects of cognition in chimpanzees *Pan troglodytes* (Hopkins et al., 2014), learning in hens *Gallus gallus domesticus* (Dudde et al., 2018) and spatial learning ability (C57BL/6Ibg and DBA/2Ibg mice *Mus musculus,* Upchurch & Wehner, 1989) all have a heritable component (but see Laumer et al., 2017).

Heritable genetic effects may also affect the development of problem solving (Figure 2.1), although this has received little attention in the literature. Elliot and Scott (1965) found that different dog *Canis lupus familiaris* breeds solved a complex barrier problem in different ways, and Audet et al. (2018) showed that an innovative species of Darwin's finches *Loxigilla barbadensis* had higher glutamate receptor expression (correlated with synaptic plasticity) than a closely related, poorly innovative species *Tiaris bicolor*. Tolman (1924) and Heron (1935) also indicated underlying genetic effects on maze-learning ability in rats, although the ability to learn a maze may not necessarily imply an ability to solve a problem (see Lagzi et al., 2010). In contrast, Quinn et al. (2016) and Bókony et al. (2017) found little measurable heritability of innovative problem-solving performance in great tits in a food-baited puzzle box and an obstacle-removal task, respectively. These studies suggest that the genetic architecture underlying problem solving may provide a rich area for future research.

### *Indirect Genetic Effects*

Indirect genetic factors, specifically epigenetic and transgenerational effects, influence how genes are read (e.g. DNA methylation, Bonduriansky & Day, 2009) or expressed (e.g. hormones activating genes during sexual maturation, Ma et al., 1992) without altering the underlying DNA. These epigenetic changes are underpinned by biochemical mechanisms that affect how easily the DNA can be transcribed (Gräff & Mansuy, 2008), subsequently influencing the development of different systems. For example, the activation of thyroid receptor genes (TRα and β) in the cerebellum of 0–19 day old chicks causes hormone-dependent neuron growth and development (Forrest et al., 1991). No studies to date have explored the effects of epigenetic factors on the development of problem solving, although this relationship can be postulated (Figure 2.1), since epigenetic factors influence the development of behaviour (e.g. maternal care, Liu et al., 2000), and cognition (e.g. memory, Miller & Sweatt, 2007). Memory is an important component of problem solving (Chapter 8; Rowell & Rymer, 2021b). Consequently, two possible routes could be inhibited via transcriptional silencing of the memory suppressor gene protein phosphatase 1 (PP1), and demethylation and transcriptional activation of the synaptic plasticity gene reelin, both of which enhance long-term potentiation. These could lead to increased memory formation (e.g. in male Sprague Dawley rats *Rattus norvegicus domesticus*, Miller & Sweatt, 2007).

Transgenerational epigenetic effects can also influence development. These effects result from parental or grandparental responses to prevailing environmental conditions, which influence how offspring and grand offspring ultimately respond to their own environment (Champagne, 2008). For example, embryonic exposure to the endocrine disruptor vinclozilin in female Sprague Dawley rats resulted in epigenetic reprogramming of hippocampal and amygdala genes for at least three generations, with the resulting F3 males showing decreased, and F3 females showing increased, anxiety-like behaviour, as adults (Skinner et al., 2008). An interesting avenue for research into transgenerational effects on the development of problem solving is the NMDA (N-methyl-D-aspartate) receptor/cAMP (cyclic adenosine monophosphate)/p38 MAP kinase (P38 mitogen-activated protein kinases) signalling cascade. Exposure of newly weaned Ras-GRF1 (growth regulating factor) knockout mice to an enriched environment enables this latent signalling pathway, rescuing defective long-term potentiation and learning ability (Li et al., 2006). These epigenetic effects may therefore influence problem-solving ability indirectly by affecting the individual's learning ability, or possibly directly by affecting the development of particular brain regions.

### *Neuroendocrine Effects—Brain Morphology*

Many developmental processes are driven by neuroendocrine factors that are, themselves, impacted by other developmental processes (Forrest et al., 1991). While the development of many of the brain's circuits (e.g. those located near the sensory or motor periphery), are governed by innate mechanisms (Knudsen, 2004), other parts (e.g. the basolateral nucleus of the amygdala and the cerebellar cortex, Medina et al., 2002; the CA1 region of the mammalian hippocampus, Malenka & Nicoll, 1999; the avian hippocampus, Sherry & Hoshooley, 2010) are considerably more plastic and more responsive to external stimuli, maintaining a high degree of neural plasticity throughout life. As these brain regions can be important for the expression of particular behaviours (e.g. the cerebellum is necessary for tool use, Iwaniuk et al., 2009), this plasticity has particular relevance for problem solving. For example, North American bird species with relatively larger forebrains were more likely to innovate when foraging than bird species with smaller forebrains (Lefebvre et al., 1997) and New Caledonian crows *C. moneduloides*, which are renowned for their tool use and problem-solving abilities, had relatively larger brains than other bird species (Mehlhorn et al., 2010). Similarly, C57BL/6J laboratory mice that received lesions to the hippocampus and medial prefrontal cortex initially showed impairments in solving a puzzle box task, although the mice ultimately solved the task over time, indicating the importance of experience and learning with repeated presentation of the task (Ben Abdallah et al., 2011).

### *Neuroendocrine Effects – Hormones*

The brain is also the central control of endocrine responses that can influence an individual's development (Figure 2.1). For example, the hypothalamic-pituitary-gonadal (HPG) axis activates gonadotropin-releasing hormone (GnRH), which stimulates the pituitary to produce luteinizing hormone (LH) and follicle-stimulating hormone (FSH, Meethal & Atwood, 2005). These hormones regulate the production of steroid hormones (testosterone and oestrogen) via the gonads (Kuiri-Hänninen et al., 2014), stimulating sexual maturity (Lincoln & Zuber, 1998). Fluctuations in steroids also influence cognitive function (Gibbs, 2005; Kimura & Hampson, 1994). For example, female rats injected neonatally with testosterone show heightened learning of a Lashley III maze (contains start box, maze, and goal box; used to test learning and memory) as adults compared to non-injected females, although the underlying impacts on neural development or neuroendocrine processes were not discussed (Stewart et al., 1975).

Endocrine responses can also feedback to brain morphology (Figure 2.1), affecting neural structure and function, which can impact behaviour, cognition, and development. The hypothalamic-pituitary-adrenocortical (HPA) axis regulates the secretion of adrenocorticotropic hormone (ACTH), which in turn regulates the secretion of glucocorticoid stress hormones (e.g. corticosterone, Belz et al., 2003) from the adrenal glands (Charmandari et al., 2005). Short-term exposure to corticosterone can improve learning, since it allows important associations to be formed, such as between threat and a behavioural response (Joëls et al., 2006). However, prolonged increased corticosterone concentrations (chronic physiological stress) reduce hippocampal neuron survival (Knapman et al., 2010), which interferes with learning (McLay et al., 1998; Yu et al., 2011), memory retrieval (Roozendaal, 2002) and problem solving. For example, house sparrows *Passer domesticus* with prolonged elevated corticosterone concentrations were less efficient problem solvers of puzzle boxes than birds with lower corticosterone concentrations, as stress impairs working memory and cognitive capacity (Bókony et al., 2014). Prolonged physiological stress can also cause detrimental developmental changes in morphology (e.g. chickens, Eriksen et al., 2003; Mashaly, 1991) and behaviour (e.g. rats, Belz et al., 2003).

In contrast to stress hormones, the mesolimbic dopaminergic system (Alcaro et al., 2007), which consists of the substantia nigra and ventral tegmental region (Brisch et al., 2014), regulates the production of dopamine, a hormone associated with motivation and reward-seeking (Laszy et al., 2005). Motivation is a physiological process (Laszy et al., 2005) that increases persistence and thereby increases the likelihood of successfully solving a problem (Griffin & Guez, 2014). Persistence is important for problem solving in foraging tasks in house sparrows (Papp et al., 2015), common pheasants *Phasianus* spp. (van Horik & Madden, 2016) and Indian mynas *Acridotheres tristis* (Lermite et al., 2017), and in puzzle box tasks in spotted hyenas *Crocuta crocuta* and lions *P. leo* (Borrego & Gaines, 2016). Changes to dopamine production can also negatively impact the development of sensorimotor integration (Nieoullon, 2002), disrupting approach, seeking and investigatory behaviours (Ikemoto & Panksepp, 1999) and acquisition of spatial discrimination (Taghzouti et al., 1985). Disruption to dopamine production, or other circuits, may also lead to an individual persisting with an inadequate strategy if the individual lacks inhibitory control (Kabadayi et al., 2017) and cannot recognise when to terminate the behaviour (Broom, 2011). Disruptions to these behaviours and cognitive functioning therefore impact foraging and exploratory behaviours (Broom, 2011; Yu et al., 2011), which can lead to undernutrition, and consequent negative impacts on growth and physical, behavioural, and cognitive development (Black et al., 2008).

Other hormones have also been implicated in the expression of problem solving. For example, both norepinephrine and serotonin likely impact problem solving, since they are related to cognitive flexibility (e.g. rhesus macaques *Macaca mulatta,* Izquierdo et al., 2007; Vallender et al., 2009), with serotonin activating, and norepinephrine deactivating, the prefrontal cortex (Fitzgerald, 2011). However, although some studies have investigated the role of these hormones in problem solving, these relationships are not clearly defined. For example, dietary deficiency in n-3 fatty acids during development increased serotonin receptor density and reduced dopamine receptor binding in the frontal cortex of rats, and it also altered dopamine metabolism (Delion et al., 1996; Zimmer et al., 1998). This dietary n-3 fatty acid deficiency also impaired problem solving in a delayed matching-to place task in the Morris water maze (Wainwright et al., 1991). However, whether problem-solving ability was impacted specifically by down-regulation of dopamine receptor binding, or up-regulation of serotonin receptor binding, is unclear.

## *Extrinsic Factors*

### *Physical Environmental Factors*

The physical environment varies in structural complexity and quality across both spatial and temporal scales (Wiens, 2000). Throughout its lifetime, an individual will experience daily and/or seasonal variation in environmental conditions (e.g. rainfall, temperature, food availability, Eccard et al., 2000), and/or when it disperses (Stamps & Swaisgood, 2007), migrates (Madsen & Shine, 1996) or travels into different areas. This variability changes the likelihood of an individual encountering positive (e.g. food, Sztainberg & Chen, 2010) or negative (e.g. predator, Husband & Bryden, 1996) stimuli, consequently influencing its development (Figure 2.1). For example, a higher density and abundance of aquatic snails results in the development of larger pharyngeal jaw muscles and stronger bones in predatory pumpkinseed sunfish *Lepomis gibbosus* (Wainwright et al., 1991).

Some studies have investigated the interplay between physical environmental conditions and problem-solving ability. Favourable environmental conditions can reduce stress (Johnstone et al., 2012), promote active and exploratory behaviours (Genaro & Schmidek, 2000) and enhance cognition (Nilsson et al., 1999), but harsh conditions may promote problem solving. For example, mountain chickadees *Poecile gambeli* living in harsher high elevation montane habitats with longer winters solved novel foraging problems significantly faster than chickadees living at lower elevations, most likely because finding food in these habitats was more challenging, and survival depends on plastic responses to these challenges (Kozlovsky et al., 2015). However, this effect on food-motivated problem-solving ability was not seen in great tits experiencing similar harsh conditions (Cole et al., 2011), suggesting that species-dependent developmental factors may be constrained by environmental effects. Urban environments may also promote the development of problem solving since they are expected to contain a higher frequency of novel problems for animals to solve. For example, house sparrows (Liker & Bókony, 2009) and house finches (Cook et al., 2017) in urban environments were more adept food-motivated problem solvers than birds from rural areas, particularly when the problem was difficult to solve (Papp et al., 2015).

### *Social Environmental Factors*

The social environment also changes throughout an individual's lifetime, and has the capacity to influence its development (Figure 2.1). Any positive (e.g. offspring suckling from mothers) or negative interactions (e.g. siblings fighting over food) between individuals can be considered social, and can vary over time scales (e.g. from daily interactions between individuals in a group, to shorter interactions between parents and offspring or mating partners, Bergman & Beehner, 2015).

For mammals, females are constrained to care for their offspring through pregnancy and suckling (Gittleman & Thompson, 1988). Consequently, the mother's physiological state and access to resources can impact offspring embryonic development prenatally through direct transfer of maternal hormones or nutrients across the placenta (Goebelsmann et al., 1972). For example, pregnant female Sprague Dawley rats exposed to unpredictable, variable stress (e.g. restraint, food restriction) during the final week of gestation produced anxious daughters and sons with impaired cognitive function (contextual memory, Schulz et al., 2011). Furthermore, maternal care during postnatal development (Liu et al., 2000), particularly the mother's diet quality, can also influence development. For example, protein deficiency in African striped mouse *Rhabdomys dilectus chakae* mothers during early postnatal development of offspring resulted in these offspring showing increased anxiety, decreased novel object recognition and increased aggression as adults compared to mice raised by mothers that did not experience nutrient deficiency (Pillay et al., 2016). Thus, detrimental developmental effects such as these may go on to impede offspring problem solving abilities.

For some species, a key developmental milestone is dispersal. Interactions with other conspecifics during this phase are often driven by dramatic developmental changes often associated with reproduction (Stamps & Swaisgood, 2007). For example, male vervet monkeys *Chlorocebus pygerythrus* leave their natal group at sexual maturity and attempt to attain dominance in another group (Cheney & Seyfarth, 1983), which could lead to increased access to food resources that can be channelled further into growth and development. This process of leaving the natal territory, and any social interactions during this time, can feedback to the individual to further affect its development. For example, in many species (e.g. brown rats), dispersing juveniles undergo a period of heightened exploration and learning, allowing them to rapidly adjust to new environmental conditions (Lynn & Brown, 2009). However, it is unknown how dispersal and other associated events impact an individual's problem-solving abilities.

Problem solving is most often studied in social animals (Bergman & Beehner, 2015), possibly because they are more conspicuous than solitary species. In some species, such as European starlings *Sturnus vulgaris* with a foraging task (Boogert et al., 2006), coyotes *Canis latrans* with a puzzle box task (Young et al., 2019) and rhesus macaques in an associative learning task (Drea & Wallen, 1999), dominant individuals are better learners and problem solvers. Similarly, the presence of an alpha individual impedes problem solving success in subordinate spotted hyenas presented with a puzzle box (Drea & Carter, 2009) and ravens in a string-pulling task (Heinrich & Bugnyar, 2005) due to direct interference and increased aggression from the dominant. However, in other species, such as blue tits *Cyanistes caeruleus* (Aplin et al., 2013), adult meerkats (Thornton & Samson, 2012) and chimpanzees (Reader & Laland, 2001), subdominants tend to be better solvers of puzzle boxes, since their lower competitive ability makes them more reliant on alternative methods for accessing resources (Kozlovsky et al., 2015). Group size may also influence problem solving, although results are equivocal. For example, larger groups of house sparrows (Liker & Bókony, 2009) and Australian magpies *Gymnorhina tibicen* (Ashton et al., 2019) in extractive foraging tasks and zebra fish *Danio rerio* in an avoidance task (Gleason et al., 1977) were better problem solvers than individuals in small groups, possibly because larger groups contained more reliable demonstrators. However, orange-winged amazons *Amazona amazonica* had similar solving success in a string-pulling task when tested in groups or in isolation (Krasheninnikova et al., 2013). Social carnivore species, such as banded mongoose *Mungos mungo*, were also less successful problem solvers of a puzzle box compared to solitary species, such as black bears *Ursus americanus* and wolverines *Gulo gulo*, suggesting that relative brain size may be more important for cognitive abilities than social environment (Holekamp et al., 2015).

Problem solving studies in solitary species are generally lacking, making it difficult to assess how social interactions may impact the development of problem solving in these species. However, it is evident that individual animals can solve problems in the absence of conspecifics. For example, black-throated monitor lizards *V. albigularis albigularis* (Manrod et al., 2008), eastern grey squirrels *Sciurus carolinensis* (Chow et al., 2016), and orangutans *Pongo pygmaeus* (Tecwyn et al., 2012) can individually solve puzzle boxes using flexible behaviours (i.e., switching strategies when necessary), persistence and learning. Similarly, North Island robins (Shaw, 2017) and brilliant-thighed poison frogs (Munteanu et al., 2016) can solve detour problem tasks when tested in their home territories. How solitary species solve problems in the presence of conspecifics, however, is an area for future investigation.

## Interacting Factors that Influence the Development of Problem Solving

### *Gene x Environment Interactions*

Genotype x environment interactions can also have a profound effect on the development of individuals (Figure 2.1). For example, the gene monoamine oxidase A (MAOA) encodes for an enzyme that impacts serotonergic activity in the central nervous system, leading to increased impulsivity and anxiety (Enoch et al., 2010). Stressful life events, or changes in social structure or status can alter the expression of this gene, leading to developmental changes during adulthood. For example, rhesus macaques raised in the absence of their parents showed increased aggression due to low MAOA enzymatic activity (Newman et al., 2005).

Although genotype x physical environment interactions have not been explored in the context of problem solving, environmental enrichment in captive bi-transgenic CK-p25 Tg laboratory mice is associated with the activation of plasticity genes, inducing chromatin modification via histone acetylation and methylation of histones 3 and 4 in the hippocampus and cortex, leading to increased numbers of dendrites and synapses (Fischer et al., 2007). This cascade of genetic and neuroendocrine processes functions to help restore learning and memory (Fischer et al., 2007), both of which are important for problem solving (Griffin & Guez, 2014; Chapter 8; Rowell & Rymer, 2021b).

Parents may also alter the environment (e.g. amount of parental care or food) their offspring experience (Champagne, 2008), which could be a consequence of genetic variation between mothers (Wolf et al., 1998) or a result of other factors (e.g. variability in resource availability, Strakovsky et al., 2011). When an offspring's development is impacted by this nongenetic parental environment, these effects are known as parental effects (Badyaev & Uller, 2009), which are specific types of indirect genetic effects (IGEs, Wolf et al., 1998). For example, female Long-Evans hooded rats that provided high levels of tactile stimulation (e.g. grooming and nursing, Liu et al., 2000) to their young produced daughters that also displayed higher levels of maternal care to their own offspring (Francis et al., 1999), indicating an IGE.

Maternal care also regulates the expression of the hippocampal glucocorticoid receptor gene by changing the acetylation of histones H3-K9 and the methylation of the NGFI-A consensus sequence on the exon 17 promoter (Fish et al., 2004). Young rats that experienced low levels of maternal tactile stimulation showed reductions in hippocampal neuron survival (Bredy et al., 2003b) and decreased hippocampal glucocorticoid receptor mRNA expression (Fish et al., 2004), leading to chronic corticosterone release as adults (Liu et al., 1997). Offspring also showed decreased exploratory behaviour (Caldji et al., 1998) and impairments in spatial learning and memory (Liu et al., 2000) and object recognition (Bredy et al., 2003a, 2003b) as adults. As for genotype x physical environment interactions, how the social environment x genotype interaction affects problem solving is a promising avenue for future research.

### *Neuroendocrine x Environment Interactions*

Habitat complexity, resource availability, and social complexity can influence development via effects on neuroendocrine systems, which can also result in changes to the social environment that may then feedback to further impact development. For example, nine-spined sticklebacks *Pungitius pungitius* preferentially shoal together in marine environments with high predation risk and patchy food resources, but prefer to swim alone when these constraints are relaxed in freshwater ponds (Herczeg et al., 2009). Marine fish with more social interactions had significantly larger olfactory bulbs and optic tecta, parts of the brain associated with sensory perception, compared to solitary fish from freshwater ponds that experienced fewer social interactions (Gonda et al., 2009b, 2009a). Rhesus macaques from larger social groups also had more grey matter and greater neural activity in the mid-superior temporal sulcus and rostral prefrontal cortex than macaques from smaller groups (Sallet et al., 2011). Similarly, structurally complex, changing environments improve survival of hippocampal cells and neurons by increasing the level of nerve growth factor in the hippocampus (Wiens, 2000), which increases hippocampal volume (Belz et al., 2003), leading to increased neural plasticity (Hoffmann et al., 2009) and a greater capacity to adjust to new environmental conditions (Berlucchi & Buchtel, 2009). Environmental enrichment has also been shown to enhance long-term potentiation in the hippocampus, which facilitates learning and memory (Arai & Feig, 2011), two important processes for problem solving (Chow et al., 2017; Griffin & Guez, 2014). Environmental enrichment has been associated with increased problem-solving ability in C57/BL6J mice in an obstruction puzzle task (O'Connor et al., 2014) and Labrador retrievers in puzzle box tasks (D'Aniello & Scandurra, 2016). This suggests causal links between the environment, the neuroendocrine system, and problem solving that are likely mediated by underlying genotype x environment interactions.

### *Age Effects*

Separating out the effects of aging and neuroendocrine or genetic effects on development is challenging. Nevertheless, age-specific effects on development, regardless of the underlying mechanisms, are an important consideration.

The nervous system shows age-dependent decreases in neurogenesis and plasticity, particularly in the dentate gyrus of the hippocampus (Shen et al., 1997), and the subventricular zone of the lateral ventricle (Smith et al., 2018), and these age-dependent changes can alter cognitive ability and behaviour (e.g. beagles, Milgram, 2003). Other neuroendocrine processes also naturally change with age. For example, as brown rats age, the ACTH response increases, glucocorticoid receptor binding capacity in the hippocampus and hypothalamus decreases, corticotropin releasing hormone (CRH) mRNA expression decreases in the paraventricular nucleus, and mineralocorticoid mRNA expression in the dentate gyrus of the hippocampus is reduced (Workel et al., 2001). These changes result in an associated attenuation of the corticosterone response to novelty (Milgram, 2003), as well as declines in spatial learning and memory (Frick et al., 1995).

Depending on the age of the individual, changes to both the physical and social environments also impact development (Arakawa, 2005). When raised in small cages with limited space, juvenile rats showed increased anxiety, and lower activity and exploration, whereas older rats did not (Arakawa, 2005). Similarly, older rats reared in larger groups were more active than juveniles, mostly likely due to increased frequency of social interactions and establishment of their rank within the social hierarchy (Arakawa, 2005).

Several studies have shown that juveniles are better problem solvers than adults, although the underlying mechanisms are currently not known. For example, juvenile Chimango caracaras *Milvago chimango* were more successful at solving a puzzle box task than adults (Biondi et al., 2010), and juvenile canaries *Serinus canaria* solved a vertical-string pulling task, whereas adults did not (Vince, 1958). Similarly, juvenile Chacma baboons *Papio ursinus* solved a hidden food task more often than adults (Carter et al., 2014), and juvenile kakas *Nestor meridionalis* showed higher innovation efficiency than adults across different tasks and contexts (Loepelt et al., 2016). Juveniles are often prone to higher levels of exploration (Arai & Feig, 2011), and are more playful (Pellis et al., 2010), than adult animals, allowing juveniles to rapidly gain motor skills (Pellis et al., 2010). This could possibly improve problem solving abilities of juveniles despite their lack of experience at solving tasks. However, results are species-specific, as Indian mynas (Griffin & Diquelou, 2015) and spotted hyenas (Benson-Amram & Holekamp, 2012) show no age-specific effects on problem solving in foraging tasks, while adult meerkats (Thornton & Samson, 2012) and black-capped chickadees (Prasher et al., 2019) were better innovators than juveniles in extractive foraging tasks.

## *Learning and Experience*

As an animal ages, it encounters predators and food resources, and interacts with conspecifics. These experiences provide a rich potential for learning, which is a critical component of problem solving. However, separating out the effects of the experience itself on development from other extrinsic and intrinsic factors, or their interactions, is challenging. Nevertheless, as in aging, an animal's development can be impacted by its experiences, particularly via learning, suggesting that experience must be considered when attempting to understand how problem solving develops.

To survive, use new resources, or avoid predators, individuals must learn to associate the experience with its significance (e.g. threat of a predator, Brown, 2003; Lönnstedt et al., 2012). Learning enables animals to acquire information about the state of their environment (Katz & Lachlan, 2003) and learning through experience allows for adjustments in physiological and behavioural responses (Brown, 2003). For example, repeated foot shock in a specific environmental location caused increases in norepinephrine and epinephrine in Sprague Dawley rats, eliciting fear and resulting in rats avoiding that location (McCarty & Kopin, 1978). Similarly, guppies decreased their time foraging in the presence of a predatory convict cichlid *Cichlasoma nigrofasciatum* (Dugatkin & Godin, 1992). Animals can learn to solve problems in different ways, such as through trial and error (e.g. rooks *C. frugilegus* across multiple foraging extraction tasks, Bird & Emery, 2009) or socially through local enhancement (e.g. common marmosets *Callithrix jacchus* in a foraging extraction task, Range & Huber, 2007), social facilitation (e.g. capuchin monkeys *Cebus apella* in a foraging extraction task, Fragaszy & Visalberghi, 1990) or copying/imitation (e.g. laboratory rats in an extractive foraging task, Heyes, 1993). Learning from previous experience is also an important component for successful problem solving. For example, grey squirrels improve their ability to solve a food-baited puzzle box with repeated exposures to the problem (Chow et al., 2017).

Similarly, North Island Robins became more efficient problem solvers of new food-extraction tasks with experience (Shaw, 2017).

### *Behavioural Flexibility and Personality*

Although development is governed by several unifying genetic and physiological mechanisms, and these processes are impacted by age and environmental effects (Diatchenko et al., 2005), the development of one individual differs considerably from that of another individual. Some of this variation can be attributed to the behavioural flexibility of each individual (Webster & Lefebvre, 2001) and/or its personality (Biondi et al., 2010), which also undergo developmental changes over the course of an individual's lifetime (Groothuis & Trillmich, 2011).

Behavioural flexibility is the ability to switch behavioural responses (likely due to cognitive flexibility, Griffin & Guez, 2014) to adjust to new situations or states (Tello-Ramos et al., 2018), and is likely governed by both genetic and non-genetic mechanisms (Kappeler & Kraus, 2010). The degree of behavioural and cognitive flexibility, and corresponding learning ability, is important for problem solving, as seen in tropical anoles (*Anolis evermanni* in an obstruction task, Leal & Powell, 2012; *A. sagrei* in a detour task, Storks & Leal, 2020), spotted hyenas in a puzzle box task (Benson-Amram & Holekamp, 2012), grey squirrels in a food-extraction task (Chow et al., 2016) and keas *N. notabilis* in a foraging extraction task (Auersperg et al., 2011). However, the degree of flexibility varies between species. For example, Indian mynas are more flexible, and are better innovative foraging problem solvers, than noisy miners *Manorina melanocephala* across a range of tasks (Griffin & Diquelou, 2015). Importantly, individual differences in behavioural and cognitive flexibility, particularly learning ability, are often attributed to physiological effects occurring during development (e.g. corticosterone exposure in nestling Florida scrub jays *Aphelocoma coerulescens*, Bebus et al., 2016).

An individual's development and experiences can also affect its personality (Miller et al., 2016), defined as consistent individual differences in behaviour shown across contexts and situations, and over time (Sih et al., 2004a). Personalities are often measured along different axes (e.g. bold/shy, Réale et al., 2007; proactive/reactive, Couchoux & Cresswell, 2012), and are mediated by hormones (Koolhaas et al., 1999). Although personality itself is influenced by intrinsic (e.g. hunger, Ariyomo & Watt, 2015) and extrinsic (e.g. environmental quality, Genaro & Schmidek, 2000) developmental factors, personality can further feedback on an individual's development through its effects on exploration (Arakawa, 2005). For example, avoidant individuals may be less willing to investigate their environment than exploratory individuals, which reduces their chances of being predated, but also reduces foraging rate, which affects growth, as seen in grey treefrog tadpoles *Hyla versicolor* (Relyea, 2003).

Personality can also impact problem solving (Cole et al., 2011). Exploratory individuals have higher interaction rates with problems, increasing their likelihood of solving innovative tasks. For example, brushtail possums *Trichosurus vulpecula* that were exploratory, active and vigilant were more likely to solve an escape-box task during the first trial, and were capable of solving a difficult task, compared to less exploratory, less active and less vigilant individuals (Wat et al., 2020). Similarly, exploratory fawn-footed mosaic-tailed rats *Melomys cervinipes* were faster problem solvers, and solved more problems, than avoidant individuals when tested with food- and escape-motivated tasks (Chapter 7; Rowell & Rymer, 2021a). Exploratory Carib grackles were also faster learners and more likely to innovate in a foraging-extraction task than avoidant individuals (Overington et al., 2011). However, this relationship is not always clearly defined. For example, both bold and shy chacma baboons improved their solving of a food extraction problem after watching a demonstrator (Carter et al., 2014). Similarly, bold meerkats that approached a puzzle box first were not always the first to solve it (Thornton & Samson, 2012), and neophobia did not significantly influence problem-solving ability in Barbary macaques *M. sylvanus* presented with puzzle boxes (Amici et al., 2019). Although relationships between personality, behavioural flexibility and problem solving are not clearly defined, such individual variation should be taken into consideration when investigating developmental effects on problem solving.

## Forgotten Components Limiting our Understanding of Problem Solving and its Development

Problem solving has been considered to rely almost exclusively on complex cognitive processes involving insightful thinking (i.e., just knowing what to do, rather than arriving at it through trial and error learning, Bird & Emery, 2009; Krasheninnikova et al., 2013), understanding of functionality or causal understanding (i.e., being able to understand rules and consequences of actions, Ortiz et al., 2019). Consequently, complex problem solving is often considered to be a consequence of relative brain size (e.g. birds and primates, Vince, 1958). However, there is little evidence that problem solving involves complicated cognitive processes (Heinrich & Bugnyar, 2005). For example, introduced black rats *R. rattus* in Australia have caused extensive damage to macadamia *Macadamia* sp. orchards (White et al., 1997). As rodents are evolutionarily constrained to gnaw due to the unrooted nature of their incisors (Hautier et al., 2011), gnawing is an effective strategy for accessing novel food resources behind barriers or hard seed coats. To solve the problem of accessing the new food, black rats required only persistence, motivation and the appropriate mechanical apparatus rather than complex cognitive abilities. While each animal's brain consists of a set of information-processing circuits that have evolved by natural selection to solve particular problems in their environment and increase their reproductive fitness (Cosmides & Tooby, 1994), without the appropriate mechanical apparatus, the animal cannot solve the problem (Tebbich et al., 2010). The ability to solve particular problems may therefore be species-specific, and morphologically constrained, specifically involving mechanical problem solving, unless animals can overcome these mechanical shortcomings (e.g. by developing tool use, Heinrich & Bugnyar, 2005).

Although problem solving has been studied in a wide variety of taxa, studies of the development of problem solving specifically have largely been restricted to birds (Kaplan, 2015), laboratory rats and mice (Iwaniuk et al., 2009; Stewart et al., 1975; Wainwright, 2002), dogs (Elliot & Scott, 1965), and primates that have been housed in captivity (Drea & Carter, 2009). This is largely due to difficulties associated with observing free-living individuals (Winkler et al., 2004) and accounting for their previous experience (Griffin & Guez, 2014). Consequently, studies rarely follow problem solving abilities over the development of individuals, instead comparing problem-solving ability between different age cohorts (Biondi et al., 2010). Such studies have shed light on the effects of intrinsic factors on the development of problem solving, but fail to consider individual variation in development.

Furthermore, the majority of studies on problem solving concern social species. Both solitary and social species need to problem solve, but the social environment could possibly influence how individuals develop their problem solving abilities. For example, social individuals may use social learning to problem solve, whereas solitary individuals would require persistence and motivation to achieve trial-and-error learning, or would rely on innovation because they are most likely unable to rely on social demonstrators for assistance (Bergman & Beehner, 2015; Carter et al., 2014), at least after weaning. Current studies therefore provide a limited view of the relevance of social conditions on problem solving development.

Finally, while the influences of environmental quality on problem-solving ability are documented, they are not well understood (Cole et al., 2011; Thornton & Samson, 2012). Animals tend to innovate under harsh conditions in times of necessity (Sol et al., 2002), yet good environmental conditions benefit problem solving by promoting neuroendocrine development (Nilsson et al., 1999) and reducing stress (Johnstone et al., 2012). The effects of the physical or social environment tend to be studied either through manipulation studies during early development, with subsequent tests occurring later on as adults in static environments (Workel et al., 2001) or via correlative studies, where individuals from different habitats are compared (Kozlovsky et al., 2015). Similarly, studies have investigated the impact of social rank (Drea & Carter, 2009), social isolation (Fone & Porkess, 2008), group size (Gleason et al., 1977; Liker & Bókony, 2009), and group composition (Benson-Amram et al., 2016; Thornton & Samson, 2012) on problem solving, but the majority of these studies have not explored the underlying developmental processes. To my knowledge, only one longitudinal study has tracked an individual's problem-solving ability in response to changing physical environments. Cole et al. (2011) found that individual performances in free-living great tits were consistent across time (seasonal variation). How problem-solving ability changes in response to changing social environments, such as when a subordinate changes dominance rank, has rarely been studied.

## An Individual-Centric Focus can be Beneficial

The ability to solve a problem relies on a combination of genetic and non-genetic factors (Miller & Sweatt, 2007), physiology (van Horik & Madden, 2016), behavioural flexibility (Griffin & Guez, 2014), general cognitive ability (Thornton & Samson, 2012), personality (Boogert et al., 2006) and mechanical ability (Chapman & Weiss, 2013). In addition, age and experience further influence problem-solving ability. Aging results in natural neuroendocrine system changes (Kuhn et al., 1996), which further affect behaviour and cognition (Smith et al., 2018). However, every individual develops along its own unique developmental trajectory within the phylogenetic constraints of the species, and the relative contribution of these intrinsic and extrinsic factors and their interactions are likely to vary considerably between individuals. Therefore, we cannot assume that individuals from the same environment (Wright et al., 2003), or even the same clutch/litter (Arnold & Bennett, 1984), will behave or respond to the environment in the same way. We only have to look at genetic clones (e.g. identical human twins displaying linguistic differences, Stromswold, 2006) to realise the uniqueness of individual developmental trajectories. This considerable variation argues strongly for focusing on individuals, particularly as they develop, learn and experience new things over their lifetimes in the context of problem solving. Therefore, when investigating problem solving abilities in the future, it may be beneficial to consider individual variation as an important aspect of the data analyses, and not just rejected as statistical 'white noise' (see Cole et al., 2011 and Shaw, 2017 for examples). Using this approach may enable future research to identify key predictors, or clusters of common predictors, of problem-solving ability.

## Conclusions

Individuals experience developmental changes over the course of their lifetimes, which impact their problem-solving abilities. The external environment, including the physical and social environments, can affect the development of problem solving via its impact on underlying genetic, non-genetic and neuroendocrine mechanisms. Problem solving has a heritable component in some species, while complex neuroendocrine processes are also involved in the development of problem solving. However, untangling the influence of these different factors on the development of problem solving is challenging, given their interdependence and complexity. Our understanding of how problem solving develops would benefit from studies of solitary species, to allow for comparisons of general causal mechanisms, since solitary species cannot rely on social learning about problems, at least after weaning. Furthermore, because environments are not static, future studies should consider the effects of changing environmental conditions over the course of an individual's lifetime on the development of problem solving. Importantly, investigating individual variation in problem-solving ability is necessary for a full understanding of the development of problem solving, which will allow us to assess the relative contributions of different developmental factors on this ability in different individuals.

# Chapter 3: Innovation in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*

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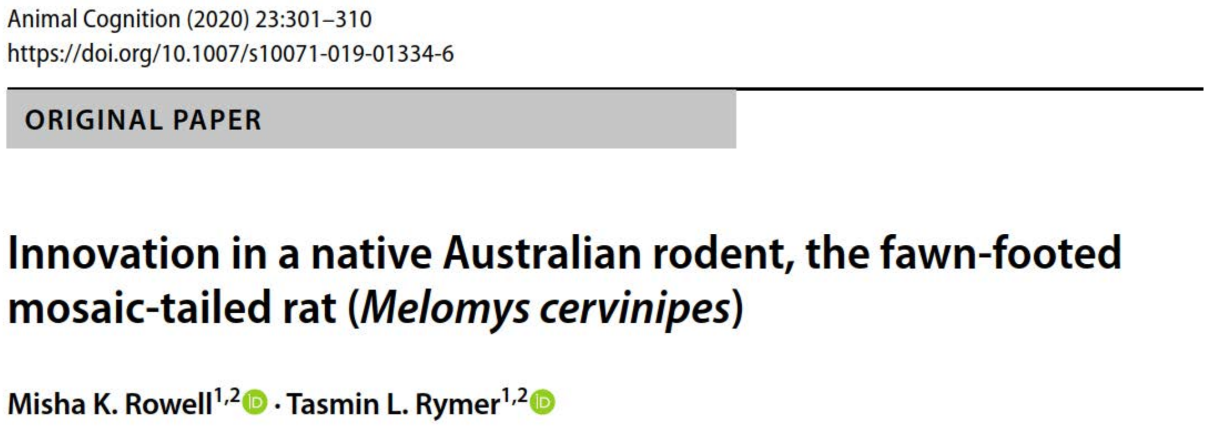

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ORIGINAL PAPER

## Innovation in a native Australian rodent, the fawn-footed mosaic-tailed rat (*Melomys cervinipes*)

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## Abstract

Innovation is the ability to use a new behaviour, or use an existing behaviour in a new context. Innovation, as an aspect of behavioural flexibility, could be important for allowing animals to cope with rapid environmental changes. Surprisingly few studies have focused on how innovation ability is affected by task complexity. I investigated innovation ability across multiple tasks of varying complexity in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*. I predicted that mosaic-tailed rats would be capable of innovating because they live in complex habitats, and can exploit disturbed and changing environments. However, I also predicted that the success rate of innovating would decrease as task complexity increased. Mosaic-tailed rats were exposed to six novel problems: cylinder, matchbox, obstruction test, pillar, tile, and lever (the last three presented in a Trixie dog activity board), which represented increasing complexity. I counted the number of individuals that could solve at least one task, compared individuals for solving efficiency and latency to solve, and compared the solving success of each task. All mosaic-tailed rats could innovate. However, solving success differed between individuals, with some solving every task and others only solving one. Solving success rate was significantly higher in the simplest task (pillar) compared to the most complicated task (lever). There was no effect of sex or sampling condition on innovation. This study is

the first to demonstrate innovation ability across task complexity in an Australian rodent, and provides promising avenues for future studies of innovation.

## Introduction

Many animals live in unpredictable environments, or environments that experience various changes. Environmental changes can be due to both natural (e.g. volcanoes) and/or anthropogenic factors (e.g. urbanisation). While natural selection provides the mechanism for populations to adjust to environmental conditions over generations (Hoffmann & Sgrò, 2011), current human-induced environmental change (HIREC) is occurring at a faster rate than adaptation will allow (Sih et al., 2016). Therefore, if individuals are to avoid extinction, they should flexibly adjust their behavioural responses to the changing conditions (Rymer et al., 2013).

An aspect of behavioural flexibility that has gained popularity recently is innovation, which is the ability of animals to use a new behaviour, or use an existing behaviour in a new context (Kummer & Goodall, 1985; Reader & Laland, 2003). For example, raccoons *Procyon lotor* exposed to a novel extractive foraging task solved the puzzle on the first presentation (Daniels et al., 2019). Similarly, guppies *Poecilia reticulata* solved an innovative foraging task without prior experience (Laland & Reader, 1999). Innovation has been recorded across multiple taxa (Laland & Reader, 1999; Lefebvre et al., 1997; Manrod et al., 2008; Reader & Laland, 2001), and is not restricted to species occupying specific ecological niches (e.g. Borrego & Gaines, 2016; Holekamp et al., 2015; Thornton & Samson, 2012) or diets (e.g. Guenther & Brust, 2017; Heinrich & Bugnyar, 2005; Tecwyn et al., 2012).

However, inter-individual variation in innovation is poorly understood. Performance has been shown to be affected by individual characteristics. A recent meta-analysis of innovation across species found that older individuals, and individuals of the larger sex, were more likely to innovate (Amici et al., 2019). Similar inter-individual differences have been found in other studies, where sex (e.g. female guppies were more likely to innovate than males, Laland & Reader, 1999), and age (e.g. adult primates were more likely to innovate than sub-adults, Reader & Laland, 2001) affect innovation rates. Other non-individual characteristics, such as sampling condition (e.g. captive spotted hyenas *Crocuta crocuta* were more likely to innovate than wild hyenas, Benson-Amram et al., 2013), or task complexity (e.g. fewer house sparrows *Passer domesticus* were capable of solving tasks when complexity increased, Papp et al., 2015), can also influence innovation propensity. However, these results are not consistent across all species. For example, Thornton & Samson (2012) found that male meerkats *Suricata suricatta* were more likely to innovate than females, and Biondi et al. (2010) found no difference in innovation propensity between juvenile and adult Chimango caracaras *Milvago chimango*.

Furthermore, few studies have explored how task complexity might impact innovation ability, with most studies only measuring innovation over one task (e.g. Borrego and Gaines, 2016). This is likely due to the difficulty of observing innovation in the wild, but may also be a consequence of a lack of consideration in studies on captive species, particularly as the literature on behavioural enrichment in captive environments often uses varying problem-solving tasks (e.g. different puzzle boxes given to lions *Panthera leo*, Borrego & Dowling, 2016; Borrego & Gaines, 2016). However, Guenther and Brust (2017) presented captive guinea pigs *Cavia porcellus* with three problem-solving tasks varying in difficulty and found that fewer individuals solved the most complex task.

To gain a greater understanding of how individuals vary in their innovation abilities, and how task-specific complexity may influence an individual's propensity to innovate, I tested the inter-individual variation of innovation ability across tasks of increasing complexity using a tropical rodent endemic to Australia, the fawn-footed mosaic-tailed rat *Melomys cervinipes*. Mosaic-tailed rats are medium-sized (72.9 ± 12.0 g) murid rodents found in forest areas along the eastern coast of Australia (Callaway et al., 2018). Mosaic-tailed rats are also common in disturbed forest edges and fragments (Laurance, 1994), which are known for having high levels of novel physical structures (e.g. increased liana presence and changing canopy connectedness, Laurance, 1994), predators (e.g. foxes *Vulpes vulpes* and feral cats *Felis catus*, Hobbs, 2001) and food sources (e.g. fruiting plants, Turner, 1996), suggesting that mosaic-tailed rats can cope with novel environmental challenges.

Individual mosaic-tailed rats were subjected to six novel problems over four testing sessions, increasing in complexity. Here, I considered complexity to be dependent on the amount of sensory information provided to the individual during solving, as well as the number of mechanical techniques required to solve the task. For example, the cylinder problem provided two types of cues (olfactory and visual), and could be solved using two techniques. Consequently, this was considered a simpler task than the matchbox task that only provided a single type of cue, but could be solved using one of three techniques. I presented mosaic-tailed rats with three tasks separately (cylinder, matchbox, and obstruction task), and three tasks concurrently (Trixie dog activity board: pillar, tile, and lever) to assess their potential to innovate. I expected that, given their capacity to exploit disturbed and changing environments, mosaic-tailed rats would be capable of innovating, and would be able to solve at least one novel problem. I further expected that the number of successful innovators would decline with increasing task complexity, as suggested by Papp et al. (2015). Due to conflicting results in the literature, I did not make *a priori* predictions regarding the direction of age effects, sex differences or sampling condition on innovation in mosaic-tailed rats.

## Methods

### *Ethical Note*

Permission to catch animals was granted by Queensland Parks and Wildlife (permit numbers WISP14530814 and WITK14530914). Mosaic-tailed rats were observed daily and weighed regularly to monitor health. Each individual received environmental enrichment, and experimental procedures did not have any negative effects on the animals. No animals experienced overt signs of stress (e.g. excessive vocalisations, seizing) during testing. Some animals experienced mild signs of stress (e.g. freezing) during the first few minutes of testing, particularly in the obstruction task. However, all individuals began moving freely soon after introduction to the different tests, apart from in the obstruction tests, where tests for two individuals were terminated as individuals remained frozen and could not easily be moved into the light compartment. Animals were monitored for 24 hours, and resumed normal behaviours and eating within this time. All animals had experienced other behavioural (but not problem solving) tests in the laboratory without any negative impacts prior to use in this study. At the end of the study, all animals were returned to the colony. The research adhered to the ABS/ASAB guidelines for the ethical treatment of animals (Vitale et al., 2018), and the Australian Code for the Care and Use of Animals for Scientific Purposes (National Health and Medical Research Council, 2013). The study was approved by the Animal Ethics Screening Committee of James Cook University (clearance number: A2539).

### *Subjects*

A colony of mosaic-tailed rats was founded in 2016 from 24 adult individuals trapped in forest areas on the James Cook University Cairns campus using Elliott traps. Subsequent to that, three additional adult females were collected between 2017 and 2018. Twenty-one offspring have currently been born in captivity. Thirty-four mosaic-tailed rats, comprising 19 (14 male and 5 female) of the original wild-caught individuals and 15 (9 male and 6 female) captive-born offspring were used in this study. All individuals were sexually mature at the time of testing, and individuals had been kept in captive conditions for at least 18 months. All mosaic-tailed rats were housed individually in wire-frame cages with a rectangular plastic base (36 cm wide ×29 cm long × 47 cm high) covered with ± 10 cm of wood shavings for bedding. A cylindrical plastic nest box (10 cm wide × 21 cm long × 10 cm high), hay and paper towel were provided for nesting material. Environmental enrichment items (e.g. plastic wheels, a cardboard roll, wire climbing platforms, and sticks and branches) were provided. Water was available *ad libitum*, and each individual was fed a diet of ± 5 g of mixed seeds and rodent chow (Vetafarm Origins), and ± 5 g of fruits or vegetables (e.g. apple, cucumber) daily.

### *Study Design*

Tests were conducted from August to December 2018. Testing occurred between 18h00 and 22h00, during the peak period of mosaic-tailed rat activity (Wood, 1971) under red light, except for the light/dark box test. Behaviour was recorded with a GoPro Hero5 or Sony HDR-CX405 Camcorder from above in the absence of observers. The duration of testing varied across the tests to allow for cross comparisons with other published studies in other species. Some tests occurred in the home cage (see below), while other tests occurred in an open field or light/dark box. Mosaic-tailed rats were given time to habituate to these novel arenas prior to testing (2 minutes in the obstruction test and 30 minutes for the activity board). They were tested individually in all cases, and returned to their home cage immediately after testing. The first three tests (see below) occurred in random order on consecutive nights, 24 hours apart. All mosaic-tailed rats received the last three tests concurrently (Trixie dog activity board; see below) one to two months later.

## *Problem Solving Tests*

No individuals had experienced problem-solving tests prior to this study. I assessed problem solving using three tests designed to be simple and solvable, using the natural movements of mosaic-tailed rats. This ensured the tests were ecologically relevant, and that they reflected the natural abilities of the animals. The tests also represented different contexts (food- vs. escape-motivated). I also assessed problem solving with an activity board that had multiple problems, representing increasing levels of complexity. In all tests, problem-solving performance was recorded as 'success' or 'failure' (1-0), which did not take into account the latency to solve the problem or interaction time (see solving success description for each puzzle below). Individuals were considered to have failed if they interacted with the task but did not solve it. I also considered the latency to solve the problem. Each problem was only presented to individuals once. All tests ended either when an individual solved a problem, or when the allocated time had elapsed (3 minutes for the obstruction test and 30 minutes for the other tests). A trial started when the individual or testing apparatus was placed in the testing space, or after the habituation period (see below).

### *Puzzle Boxes*

I used two food-baited puzzle boxes placed within the individuals' home cages to assess innovation in relation to foraging. The first puzzle box was a clear, cylindrical plastic tube (2 cm wide × 4 cm long × 2 cm high), with one closed end (Figure 3.1a). Small holes were made in the sides of the tube. 2 g of banana (a favoured food) was placed in the middle of the tube, and the open end was covered with a piece of tinfoil and secured with an elastic band. The cylinder was secured to a wire platform within the home cage of the animal to prevent the animal from manipulating it and moving it away. The rat could solve the problem by either pushing through the tinfoil or pulling the tinfoil off.

The second puzzle box was a cardboard matchbox (Redheads brand; 4 cm wide × 5 cm long × 1 cm high; Figure 3.1b). 2 g of banana was placed in the centre of the box, which was then placed in the matchbox sleeve. The matchbox was secured to the wire platform in the home cage. The rat could solve the problem by pulling or pushing the box out the cardboard sleeve, or chewing through the cardboard.

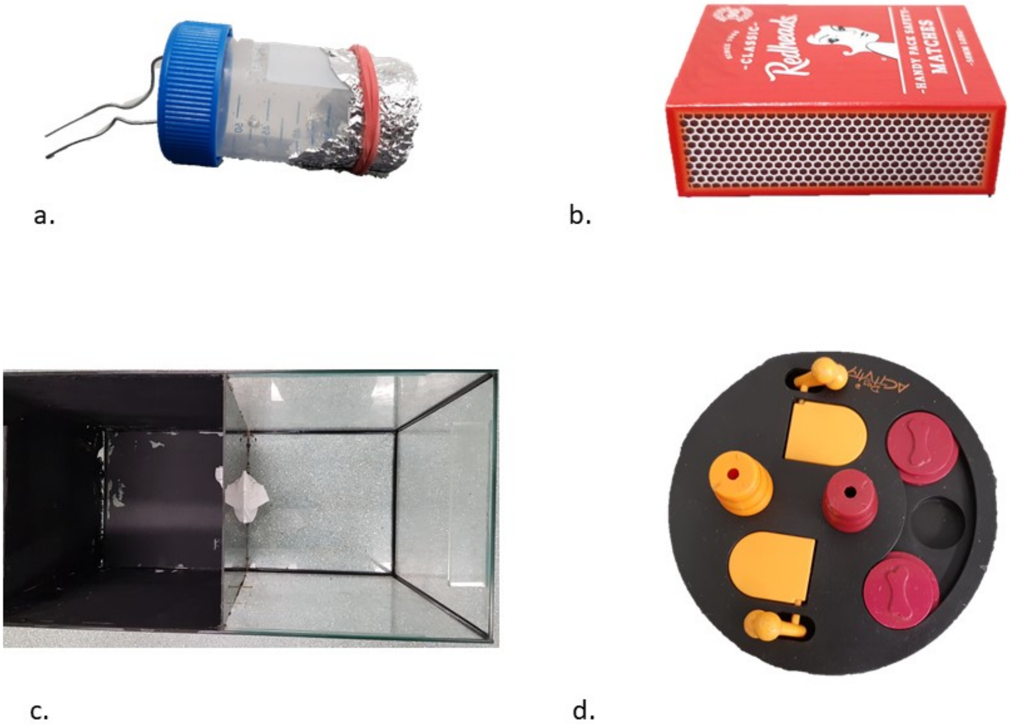

**Figure 3.1.** Problem-solving tests given to mosaic-tailed rats *Melomys cervinipes.* a) cylinder test: a plastic tube (2 × 4 × 2 cm) with food reward inside, tinfoil on one end and the other secured closed, with small holes poked in the plastic (placed directly in home cage); b) matchbox test: Redheads brand (4 × 5 × 1 cm) with food reward inside the cardboard sleeve (placed directly in home cage); c) obstruction test: light/dark box: glass tank (61 × 38 × 30 cm) divided in half with a plastic barrier, with one side painted black (dark compartment), the other side left clear (light compartment), a small door (10 × 10 cm) cut in the centre, and a piece of crumpled paper placed in the doorway; d) commercial Trixie dog activity board (level 2), with two pillars, two tiles and two levers of two colours (yellow and red).

### *Obstruction Test*

The obstruction test was conducted in a light/dark box (Ben Abdallah et al., 2011; O'Connor et al., 2014), to assess innovation in relation to perceived predation risk, as mosaic-tailed rats are nocturnal (Wood, 1971), and numerous nocturnal rodents are known to reduce activity under bright moonlight as this increases perceived predation risk (Daly et al., 1992; Wolfe & Summerlin, 1989). The light/dark box consisted of a glass tank (61cm long × 30 cm wide × 38 cm high) divided in half with a plastic barrier (Figure 3.1c). One side of the tank was painted black (dark compartment), and the other side remained clear (light compartment). A small door (10 × 10 cm) was cut into the barrier, and allowed the animal to move freely between compartments. A bright LED light was focused on the light compartment to simulate moonlight and heightened predation risk.

An individual was placed in the light compartment with the doorway open. Individuals were allowed to habituate to the light/dark box for two minutes, and could move freely between the light and dark compartments during this time. Thereafter, the animal was gently moved into the light compartment (if not there already), and the doorway was blocked with a crumpled piece of paper. The individual was then given three trials to solve the task in line with other studies (Ben Abdallah et al., 2011; O'Connor et al., 2014). In addition, as this test was expected to induce a freezing response under the light conditions (Delarue et al., 2020), repeating the trial multiple times increased the probability of measuring natural problem solving ability. Each trial lasted three minutes, with a two-minute rest period in between. This rest period is not sufficient for learning to properly occur, as memories take 1 to 2 hours to form (Euston et al., 2012), but allows a small respite from the stressful situation. The rat could solve the problem by either pushing the paper through the door into the dark compartment, or pulling the paper out the door into the light compartment.

### *Trixie Dog Activity Board*

Puzzle boxes containing multiple solving options or food chambers have been used to assess problem-solving ability with increasing complexity (Biondi et al., 2010). I used a level 2 Trixie dog activity board (similar to that used by Guenther & Brust, 2017) that had three types of problems: two pillars to push over, two tiles to slide, and two levers to pull that lifted up doors (Figure 3.1d). The activity board represented increasing levels of difficulty, from pushing over the pillars (simple) to manipulating the levers (hard).

The activity board was presented to individuals in an open field arena (57 cm long × 33 cm wide× 40 cm high). The board was presented to each individual for 30 minutes the night before testing to reduce neophobia to the novel arena and the board, and increasing the likelihood that the rats would interact with the board. Two sunflower seeds (a preferred seed type) were placed near each puzzle, and each puzzle was left open. Tasks could not be solved on this night as a result. Sunflower seeds were used in place of fruit, as pieces of fruit could be trapped in some of the puzzle mechanisms, making it difficult to clean and potentially leaving odour cues that could be used later.

The following night, two sunflower seeds were placed in each puzzle compartment, and the puzzles were closed. Individuals had access to all problems (two pillars, two tiles, and two levers) during this one testing session. The individual had to solve at least one of each task (pillar, tile, and lever) to be recorded as innovating for that individual task.

Because individuals had only 30 minutes to explore the board, I also measured the duration of time spent interacting with each puzzle (in seconds). I recorded the total time spent interacting with each puzzle type (pillar, tile, lever). Interactions included closely sniffing the puzzles, biting the puzzles, or physically manipulating the puzzles with the fore paws.

### *Statistical Analyses*

All analyses were performed 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 $\alpha = 0.05$. Two mosaic-tailed rats in each of the cylinder and matchbox tasks did not participate (i.e. did not interact with the task), while six individuals did not participate in the obstruction task. Because non-participation does not necessarily equate to an inability to innovate, data were adjusted accordingly prior to statistical analysis, and these data from these individuals for these tasks were excluded from analyses.

To determine if increasing task complexity affected the ability to innovate, I ran a general linear mixed effects model (lmerTest package; Kuznetsova et al., 2015) with binomial distribution and logit link function. Solving success (0 = failure; 1 = success) was the dependent variable. Sampling condition (captive-born or wild-caught), sex, and task (matchbox, cylinder, obstruction, pillar, tile and lever) were fixed factors, body mass was a continuous predictor and individual identity (ID) was the random factor. I did not include all interactions between fixed factors as the model failed to converge. To investigate the effect of individual identity on solving success, I conducted likelihood ratio tests and compared the model with the random factor of ID to a model without it. A Tukey's *post hoc* test was used to identify specific differences for significant predictors using the differences of least squares means method (lsmeans package: Lenth & Love, 2018).

I ran two general linear mixed effect models with negative binomial distribution (lmerTest package) to assess whether individuals interacted with the tasks for a different amount of time in the activity board, and whether the latency to solve all puzzles differed as a function of the complexity of the puzzle. In both models, sampling condition (captive-born or wild-caught), sex, and task (pillar, tile, and lever) were fixed factors, body mass was a continuous predictor and ID was the random factor. To investigate whether there was an effect of ID on the duration of interaction and the latency, I conducted likelihood ratio tests comparing each model with and without the random factor of ID. A Tukey's *post hoc* test was used to identify specific differences for significant predictors using the differences of least squares means method (lsmeans package).

## Results

All mosaic-tailed rats (34/34) were able to solve at least one task, indicating that they were capable of innovating (Figure 3.2). However, there were differences in the innovation abilities between individuals (Figure 3.2). Of the individuals that participated, four individuals (11.8%) solved all six tasks, 10 individuals (29.4%) solved five tasks, six individuals (17.6%) solved four tasks, three individuals (8.8%) solved three tasks, one individual (2.9%) solved two tasks and two individuals (5.9%) solved only one task (Figure 3.2). The solving performance of the top four innovators was significantly greater than the solving performance of the bottom two innovators (GLMER: $\chi^2_1 = 13.13$, $p < 0.001$; Figure 3.2).

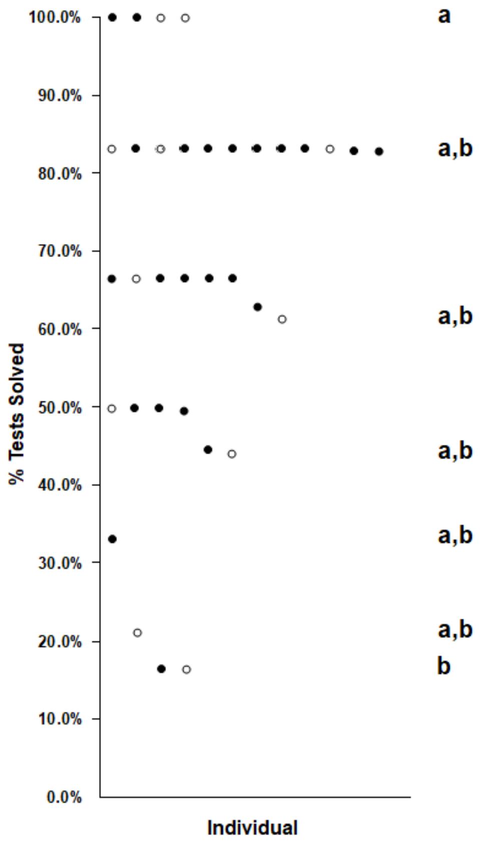

**Figure 3.2.** Solving success (%) of individual fawn-footed mosaic-tailed rats *Melomys cervinipes* across six problem-solving tasks (matchbox, cylinder, obstruction, pillar, tile, and lever). Each point represents a single individual. Males are represented as black circles and females are represented as white circles. Groups with the same letters indicate non-significant differences (Tukey's *post hoc* tests).

Task had a significant effect on solving success (GLMER: $\chi^2_5 = 34.54$, $p < 0.001$; Figure 3.3). Significantly fewer individuals were able to solve the lever task compared to all other tests (17.7% success), and significantly more individuals were capable of solving the pillar task (94.1%) and the cylinder task (87.5%) compared to the tile task (55.9%; Figure 3.3). I found no significant effect of body mass ($\chi^2_1 = 0.33$, $p = 0.567$), sex ($\chi^2_1 = 0.30$, $p = 0.584$) or sampling condition ($\chi^2_1 = 3.05$, $p = 0.081$) on solving success.

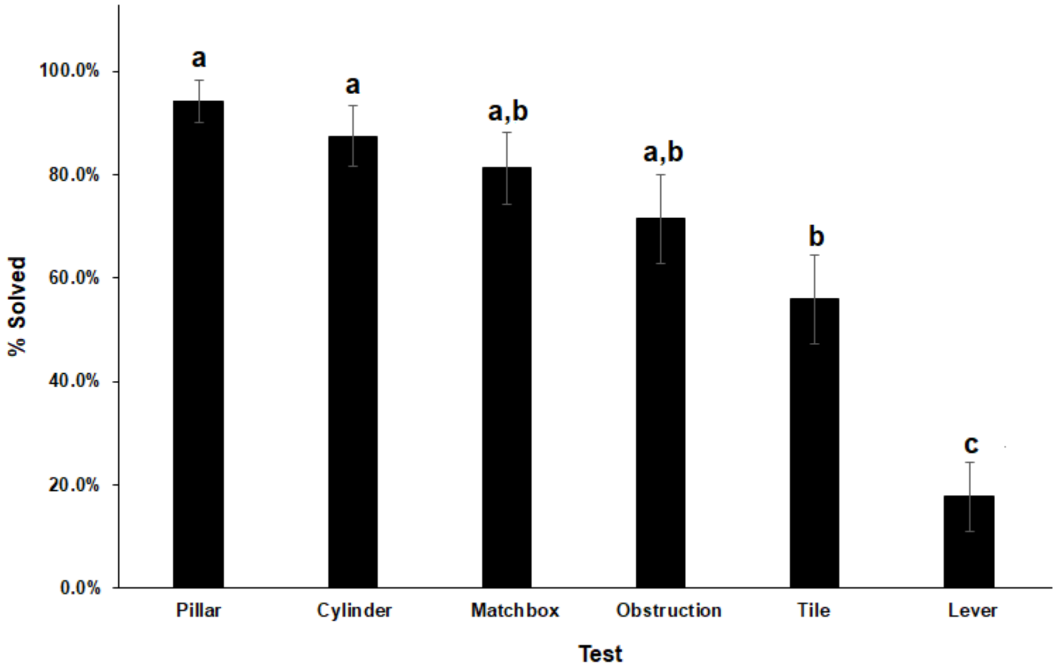

**Figure 3.3.** Mean ± SE solving success (%) of six problem tasks (matchbox, cylinder, obstruction, pillar, tile and lever) by mosaic-tailed rats *Melomys cervinipes*. Bars with the same letters indicate non-significant differences (Tukey's *post hoc* tests).

Task was a significant predictor of duration of interactions in the Trixie dog activity board ($\chi^2_2 = 37.69$, $p < 0.001$). Mosaic-tailed rats spent significantly more time interacting with the most complex lever task compared to the simpler pillar and tile tasks (Figure 3.4). I found no significant effect of body mass ($\chi^2_1 = 0.05$, $p = 0.831$), sex ($\chi^2_1 = 0.04$, $p = 0.839$) or sampling condition ($\chi^2_1 = 0.00$, $p = 0.951$) on duration of interactions.

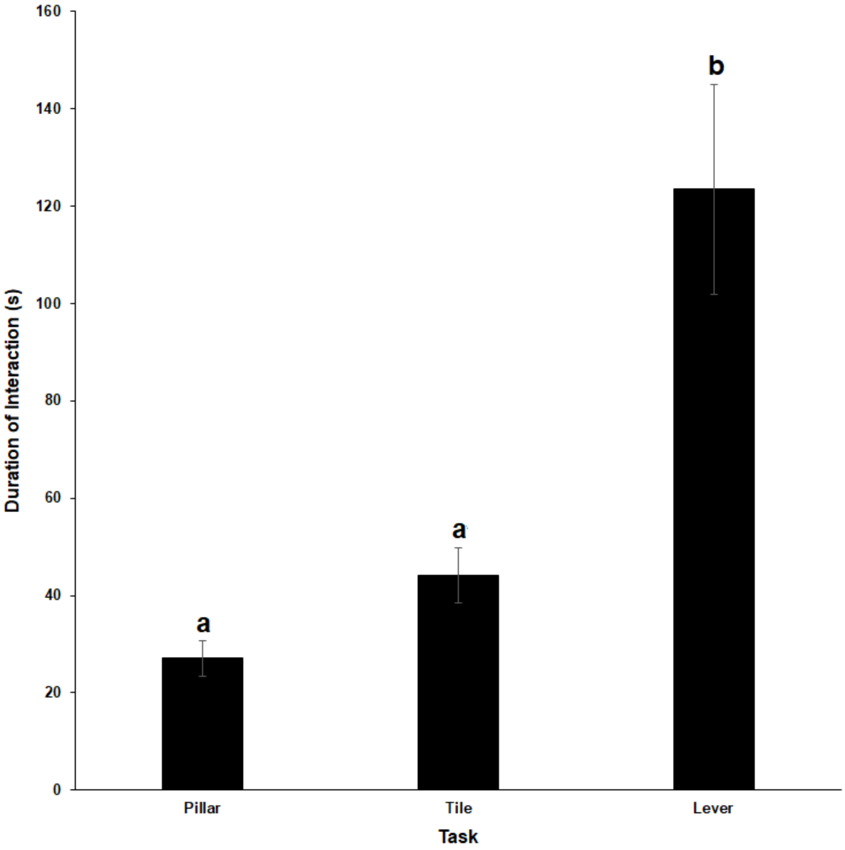

**Figure 3.4.** Mean ± SE duration of time (s) spent interacting with the puzzles in the Trixie dog activity board task (pillar, tile and lever) by mosaic-tailed rats *Melomys cervinipes*. Bars with the same letters indicate non-significant differences (Tukey's *post hoc* tests).

Task was a significant predictor of the latency to solve the puzzle ($\chi^2_5 = 88.06$, $p < 0.001$). Mosaic-tailed rats solved the obstruction task significantly faster than all other tasks (Figure 3.5). Mosaic-tailed rats also took significantly longer to solve the lever task compared to all other tasks, except the tile task (Figure 3.5). I found no significant effect of body mass ($\chi^2_1 = 0.31$, $p = 0.575$), sex ($\chi^2_1 = 1.64$, $p = 0.200$) or sampling condition ($\chi^2_1 = 2.14$, $p = 0.144$) on latency to solve a puzzle.

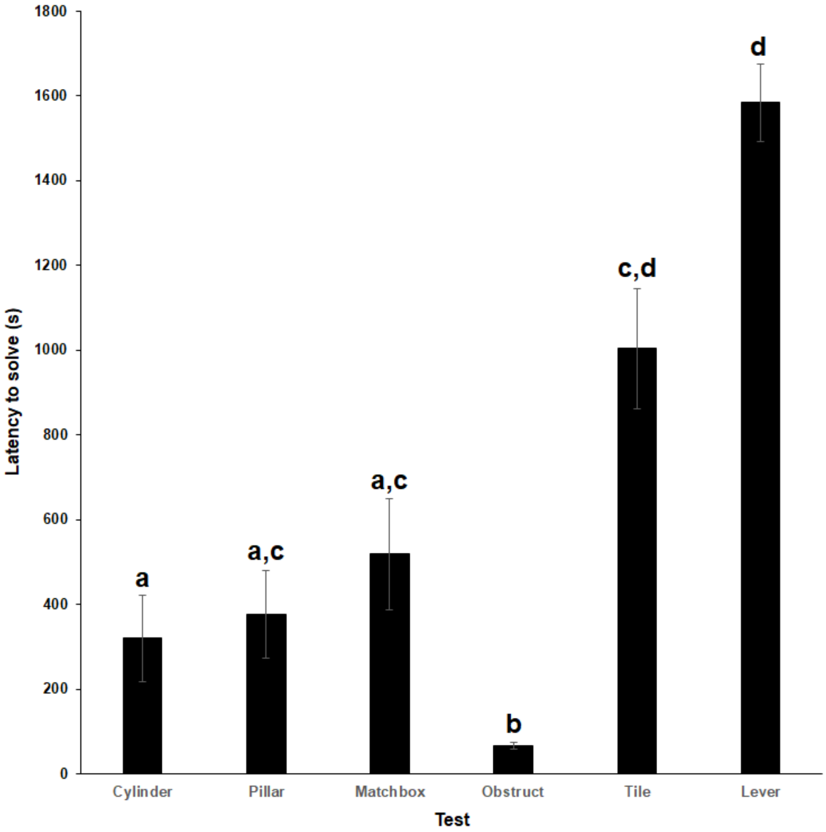

**Figure 3.5.** Mean ± SE latency (s) to solve six problem tasks (matchbox, cylinder, obstruction, pillar, tile and lever) by mosaic-tailed rats *Melomys cervinipes*. Bars with the same letters indicate non-significant differences (Tukey's *post hoc* tests).

## Discussion

Few studies have investigated problem-solving ability using multiple tasks, with even less considering how task complexity might impact innovation ability (but see Chow et al., 2018; Papp et al., 2015). Therefore, I investigated innovation ability in a native Australian rodent in six tasks that showed increases in complexity. As predicted, all mosaic-tailed rats were able to innovate and solve at least one novel problem without prior experience or training. The ability to innovate has been found in a variety of mammals (Griffin & Guez, 2014), such as meerkats (Thornton & Samson, 2012) and spotted hyenas (Benson-Amram et al., 2013). Furthermore, a few studies in rodents have also shown innovation ability. Solving success was comparable to these other studies (25-64% in guinea pigs, Guenther & Brust, 2017; 50-90% in squirrels, Chow et al., 2018).

As expected, I also found that the number of successful innovators decreased as the complexity of the task increased. This is consistent with Chow et al. (2018), who found that 50-93% of squirrels solved an easy task compared to 29-64% of squirrels that solved a more difficult task. Individuals within a species (Holekamp et al., 2015), and even within populations (Benson-Amram & Holekamp, 2012), have different innovation abilities, with some individuals being ‘good’ innovators that are able to solve more complex tasks than others. This could be due to differences in persistence (Griffin & Guez, 2014), motivation (van Horik & Madden, 2016) and general cognitive ability (Griffin & Guez, 2014). In addition, personality has been suggested to be a factor influencing problem-solving ability, with more exploratory, less neophobic individuals being more likely to innovate (Guenther & Brust, 2017). I found that mosaic-tailed rats spent more time interacting with the most difficult lever task in the activity board test, suggesting that the lower solving success for this task was not due to a lack of persistence or motivation by the rats in general. However, some individuals spent less time interacting with all tests, suggesting individual variation in cognitive abilities, personalities or motivation could be affecting how they interact with tasks in general. Which factor(s) could be contributing to the differences in innovation ability between mosaic-tailed rats remains to be tested.

The latency to solve the puzzle was affected by the type of puzzle. Interestingly, mosaic-tailed rats solved the obstruction task significantly faster than all other tasks, even though I considered it to be more complex than some other tasks. It is likely that the nature of the task, rather than its level of complexity, affected the latency to solve it. It was the only task that was not food motivated, and it simulated a high predation risk environment. Consequently, mosaic-tailed rats may have been more motivated to solve this task because of the stress and risk associated with the task (Ben Abdallah et al., 2011), rather than its complexity *per se.*

Interestingly, there were no sex differences in innovation. Laland & Reader (1999) suggested that female guppies are more likely to innovate than males, while Reader & Laland (2001) and Guenther & Brust (2017) suggested that male primates and guinea pigs are more likely to innovate than females. Fluctuations in sex hormones (testosterone and oestradiol) are known to influence cognitive function in people (Kimura & Hampson, 1994) and Sprague-Dawley rats (Gibbs, 2005), suggesting potential impacts on problem solving and innovation. However, Kozlovsky et al. (2015) found no sex differences in problem-solving ability in mountain chickadees *Poecile gambeli*. Sex differences are thought to evolve over long evolutionary time scales, needing strong selection pressures to evolve (Sherry et al., 1992). It is possible that there is no selective advantage for one sex having better innovation abilities than the other in mosaic-tailed rats. However, this requires specific testing.

Innovation success rate was not influenced by sampling condition, and captive-born individuals did not solve significantly more tasks than wild-born individuals that had been in captivity for at least 18 months. However, although not significantly different, 74% of captive-born individuals solved the tasks compared to only 63% of wild-caught individuals. This is consistent with other studies, showing that captive individuals are more innovative due to lowered neophobia and greater exploration than wild individuals (Benson-Amram et al., 2013). One reason why there was no effect of sampling condition in this study could be due to the length of time individuals had been housed in captivity prior to testing. All individuals had been living in laboratory conditions for at least 18 months, suggesting that the effects of captivity could mitigate changes in innovation capacity. Alternatively, early life conditions, rather than adult experiences, could be more influential in impacting innovation success. Some studies (e.g. hyenas, Benson-Amram & Holekamp, 2012; meerkats, Thornton & Samson, 2012) show age-specific differences in innovation ability. All mosaic-tailed rats in this study were over one year old at testing, and all were sexually mature. I could not include specific age in the model, as I could not determine with accuracy the age of wild-caught individuals. However, it would be beneficial to assess the effects of age on innovation ability in future studies.

I found that mosaic-tailed rats are capable of solving novel problems, indicating that they can innovate. Furthermore, I found that individuals varied considerably in their ability to innovate and solve the problems presented to them, and that the likelihood of solving a problem decreased with increased complexity. While rodents are exceptionally diverse, the innovation ability of wild rodents is understudied, and Australian rodents in particular appear to be particularly poorly studied. To my knowledge, this is the first reported study of innovation in an Australian rodent species. The high levels of innovation observed in this study suggest that mosaic-tailed rats could be a good model species for investigating cognition in general.

# Chapter 4: Is problem solving in fawn-footed mosaic-tailed rats *Melomys cervinipes* influenced by maternal care or genetic effects?

## Abstract

Innovative problem solving is thought to be a flexible trait that allows animals to adjust to changing or challenging environmental conditions. However, it is not known how problem solving develops during an animal's early life, or whether it may have a heritable component. I investigated whether maternal genetic and non-genetic effects influenced problem solving ability in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*. I measured direct (time spent grooming and huddling), indirect (time spent nesting), and total amount of maternal care received across pup development (postnatal days 1-13). I measured problem solving in juveniles using matchbox tasks, and in mothers and adult offspring using six tasks of varying complexity (matchbox, cylinder, obstruction, pillar, tile, and lever tasks). I found no relationship between any maternal care measures and problem solving abilities across multiple tests. I also found that problem solving only had a small heritable, non-significant, component in some tasks, but this requires further investigation. These results suggest that problem solving is unlikely to be constrained by maternal effects experienced during early development, and is, instead, more likely to be influenced by other factors (e.g. experience) later in an individual's lifetime.

## Introduction

Behavioural and cognitive traits can allow animals to rapidly adjust to changing environmental conditions (Sol et al., 2002), and to cope with harsh conditions (Kozlovsky et al., 2015). While these traits are often flexible (Blackenhorn & Perner, 1994), changing throughout an individual's lifetime as it develops and experiences new situations, there may be some constraints on how much a trait can change over time. Many behavioural and cognitive traits have a genetic basis (Barlow, 1991) For example, exploratory behaviour in great tits *Parus major* (Dingemanse et al., 2002), and spatial learning ability in C57BL/6Ibg and DBA/2Ibg mice *Mus musculus* (Upchurch & Wehner, 1989) both have a heritable component, which may limit the flexibility of behaviour or cognition in offspring.

The development of behavioural and cognitive traits may be affected by non-genetic effects experienced during early life. In mammals, behavioural and cognitive development can be affected by the mother's physiological state *in utero* (Liu et al., 1997), as hormones (e.g. cortisol, Van den Bergh et al., 2005) can be transferred from the mother to the offspring via the placenta. These physiological changes can then impact neural development, physiological states, and behavioural phenotypes of the offspring (Rymer & Pillay, 2013). Once the offspring are born, the quality and quantity of care provided by the parents can further affect how the offspring develop via epigenetic factors. For example, female Long-Evans hooded rats *Rattus norvegicus* differ in the amount of tactile stimulation (licking and grooming) they provide to offspring (Liu et al., 2000). Offspring that receive low levels of stimulation show a chronic stress response (Liu et al., 1997), lower exploratory behaviour (Caldji et al., 1998), and impaired spatial learning and memory (Liu et al., 2000) as adults compared to offspring that receive high levels of licking and grooming.

While genetic and non-genetic parental effects on offspring behavioural and cognitive development have been widely considered (e.g. Francis & Meaney, 1999; Kikusui et al., 2005), little attention has been given to genetic and non-genetic parental effects on innovative problem solving. Problem solving is an animal's ability to move itself or an object to overcome an obstacle or barrier and access a desired goal (Rowell et al., 2021). As problem solving is largely dependent on an individual's exploratory behaviour and learning ability (Griffin & Guez, 2014), which both have a heritable component in some species (Dingemanse et al., 2002; Upchurch & Wehner, 1989), it is possible that problem solving could, at least partially, be heritable. However, the few studies that have investigated these relationships have only focused on birds. Quinn et al. (2016) and Bókony et al. (2017) both found that problem solving measures had low or no heritable component in wild great tits. Furthermore, exploration and learning are also impaired by poor maternal care (Caldji et al., 1998; Liu et al., 2000), suggesting that non-genetic effects may also impair problem solving. However, maternal feeding behaviour in great tits did not significantly affect the problem solving performance of offspring (Quinn et al., 2016). Therefore, the lack of studies makes broader generalisations challenging. In addition, no studies have investigated both genetic and non-genetic effects simultaneously.

Therefore, we investigated the influence of maternal genetic and non-genetic effects on innovative problem solving in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*. Mosaic-tailed rats are commonly found in various types of forests along the eastern coast of Australia (Moore et al., 2008). They are an endemic rodent, and females have up to 4 pups per litter and show a prolonged period of pre- and post-natal care (Callaway et al., 2018). Pups nipple cling to the mother at least until their eyes open (approx. 9 days old, Rowell & Rymer, 2020a), suggesting a heightened level of maternal care may be present. Mosaic-tailed rats are capable of solving problems even as juveniles (unpub. data) and adults show individual differences in solving ability (Rowell & Rymer, 2020b), possibly due to genetic and epigenetic effects.

Mosaic-tailed rat pups used in this study were raised in captivity by their mothers. I quantified maternal care (grooming, huddling, nesting) given to the pups in each litter. Thereafter, I exposed pups to three trials of problem solving tests using food-baited matchbox tasks, with each testing session lasting 20 minutes. I measured how long it took pups to first solve the task across the three trials (i.e. maximum of 3600 seconds) and compared this to the level of maternal care received. I also tested problem solving performance of mothers and pups as adults across six tasks (matchbox task, cylinder task, pillar task, tile task, lever task, and obstruction task) to estimate the narrow-sense heritability of problem solving and to assess long-term effects of maternal care on problem solving. While there are only a few studies exploring maternal genetic and non-genetic effects on problem solving, many studies have looked at how these factors influence other behaviours that are known to be important for problem solving (e.g. exploratory behaviour, Champagne, 2008; Dingemanse et al., 2002; learning, Liu et al., 2000; Upchurch & Wehner, 1989). I hypothesised that both maternal genetic and non-genetic effects would influence offspring problem solving performance. I predicted that pups born to mothers that provided high levels of care would be better problem solvers than pups born to mothers that provided less care, indicating a non-genetic maternal effect, as increased care is associated with more exploratory offspring (Champagne, 2008). I also predicted that mothers that were good problem solvers would have offspring that were also good problem solvers, indicating a heritable component for problem solving, as exploratory behaviour (Dingemanse et al., 2002) and learning ability (Upchurch & Wehner, 1989) have heritable components in other species.

## Methods

### *Ethical Note*

Adult female mosaic-tailed rats were trapped with permission from the Queensland Department of Environment of Science (permit numbers WISP14530814, WITK14530914, WA0014502 and PTU19-001632). All mosaic-tailed rats were maintained in captivity as part of a breeding colony in accordance with James Cook University Animal Ethics Screening (clearance number A2539). The research and husbandry methodologies followed the ABS/ASAB guidelines for the ethical treatment of animals (Bee et al., 2020), and the Australian Code for the Care and Use of Animals for Scientific Purposes (National Health and Medical Research Council (NHMRC), 2013). No signs of excessive stress were recorded in any of the animals, and experimental procedures did not have any negative impacts on the animals (e.g. excessive vocalising, sudden weight changes).

### *Animal Husbandry*

Ten adult female mosaic-tailed rats and their offspring (n = 21) were used for the maternal care experiment (described below). During this time, animals were kept in glass tanks (44 x 35 x 32 cm) under a 12:12 h light/dark cycle in partially controlled temperature conditions (22 – 26 °C). Tanks contained approximately 5 cm of wood shavings, and a cylindrical plastic nest box (11 x 11 x 20 cm) filled with a handful of pasture hay and two pieces of paper towel for nesting material. Cardboard rolls for chewing and sticks for climbing were provided for behavioural enrichment (Rader & Krockenberger, 2006). While with pups, females were fed daily 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), depending on the size, age, and health of the pups. Water was available *ad libitum*. Pups were briefly removed from their mothers every second day from 3 days old to measure behavioural and physical development (see Rowell & Rymer, 2020a). Pups were returned to their mothers after measurements. Pups were weaned from their mothers at 21 days old. Mothers were removed from the tanks and housed individually in wireframe cages (described below). Siblings were kept together in the tank until juvenile testing was complete (see below).

These individuals (n = 31), and a further six adult females and their adult offspring (n = 13) were also used in the heritability experiment (described below). For this study, animals were individually housed in wireframe cages (34.5 × 28 × 38 cm) with deep plastic bases (34.5 × 28 × 11 cm) containing approximately 10 cm of wood shavings. Nesting and enrichment items as described above were placed in the cages, as well as a wire shelf to facilitate climbing. Individuals were each given 5 g of mixed seed and rodent chow, and 5 g vegetable/fruit daily.

## *General Testing Procedures*

Data collection occurred between August 2018 and March 2021. Tests were conducted during the peak activity period of mosaic-tailed rats (18h00-22h00, Wood, 1971) under red light (except for the obstruction test, see below), which does not interfere with mosaic-tailed rat behaviours (Paulling et al., 2019; Rowell & Rymer, 2021a, 2021b). To encourage animals to interact with the food-related puzzle tests, animals were not fed on the days of these tests until after the tests were complete.

### *Maternal Care*

Maternal care was quantified every second night, for a total of six sessions, commencing when pups were two days old. Mothers and pups were briefly moved out of the nest and placed in an empty plastic box. The nesting cylinder was placed back in the tank, and the nesting material (except for a few strips of paper towel) was removed for the duration of the test to allow the mother to be easily filmed. The mother and pups were then gently returned to the front of the nest box. I recorded the mother's behaviour for 20 minutes, including time spent huddling over the pups, time spent licking and grooming pups, and time spent moving the nesting material around. I combined the time spent grooming and the time spent huddling over pups across all nights to produce a total direct care measure. I also combined the time spent nesting across all nights to produce a total indirect care value. The total duration of all three behaviours for each night were also added together to produce a total measure of maternal care. As I could not tell which specific pup was receiving care at any time, these care measures were divided by the number of pups in each litter to calculate the average amount of care given to each individual pup.

### *Juvenile Problem Solving*

Juvenile mosaic-tailed rats experienced three problem solving sessions while they were between 16 and 56 days old to investigate the effects of maternal care on early experiences of problem solving. Each testing session was conducted 10 days apart. For these tests, juveniles were placed in an open field arena (57 x 33 x 40 cm) with two food-baited cardboard matchboxes scaled to body size (small: 4 x 2 x 1, medium: 6 x 3 x 1.5, large: 7 x 5 x 2 cm). Juveniles could push or pull the box out of the sleeve, or could chew through the sleeve, to access the food reward. Juveniles were each given 20 minutes for each testing session. Juveniles were originally divided into two groups, where one group was tested earlier in development (16- to 36-days old), and the other was tested later in development (36- to 56-days old). However, as I found no age-effects on solving ability, individuals were combined into one group for the analyses. I recorded the latency to first solve the task, regardless of what session it was solved in (i.e. up to 3600 seconds), to avoid the effects of learning and experience on problem solving.

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### *Adult Problem Solving*

All mosaic-tailed rats were also tested in six problem solving tasks (Rowell & Rymer, 2020b) as adults to determine the heritability of problem solving and to investigate whether maternal care effects on problem solving were manifested during adulthood. For each problem, I measured the latency to solve each task after making first contact with it as a proportion of test duration, and time spent interacting with the problem. Individuals that did not solve the problem were given the maximum latency. For problems repeated in duplicate (e.g. two pillars on the activity board), I recorded the latency to solve the first duplicate, and used the average time spent interacting between duplicates. The average time spent interacting was used because individuals could interact with both duplicates and gain information from both, to then go on and solve only one of the duplicates. Animals were presented with two food-baited puzzle boxes in the home cage (a cardboard matchbox that could be pulled/pushed open or chewed through, and a plastic cylinder with one open end covered by tin foil that could be pulled off or pushed through), an obstruction task in a light/dark box arena under an LED light (where rats had to push or pull a piece of crumpled paper out of the doorway to escape to a darkened side), and three food-baited problems on a Trixie Dog Activity Board (Level 2) given in an open arena (two pillars to push over, two tiles to slide, and two levers to pull up flaps).

## Statistical Analyses

Statistical analyses were performed using R version 4.0.2 (R Core Team, 2020). For each model, the effect size (Cohen's d) was calculated (effsize package, Torchiano & Torchiano, 2020) and used to estimate the power of each two-level factor in the models (pwr package, Champely et al., 2018), with a power estimate of 0.80 or above indicating a strong model. The proportional variance explained by each independent factor used in the linear models was calculated by dividing the factor sum of squares by the total sum of squares for the model (factor + residual). The proportional variance could not be calculated for factors used in beta regression models due to large differences in variable ranges.

### *Maternal Care and Offspring Problem Solving*

I considered the effect of maternal care on the solving latencies of offspring as juveniles and adults (juvenile: matchbox task; adults: matchbox, cylinder, obstruction, pillar, tile, lever tasks). I first used the descdist function (fitdistrplus package, Delignette-Muller & Dutang, 2015) to assess the best model distribution to use for the data. Based on this, I used separate models with beta distributions ('betareg' package, Cribari-Neto & Zeileis, 2010) for all maternal care measures to determine whether the proportional solving latencies of offspring (dependent variables) were influenced by the different measures of maternal care (total, direct, and indirect) they received (continuous predictors in separate models). In all three models, offspring sex and problem type were included as fixed factors.

### *Heritability of Problem Solving*

Parent-offspring regressions are commonly used to estimate the narrow-sense heritability ($h^2$) of an unknown continuous trait (Haldane, 1996). $h^2$ refers to the proportion of phenotypic variance controlled by heritable genetic effects (Hoffmann & Merilä, 1999). As problem solving latency is a continuous behavioural measurement, and its heritability is unknown, I calculated the narrow-sense heritability of problem solving in each task by regressing the scaled average offspring latency value for each litter (the mid-offspring value) on the scaled mothers' latency (lmtest package, Zeileis & Hothorn, 2002), hereafter referred to as parent-offspring regressions. I used the scale function to standardise each factor based on its mean and standard deviation, thereby allowing the beta coefficient to be calculated for each regression model (Cheng & Wu, 1994). The average pup latency was the dependent variable and the mother's latency to solve was the independent variable for each model.

I also considered whether the time spent interacting with the problems was heritable, as this could influence the solving success of the mosaic-tailed rats (Rowell & Rymer, 2021a). Again, I used separate parent-offspring regressions to investigate whether the scaled mother's time spent interacting (independent variable) was a significant predictor of the scaled mid-offspring value for the time spent interacting (dependent variable) for each problem type.

I used the beta coefficient of the parent-offspring regressions to estimate the maternal genetic contributions of problem solving latency and time spent interacting in each task. I was not able to measure the solving abilities of the fathers, as the majority were unknown. As the genetic contribution from parents to offspring may not necessarily be equal (Changxin, 1993), I could not assume that the maternal genetic contribution represented only ½ $h^2$. Therefore, as I could not estimate the total heritability values of problem solving, I simply present the maternal $h^2$ (the beta coefficient). I calculated the correlation of each parent-offspring aggression using $\sqrt{½h^2}$ (Wray & Visscher, 2008). I assumed that negative heritability estimates were zero (Robinson et al., 1955), but I still present them here, as suggested by Dudley & Moll (1969).

## Results

### *Problem Solving Ability*

Successful problem solving rates were low in juvenile mosaic-tailed rats, with only 12 of the 21 (57%) individuals solving the matchbox task at some point over the three trials. However, all individuals were capable of problem solving as adults, although this varied by task complexity (Rowell & Rymer, 2020b).

### *Maternal Care and Offspring Problem Solving*

When offspring were tested in their problem solving ability as juveniles and adults, the total amount of maternal care received, the amount of direct care received, and the amount of indirect maternal care received did not significantly affect the latency to first solve the matchbox task (Table 4.1). However, problem type significantly impacted the latency to solve in all models (Table 4.1), with offspring taking significantly longer to solve the lever task than any other problem (Figure 4.1). The amount of maternal care (direct, indirect, total) received did not significantly affect offspring solving in the remaining tasks (Table 4.1).

**Table 4.1.** Statistical outputs, power estimates and R-squared values for maternal care models for problem solving in fawn-footed mosaic-tailed rat *Melomys cervinipes* offspring. Significant results are shown in bold.

| Maternal Care Measure | Variable | Statistical Output | Power Estimate | Model R-squared |
|---|---|---|---|---|
| Total Care | Care | $\chi^2_1 = 0.65, p = 0.421$ | 1.000 | 0.349 |
| | Sex | $\chi^2_1 = 0.02, p = 0.879$ | 0.207 | |
| | Test | **$\chi^2_6 = 78.88, p < 0.001$** | - | |
| Direct Care | Care | $\chi^2_1 = 0.10, p = 0.753$ | 1.000 | 0.347 |
| | Sex | $\chi^2_1 = 0.00, p = 0.998$ | 0.207 | |
| | Test | **$\chi^2_6 = 78.40, p < 0.001$** | - | |
| Indirect Care | Care | $\chi^2_1 = 0.82, p = 0.364$ | 0.999 | 0.352 |
| | Sex | $\chi^2_1 < 0.01, p = 0.959$ | 0.207 | |
| | Test | **$\chi^2_6 = 78.07, p < 0.001$** | - | |

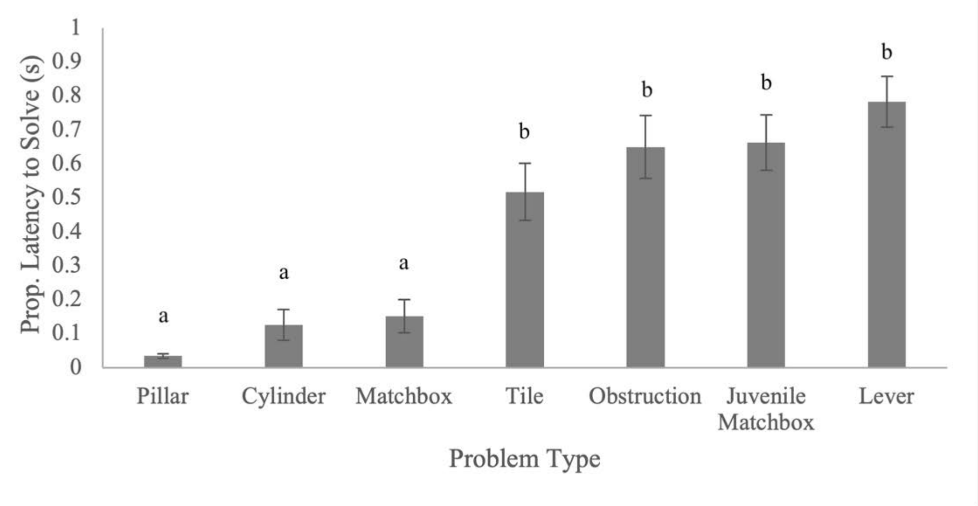

**Figure 4.1.** The proportional latency to solve (s) of offspring fawn-footed mosaic-tailed rats *Melomys cervinipes* across seven different problem solving tests.

### *Heritability of Problem Solving*

I found a trend for heritability of problem solving, albeit it was non-significant, in the latency to solve the cylinder, tile, and lever tasks (Table 4.2). I also found a trend in the time spent interacting in all the tasks, apart from the pillar task, between mothers and offspring, suggesting a possible heritable component (Table 4.2). For all other models, the problem solving ability of pups (latency to solve and time spent interacting with the task) was not related to the mothers' problem solving, suggesting that these traits do not have a heritable component (Table 4.2). The proportion of variance explained by the latency to solve a task or the time spent interacting with a task rarely contributed more than 10%, except for the time spent interacting with the obstruction task and latency to solve the lever task (Table 4.2).

**Table 4.2**. Narrow sense heritability ($h^2$) as estimated by beta coefficients and statistical outputs of parent-offspring regression models of problem solving in fawn-footed mosaic-tailed rats *Melomys cervinipes*

| **Solving Task** | **Measurement** | **$h^2$ (β ± SE)** | **Correlation** | **Statistics** | **Power** | **Prop. Variation** |
|---|---|---|---|---|---|---|
| Matchbox | Latency | -0.12 ± 0.27 | 0.35 | $F_{1,14} = 0.20$, $p = 0.660$ | 0.509 | 0.014 |
| | Time Interacting | 0.21 ± 0.26 | 0.46 | $F_{1,14} = 0.62$, $p = 0.445$ | 0.652 | 0.042 |
| Cylinder | Latency | 0.32 ± 0.25 | 0.57 | $F_{1,14} = 1.60$, $p = 0.226$ | 0.343 | 0.103 |
| | Time Interacting | 0.14 ± 0.26 | 0.37 | $F_{1,14} = 0.26$, $p = 0.619$ | 0.865 | 0.018 |
| Obstruction | Latency | -0.28 ± 0.26 | -0.53 | $F_{1,14} = 1.17$, $p = 0.295$ | 0.681 | 0.078 |
| | Time Interacting | 0.35 ± 0.25 | 0.59 | $F_{1,14} = 1.965$, $p = 0.183$ | 0.256 | 0.123 |
| Pillar | Latency | -0.07 ± 0.27 | -0.26 | $F_{1,14} = 0.07$, $p = 0.789$ | 0.733 | 0.005 |
| | Time Interacting | -0.03 ± 0.27 | -0.17 | $F_{1,14} = 0.01$, $p = 0.915$ | 0.839 | <0.001 |
| Tile | Latency | 0.25 ± 0.26 | 0.50 | $F_{1,14} = 0.93$, $p = 0.351$ | 0.743 | 0.062 |
| | Time Interacting | 0.25 ± 0.26 | 0.50 | $F_{1,14} = 0.972$, $p = 0.341$ | 0.806 | 0.065 |
| Lever | Latency | 0.40 ± 0.25 | 0.63 | $F_{1,14} = 2.64$, $p = 0.126$ | 0.455 | 0.159 |
| | Time Interacting | 0.32 ± 0.25 | 0.57 | $F_{1,14} = 1.61$, $p = 0.225$ | 0.503 | 0.103 |

## Discussion

In this study, I investigated genetic and non-genetic maternal effects on offspring problem solving, an area that has received little attention despite several studies showing genetic and non-genetic maternal effects on offspring behavioural and cognitive development in general (e.g. Francis & Meaney, 1999; Kikusui et al., 2005). I found that the amount of maternal care received during the early postnatal period, irrespective of whether it was direct or indirect, did not significantly impact the problem solving abilities of juveniles. This could be due to the extensive postnatal care provided by mothers. Mosaic-tailed rat pups nipple cling to their mothers until their eyes open (Callaway et al., 2018) and, as a result, huddling by mothers was high, irrespective of whether they were actively providing other forms of care (e.g. grooming pups) or not. Mosaic-tailed rats also have small litters, generally only producing two pups (although females have 2 pairs of inguinal nipples, Callaway et al., 2018), which suggests that females likely invest more time in caring for their offspring (showing a K-selected reproductive strategy, Rowell & Rymer, 2020a) than other similar-sized species. All mothers producing high amounts of care could have resulted in offspring developing along similar trajectories, preventing a large variation in problem solving performance from being shown at this stage. While it is possible that the juveniles may have been too young at the time of testing to successfully solve problems, that some individuals were capable of solving the problems from 16-days old (Rowell & Rymer, in review) suggests that rats at this age are likely physically and cognitively developed enough to solve problems generally, and individual variation in solving abilities may have been due to other factors (e.g. differences in personality; Rowell & Rymer, 2021a).

I found no significant influences of non-genetic maternal care effects on adult problem solving behaviour. While tactile stimulation from mothers is known to improve physiological, behavioural, and cognitive responses in offspring when they reach adulthood in other rodents (Champagne, 2008; Rymer & Pillay, 2011), my results suggest that problem solving is not constrained by offspring neural development. Instead, problem solving is likely a flexible response that changes throughout an individual’s lifetime (Rowell et al., 2021). For example, North Island robins *Petroica longipes* with previous problem-solving experience were better solvers than naïve individuals (Shaw, 2017). Problem solving ability could also be dependent on other individual characteristics, such as persistence and behavioural flexibility (Griffin & Guez, 2014). For example, pheasant *Phasianus colchicus* chicks that were more motivated were more likely to solve a food-baited problem than less motivated individuals (van Horik & Madden, 2016). However, these characteristics themselves could also be heritable, thereby indirectly influencing problem solving (Rowell et al., 2021).

My results suggest that there may only be a small heritable component for some problem solving behaviours (latency to solve the cylinder, lever, and tile tasks, time spent interacting with most tasks), although the results failed to reach significance, possibly due to small sample size (as suggested by some low power estimates). This is similar to the findings of  Quinn et al. (2016) for great tits, where problem solving ability also had low heritability estimates, and was suggested to be a flexible trait influenced by environmental conditions (Quinn et al., 2016). Problem solving ability in mosaic-tailed rats has been linked to exploratory behaviour, including time spent interacting (Rowell & Rymer, 2020a), and some forms of cognition (learning and memory, Rowell & Rymer, 2021b), both of which are known to be heritable in other species (Dingemanse et al., 2002; Upchurch & Wehner, 1989). Therefore, under certain contexts and task complexities, it is likely that it is the underlying behaviours or forms of cognition that are heritable, and not problem solving in its entirety *per se*. The next step would be to assess relative heritability of these underlying components, to gain a broader understanding of how problem solving is ultimately affected by genetic effects, even if not directly.

These results suggest that problem solving ability in adult mosaic-tailed rats are not largely constrained by genetic effects, most likely because of its multi-faceted nature, including its reliance on behavioural and cognitive components, including exploration and learning. This complexity could explain why there may be slight genetic effects for some tasks that utilise these traits, but not others. As such, female mosaic-tailed rats may only have a small organisational effect on the developmental trajectories of their offspring. The development of problem solving, however, is more likely altered by the experiences and information gained throughout development (Rowell et al., 2021), as suggested by the low contribution to the overall variances produced in the models. There is therefore also a level of flexibility in how offspring respond to environmental challenges and, as a result, an individual should be capable of solving problems regardless of its mother's abilities because the environment it experiences is unlikely to be the same as the one its mother experienced.

# Chapter 5: Experience is more important than age for successful problem solving in juvenile fawn-footed mosaic-tailed rats *Melomys cervinipes*

## Abstract

Problem solving could be important for survival in animals. However, untangling the relevant effects of age and experience on problem solving ability is challenging. I tested how age and experience affected problem solving in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes* using a novel experimental design to tease apart these effects. Juveniles were divided into two developmental groups (Group 1 tested early in development; Group 2 tested late in development) and received a food-baited cardboard matchbox at three time points. I then compared juveniles from each group when age and experience level was constant, as well as investigating how problem solving changed over time. Problem solving ability of naïve juveniles was also compared to problem solving ability of naïve adults, and problem solving of naïve adults was also compared to adults that had experience solving problems as juveniles. Juveniles with more experience solved the task faster than less-experienced juveniles. However, adults were significantly better solvers than juveniles. Interestingly, early-life experience of solving particular types of problem did not provide adults with an advantage. While previous experience with a problem may be important for short term solving during early development, more general experience at manipulating objects may ultimately be more important for problem solving success in adulthood.

## Introduction

Animals experience dramatic changes in their physiology (Forrest et al., 1991), behaviour (Lynn & Brown, 2009), cognition (Brown & Kraemer, 1997), and brain morphology (Fischer et al., 2007) as they develop, which changes how they interact with the environment. For example, juveniles are often more exploratory (Griffin & Guez, 2014) than adults, allowing them to quickly gather and learn new information (Lynn & Brown, 2009). However, adults are more developed than juveniles, both physically (Thornton & Samson, 2012) and cognitively (Healy et al., 1994), which enhances their survival (e.g. increased hippocampal development in adult marsh tits *Parus palustris*, Healy et al., 1994). These different patterns of behaviour and cognition can, therefore, affect the survival of different age classes. How individuals of different ages cope with challenges using their problem solving abilities has been a growing area of interest.

Problem solving is an animal's ability to use prior information (knowledge or behaviour) to move itself, or manipulate an object, to overcome a barrier, negative state or agent, and access a goal (Chapter 2; Rowell et al., 2021). The ability to solve a problem relies on behavioural (exploration, Benson-Amram et al., 2013; Rowell & Rymer, 2021a), cognitive (learning and memory, Griffin & Guez, 2014; Rowell & Rymer, 2021b) and physical (dexterity, manipulation, Thornton & Samson, 2012) components. These components are not static, and can change over an animal's lifetime as it undergoes changes in physiology and morphology. For example, ageing brown rats *Rattus norvegicus* experience a suite of neurological changes across multiple brain regions (i.e. decreased glucocorticoid receptor binding capacity in the hippocampus), resulting in impaired spatial learning and memory (Frick et al., 1995). It is therefore expected that an individual's problem solving ability likely also changes throughout its lifetime.

Previous studies have found mixed results on the impact of age on problem solving ability in animals. Juveniles are often more successful at problem solving than adults due to a period of heightened exploration and increased persistence (e.g. Chimango caracara *Milvago chimango*, Biondi et al., 2010; blue tits *Cyanistes caeruleus*, Aplin et al., 2013; Indian mynas *Sturnus tristis*, Griffin et al., 2014). However, other studies have found that juveniles are not more likely to solve puzzles, or are slower at solving puzzles, than adults (e.g. satin bowerbirds *Ptilonorhynchus violaceus*,Keagy et al., 2009; great tits *Parus major*, Cole et al., 2011; meerkats *Suricata suricatta*, Thornton & Samson, 2012; spotted hyenas *Crocuta crocuta,* Benson-Amram & Holekamp, 2012). Age was also not important for problem solving ability when comparing different ages of adults (e.g. adult chimpanzees *Pan troglodytes* between 14 – 47 years old, Hopper et al., 2014). An important consideration for these study designs is the underlying foraging experience that individuals have at the time of testing. In some species (e.g. birds being tested after fledging), despite being juveniles, these individuals were still capable foragers at the time of testing (Griffin & Guez, 2014), and inherently had previous experience in manipulating food. Level of previous experience therefore also needs to be considered to understand how problem solving develops.

As individuals explore their environments, they gain experience in manipulating objects, foraging, and interacting with other individuals. As such, an individual's level of experience, rather than its physical age, may be more important for successful problem solving. Performance in solving problems often increases over repeated sessions through trial-and-error learning (Thornton & Samson, 2012). For example, Chimango caracaras became faster at solving foraging tasks over repeated sessions (Biondi et al., 2010) and North Island robins *Petroica longipes* that had previous experience at solving different problems were more likely to solve a novel problem than naïve individuals (Shaw, 2017). Experience can also allow individuals to gain new motor skills required for problem solving (Griffin & Guez, 2014). However, the experience level of wild animals cannot always be known or standardised (van Horik & Madden, 2016). Consequently, an individual's age is often used as a proxy for experience, and cohorts of different individuals are compared to each other (e.g. adults vs. juveniles), with adults being assumed to be more experienced than juveniles. However, this approach does not account for other sources of individual variation, such as differences in motivation (van Horik & Madden, 2016), personality (Rowell & Rymer, 2021a) or cognitive ability (Boogert et al., 2008), which are also known to affect problem solving (Griffin & Guez, 2014). Therefore, it is unclear whether problem solving is affected more by an individual's age or by its level of experience.

I investigated whether individual age or previous experience in solving problems was more important for successful problem solving in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*. To do this, I raised mosaic-tailed rats in captivity, where age was known and problem solving experience could be controlled, and presented juveniles with a food-baited puzzle box on three occasions. I also presented the same task to these experienced individuals, as well as naïve adults. Previous studies have found that adult mosaic-tailed rats are efficient problem solvers, and show individual variation in solving performance (Rowell & Rymer, 2020b), suggesting that early life conditions may influence this ability. I hypothesised that problem solving ability would be affected by both age and experience (Griffin & Guez, 2014), as physiological and morphological changes during aging impact behaviour and cognition (Moriceau et al., 2010), and increased experience facilitates trial-and-error learning (Thornton & Samson, 2012). I expected that individuals would improve in solving problems as they aged due to having more developed brains (Moriceau et al., 2010), and as they gained experience due to having more opportunities to learn to solve tasks in general (Biondi et al., 2010).

## Methods

### Ethical Note

Permission to trap adult females was granted by the Queensland Department of Environment and Science (permit numbers WA0014502 and PTU19-001632). See Chapter 3 (Rowell & Rymer, 2020b) for details on the trapping methodology. Adult mosaic-tailed rats were observed daily and weighed regularly to monitor health. Experimental procedures did not have any negative effects on the animals. Mothers did not display any aggressive behaviours towards pups, and pups continued to grow well during the testing period. No animals experienced overt signs of stress (e.g. excessive vocalisations, seizing) during testing. Animals were monitored for 24 h and resumed normal behaviours within this time. At the end of the study, all animals were returned to the colony. The research adhered to the ABS/ASAB guidelines for the ethical treatment of animals (Bee et al., 2020), and 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).

### Animal Husbandry

Ten adult female fawn-footed mosaic-tailed rats (wild caught = 8, captive born = 2) and their offspring (n = 21) were used in this study. Mosaic-tailed rats were kept in glass tanks (44 x 35 x 32 cm) under partially controlled environmental conditions (12:12 h light cycle; 22–26C; 50–65% relative humidity). Tanks contained approximately 5 cm of wood shavings, and a cylindrical plastic nest box (11 x 11 x 20 cm) filled with a handful of pasture hay and two pieces of paper towel for nesting material. Cardboard rolls for chewing and sticks for climbing were provided for behavioural enrichment (Rader & Krockenberger, 2006). Once females gave birth, up to 10 g of mixed seed and rodent chow (Vetafarm Origins) and 15 g of vegetable/fruit (e.g. sweet potato, apple) were given to each female, depending on litter size, age and condition. Water was available *ad libitum*. Pups were removed from their mothers briefly every second day from 3 days old to assess behavioural and physical development (see Rowell & Rymer, 2020a). Pups were returned to their mothers after measurements were taken without any incidents. Mosaic-tailed rat pups were kept with their mothers until they were 21 days old when they were weaned

(Rowell & Rymer, 2020a). Thereafter, the mother was removed from the tank, and siblings were kept together until completion of testing.

Fifty-nine adult mosaic-tailed rats from the James Cook University Animal Behaviour laboratory breeding colony were used for the adult testing paradigm. Adult individuals were given the same enrichment and nesting material as described above, but were housed individually in wire cages (34.5 x 28 x 38 cm) with deep plastic bases (34.5 x 28 x 11 cm) containing 10 cm of wood shavings, and a wire platform to better facilitate climbing. Each individual was given 5 g of vegetable/fruit and 5 g of mixed seed and rodent chow daily, and water was available *ad libitum*.

### *General Juvenile Problem Solving Testing Procedure*

Tests were conducted from October 2018 to March 2021. Testing occurred between 18h00 and 22h00, during the peak period of mosaic-tailed rat activity (Wood, 1971) under red light which does not influence mosaic-tailed rat behaviour (Paulling et al., 2019). Behavioural trials were recorded with a Sony HDR-CX405 Camcorder from above in the absence of observers. Behavioural data were extracted using the software BORIS (Friard & Gamba, 2016). As the task was a food-motivated task, mosaic-tailed rats were not fed on the day of testing until after testing was complete, encouraging individuals to interact with the puzzles.

Prior to problem-solving testing (either postnatal day (PND) 15 or PND 35; see below), mosaic-tailed rat pups were placed in an open field arena (57 cm long × 33 cm wide × 40 cm high) for 20 minutes, with a novel object present for the last 10 minutes, to reduce neophobia to the novel arena and objects, and to increase the likelihood that they would interact with the puzzles in the problem-solving tasks. The following night (either PND 16 or PND 36; see below), pups were presented with two cardboard matchbox tasks for 20 minutes in the open field arena. The matchboxes were scaled to body size (16 days old: 4 x 2 x 1 cm; 26 days old: 6 x 3 x 1.5 cm; 36 days old and above: 7 x 5 x 2 cm), and each matchbox was baited with 1 g of fruit. Pups could push or pull the box out of the sleeve, or chew through the sleeve, to solve the task. I measured the latency of pups to first solve one of the matchbox tasks, and how many matchboxes were solved during the test. Two matchbox tasks were presented to each individual for three sessions, each session being 10 days apart (see below).

### *Controlling for Age and Experience*

Litter sizes in mosaic-tailed rats range from 2-4, generally with a sex ratio of 50:50 (Callaway et al., 2018). Half of the pups from each litter (n = 11) were allocated to Group 1, while the other half (n = 10) were placed into Group 2, keeping sexes balanced between the groups (Group 1: F = 7, M = 4, Group 2: F = 7, M = 3). Group 1 pups were tested earlier in their development than Group 2 pups. Pup eyes fully open approximately 9 days after birth (Rowell & Rymer, 2020a). Therefore, the first testing session occurred 7 days later (approximately PND 16). The second and third testing sessions occurred in 10 day increments, at approximately PND 26 and PND 36 (Figure 5.1). As these tests were food-motivated, juveniles needed to be old enough to be eating solid food. Pups in Group 1 were first tested when they were still initially reliant on their mothers (PND 16), tested again soon after weaning (PND 26), and then tested a third time after independently foraging for nearly 2 weeks (PND 36).

Group 2 pups were tested later in development than Group 1 pups. They were tested at approximately PND 36, PND 46, and PND 56 (Figure 5.1). This design allowed me to test for the effects of age (by comparing Group 1 at PND 16 and Group 2 at PND 36) and experience (by comparing both Groups 1 and 2 at PND 36 days) independently, as well as explore interaction effects (within and between groups; Figure 5.1).

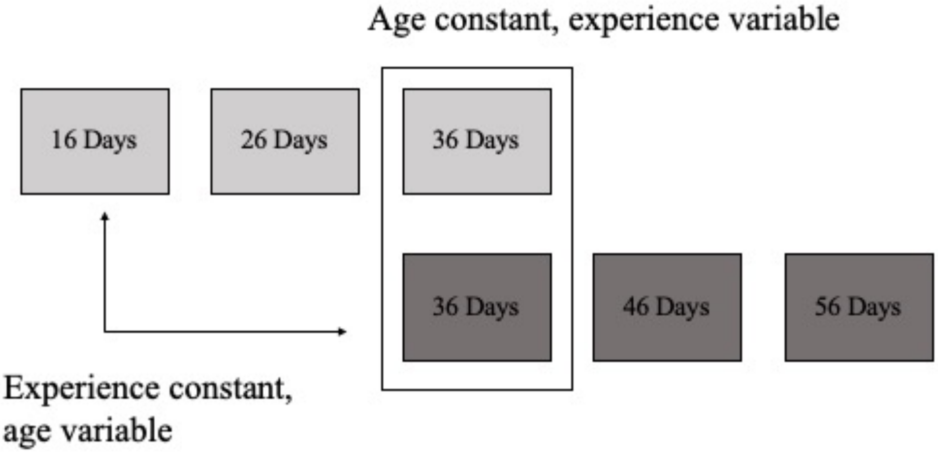

**Figure 5.1.** Testing paradigm to separate out age and experience effects on problem solving ability of fawn-footed mosaic-tailed rat *Melomys cervinipes* pups. The light grey boxes represent Group 1 juveniles and the dark grey boxes represent Group 2 juveniles. Days represent days since birth (postnatal day = PND).

### *Adult Problem Solving Testing*

Performance in the matchbox task was measured again once mosaic-tailed rats were at least 5 months old (when sexual maturity is reached, Yom-Tov, 1985). I tested individuals that had undergone the juvenile testing described above (n = 17), as well as naïve individuals that had not been tested as juveniles (n = 42). For this test, a large cardboard matchbox (7 x 5 x 2 cm) baited with 2 g of fruit was secured with tape to a wire shelf at the top of each individual's home cage (Rowell & Rymer, 2020b). I gave the mosaic-tailed rats 30 minutes to solve the task. Again, I measured the latency to solve the task. Individuals that did not solve the task were given the maximum latency (i.e. 1800 seconds, Liker & Bókony, 2009).

### *Statistical Analyses*

Statistical analyses were performed using R version 3.5.0 (R Core Team, 2020). The model-level significance was set at $\alpha = 0.05$. Data and models were tested for normality (Shapiro-Wilk test). Figures are displayed with means and standard errors. Significant differences in the main effects were identified using Tukey's *post hoc* tests (emmeans package, Lenth et al., 2020). In all cases, I initially used the descdist function (fitdistrplus package, Delignette-Muller & Dutang, 2015) to find the best model distribution for my data. I first considered the latency to solve and the number of boxes solved within the age-constant (Group 1 PND 36 vs. Group 2 PND 36) and experience-constant (Group 1 PND 16 vs. Group 2 PND 36) groups of juveniles. The variances of the data were compared using F tests, and the averages of each group (age-constant; experience-constant) were then compared using either two sample t-tests (if normally distributed) or Wilcoxon rank sum tests (if not normally distributed).

I then considered how juveniles changed in their solving performance over time, irrespective of whether they were assigned to Group 1 or Group 2. To do this, I only included individuals that were capable of solving the task at least once (n = 12). I ran a general linear mixed effects model (GLMER, lmerTest package, Kuznetsova et al., 2015) with a binomial distribution to investigate how solving success (1 = solved, 0 = not solved) was impacted by individual identity (random factor), test session number, and pup sex (both fixed factors). Individual effects on solving success were calculated using the lrtest function. I used a beta regression model to assess the latency to solve (as a proportion) in response to pup sex and test session number, which were included as fixed factors. Individual identity could not be included as a random effect in this type of model.

I also explored how age impacted performance in the first solving trial over the longer time frame into adulthood. Only naïve adults that did not receive testing as juveniles were used in the adult category. I ran a GLM with a binomial distribution to investigate how age category at first testing (PND 16, PND 36, adult) and sex impacted solving success (1 = solved, 0 = not solved). I then used a GLM with a negative binomial distribution with age category (PND 16, PND 36, adult) and sex included as fixed factors to assess first latency to solve the matchbox task.

Finally, I compared adult problem solving performance between individuals that had first experienced the matchbox as juveniles and individuals that only received the test as adults. I used a beta regression model to assess latency to solve (as a proportion) in response to experience group (juvenile vs. adult), birth origin, sex, and mass, which were included as fixed factors.

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## Results

### *General Problem Solving Performance*

Only 12 of the 21 mosaic-tailed rat pups (57%) tested were capable of solving the matchbox task at least once. Of these 12 solvers, 5 individuals (42%) first solved the matchbox in the first testing session, 3 individuals (25%) first solved the matchbox in the second session, and 4 individuals (33%) first solved the matchbox in the third session. When first tested as adults, 34 of the 42 mosaic-tailed rats (81%) solved the matchbox task.

### *Age-constant and Experience-constant Group Comparisons*

There were no significant differences in the latency to solve the matchbox task ($t_{18.94} = 0.26$, $p = 0.799$) or the number of tasks solved ($t_{18.44} = -0.66$, $p = 0.515$) between the 36-day old pups from Group 1 (experienced) and the 36-day old pups from Group 2 (no experience). Similarly, there were no significant differences in the latency to solve the matchbox task ($W_{1,21} = 64.5$, $p = 0.396$) or the number of tasks solved ($t_{14.13} = -0.86$, $p = 0.402$) between the 16-day old pups from Group 1 and the 36-day old pups from Group 2.

## *Change in Performance Over Time*

Regardless of pup age, the latency to solve the matchbox task was significantly affected by test session (z = -3.16, n = 36, *p* = 0.002), with pups solving the task on average 2.5 x faster in the third trial (0.31 ± 0.10 s) than in the first trial (0.78 ± 0.10 s; Figure 5.2). Pup sex did not significantly affect the latency to solve the matchbox task (z = 0.62, n = 36, *p* = 0.538). Solving success in the matchbox task was not significantly affected by test session number ($\chi^2_1$= 0.21, *p* = 0.647), pup sex ($\chi^2_1$= 0.07, *p* = 0.797) or individual identity ($\chi^2_1$= 0.19, *p* = 0.659).

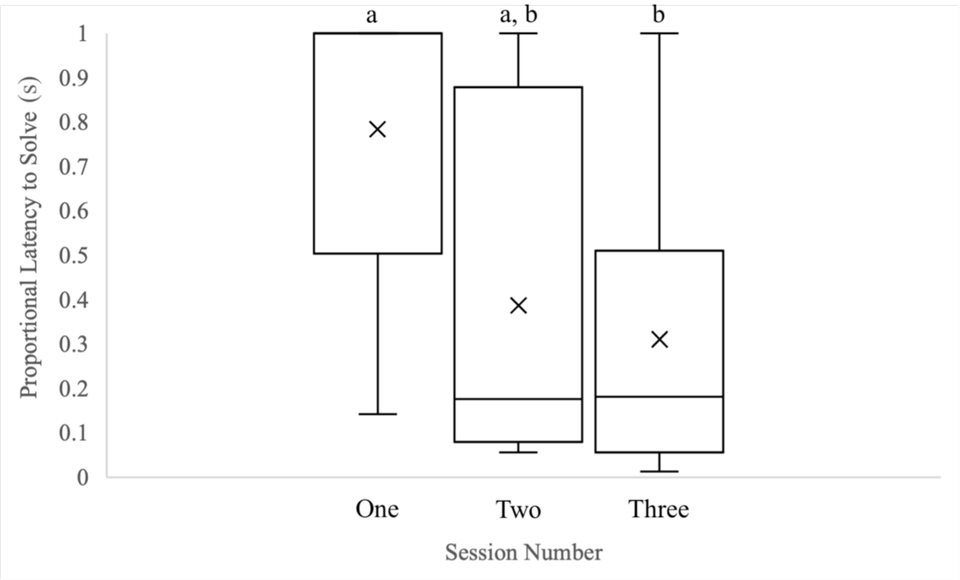

**Figure 5.2.** Mean ± SE latency (as a proportion) to solve a matchbox task (s) by fawn-footed mosaic-tailed rat *Melomys cervinipes* pups across three testing sessions. The x in each bar represents the mean value. Different letters indicate significant differences.

## *Age and First Solving Performance*

Naïve adult mosaic-tailed rats were significantly more likely to solve the matchbox task (81% ± 0.96; $\chi^2_1$= 19.65, *p* < 0.001) than both 16-day old (18% ± 0.10) and 36-day old naïve juveniles (30% ± 0.15; Figure 5.3). Adults also solved the matchbox task significantly faster (498.22 ± 100.26 s; $\chi^2_1$ = 7.50, *p* = 0.024) than 16-day old juveniles (1170.57 ± 19.92 s), but not 36-day old juveniles (921.10 ± 144.24 s; Figure 5.4). Sex did not significantly impact solving success ($\chi^2_1$= 0.03, *p* = 0.874) or the latency to first solve the problem ($\chi^2_1$ = 0.53, *p* = 0.467).

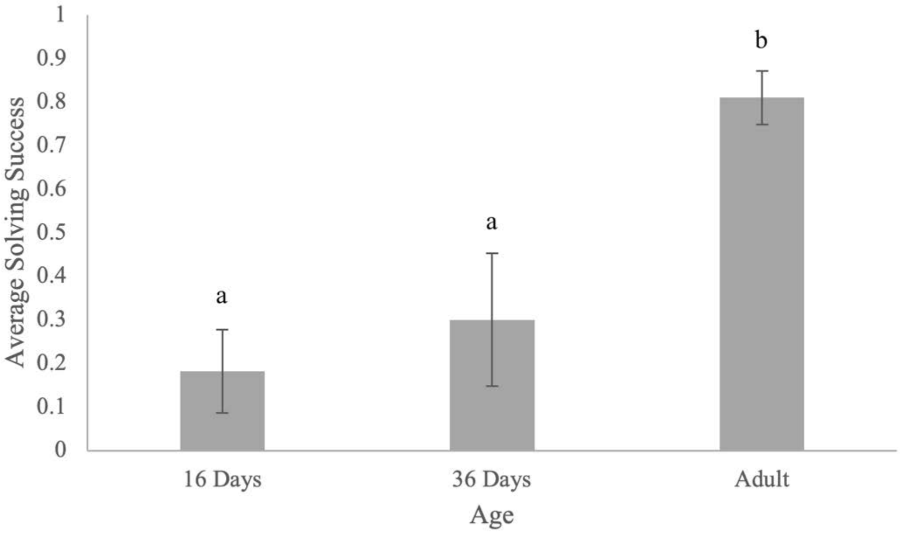

**Figure 5.3.** Mean ± SE solving success in the first presentation of the matchbox task to fawn-footed mosaic-tailed rats *Melomys cervinipes* across three age categories. Different letters indicate significant differences.

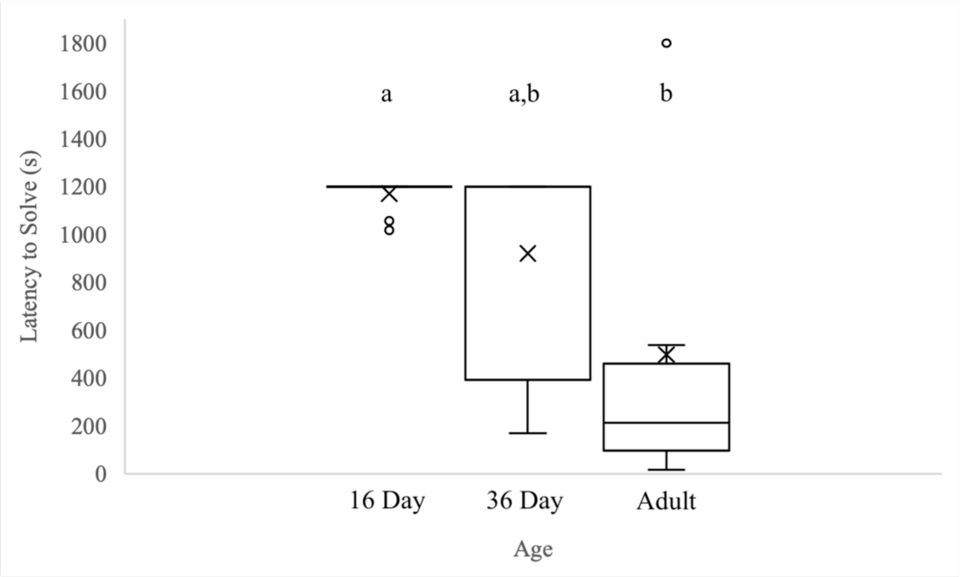

**Figure 5.4.** Mean ± SE latency to solve the matchbox task (s) on first presentation to fawn-footed mosaic-tailed rats *Melomys cervinipes* across three age categories. The x in each bar represents the mean value. Different letters indicate significant differences.

## *Adult Problem Solving Testing*

The latency to solve the matchbox did not differ significantly between adults that experienced the tests as juveniles and adults that were naïve at first testing (juvenile: 0.169 ± 0.06 s, adult: 0.277 ± 0.05 s; z = 0.39, *p* = 0.070). In addition, the latency to solve the matchbox task was not significantly affected by sex (male: 0.254 ± 0.063 s, female: 0.237 ± 0.06 s; z = -0.29, n = 59, *p* = 0.769), birth origin (captive-born: 0.194 ± 0.05 s, wild-caught: 0.302 ± 0.07 s; z = 0.91, n = 59, $p = 0.364$), or mass (z = 1.88, n = 59, $p = 0.060$). Similarly, solving success between individuals tested as juveniles and individuals only tested as adults was not significantly different (juvenile: 94.1% ± 0.06, adult: 81.0% ± 0.07; $\chi^2_1 = 2.85$, $p = 0.091$), and was also not significantly affected by sex (male: 83.3% ± 0.07, female: 86.2% ± 0.07; $\chi^2_1 < 0.01$, $p = 0.999$), birth origin (captive-born: 90.3% ± 0.05, wild-caught: 78.6% ± 0.08; $\chi^2_1 = 0.65$, $p = 0.420$), or mass ($\chi^2_1 < 0.01$, $p = 0.998$).

## Discussion

I designed an experimental protocol that tracked developing individuals and controlled for previous experience in problem solving, allowing the independent effects of age and experience on problem solving ability to be properly considered. I found that some juvenile fawn-footed mosaic-tailed rats were capable of solving the matchbox puzzle box from just 16-days old, and with no prior experience. However, solving success rates were generally low in juveniles, with only 57% individuals solving the puzzle at least once. This suggests that the testing time frame (16-days old to 56-days old) may not have been long enough to separate out developmental effects of age or experience on problem solving. Alternatively, the sample size (n = 21) may have been too small to compare different cohorts of individuals (e.g. experienced vs. not experienced), but this is unlikely, due to high power estimates (up to 0.91) being calculated. Furthermore, because some individuals were capable of problem solving at 16 days, this suggests that mosaic-tailed rats are generally developmentally capable of solving problems prior to weaning, which suggests that other factors might provide better explanations as to the lack of solving in some individuals.

When I tested how individual problem solving changed over development, I found that mosaic-tailed rats solved the matchbox task in their third trial significantly faster than in their first trial, irrespective of age group. This suggests that individuals were learning through trial-and-error across the testing sessions, allowing them to become more efficient at problem solving over time. Similar results have been found in Chimango caracaras (Biondi et al., 2010) and lions *Panthera leo* (Borrego & Dowling, 2016). While the speed of problem solving changed over time, trial number did not significantly affect the probability of solving the task, with some juveniles innovating during their first trial, and others requiring multiple sessions before being successful solvers. Adult mosaic-tailed rats can innovate, and individual differences are present (Chapter 3; Rowell & Rymer, 2020b).

Therefore, it is not surprising that juveniles also show variation in their ability to innovate. Individual variation in problem-solving ability in adult mosaic-tailed is, at least partially, due to differences in personality (Chapter 7; Rowell & Rymer, 2021a) and cognitive ability (Chapter 8; Rowell & Rymer, 2021b), and it is likely that the developmental processes associated with personality and cognition are linked to those associated with problem solving.

While some juveniles were capable of innovating, naïve adult mosaic-tailed rats were more likely to solve the matchbox task on first presentation, and were also faster at solving it, than juveniles. This increased solving ability could be due to the adults simply having more experience in general in manipulating objects and food while foraging than juveniles (Griffin & Guez, 2014). At the time of testing, the 16-day old individuals had only been eating solid food for approximately 7 days, whereas the adults had been eating solid food for at least 5 months. This suggests that the motor skills, dexterity and/or strength in juveniles may have required more development to allow for manipulation and solving to occur successfully at least in some individuals, as suggested by Thornton & Samson (2012) for meerkats. While I tried to account for this by scaling the puzzles to the body size of the juveniles, the ability to pull out or push on the box may still have been dependent on body mass and, therefore, developmental stage. Alternatively, adult mosaic-tailed rats may have had enhanced cognitive abilities, which are known to impact problem solving ability, compared to the juveniles, which were still developing (Healy et al., 1994). For example, while the relationship between cognition and problem solving has not been tested in juveniles, memory and learning were found to be important for problem solving in adult mosaic-tailed rats (Chapter 8; Rowell & Rymer, 2021b). This could mean that adults learn faster from trial-and-error, and retain memories better, than juveniles.

When comparing the performance of experienced adults (those that had been tested as juveniles) and naïve adults, I found that early exposure to the matchbox task did not enhance problem solving performance or speed at solving the task. This suggests that, as problem solving is a flexible trait (Rowell et al., 2021), recent information (e.g. about current food items) could be more important for successful solving than early life experiences, which may contain outdated information. While long-term memory can improve problem solving performance when individuals receive tests as adults (Chow et al., 2017; Shaw, 2017), the influence of memory on solving ability has not been tested across a drastic developmental gradient (e.g. dependent juvenile to independent adult). Research suggests that adult rodents may not even be capable of remembering information gained as pups (Guskjolen et al., 2018) due to developmental changes that occur in the brain (e.g. accelerated rates of hippocampal neuron regeneration in laboratory mice, Akers et al., 2014). As such, it may not have been possible for mosaic-tailed rats in this experiment to use the memories gained from testing early in their development.

My study is one of the first to appropriately measure and control for the effects of age and previous experience on individual problem solving ability. At least for juvenile mosaic-tailed rats, previous experience is more important than age for successful solving. However, adults were more efficient problem solvers than juveniles, possibly due to having more experience in manipulating objects in general, and/or having greater dexterity, and the ability to successfully problem solve as an adult was not dependent on juvenile experience. Because an individual's problem solving ability may also be influenced by other factors (e.g. personality, cognition) that develop along their own trajectories as the animal ages and gains experience (Rowell et al., 2021), and these factors may also interact with each other to indirectly influence an individual's problem solving ability (Rowell et al., 2021), untangling the role that developmental effects play in problem solving is a difficult and challenging task.

# Chapter 6: Corticosterone metabolite concentration is not related to problem solving in the fawn-footed mosaic-tailed rat *Melomys cervinipes*

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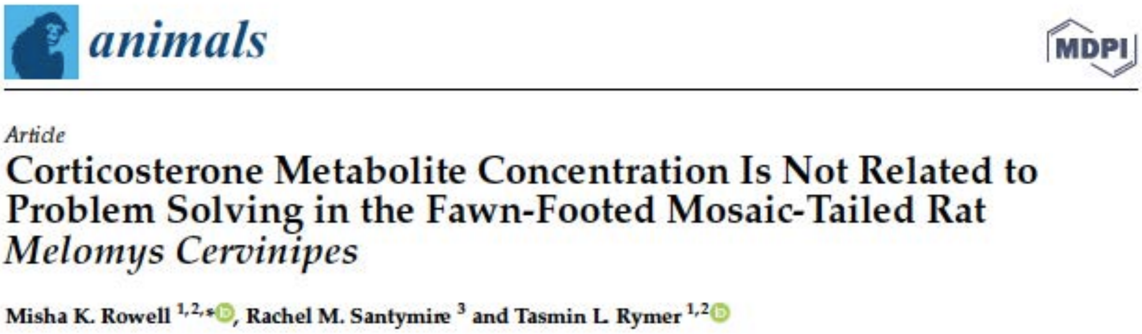

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## Corticosterone Metabolite Concentration Is Not Related to Problem Solving in the Fawn-Footed Mosaic-Tailed Rat *Melomys Cervinipes*

**Misha K. Rowell [1,2,*], Rachel M. Santymire [3] and Tasmin L. Rymer [1,2]**

## Abstract

Animals can respond physiologically, such as by adjusting glucocorticoid hormone concentrations, to sudden environmental challenges. These physiological changes can then affect behavioural and cognitive responses. While the relationships between adrenocortical activity and behaviour and cognition are well documented, results are equivocal, suggesting species-specific responses. I investigated whether adrenocortical activity, measured using corticosterone metabolite concentration, was related to problem solving in an Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*. Mosaic-tailed rats live in complex environments that are prone to disturbance, suggesting a potential need to solve novel problems, and have been found to show relationships between physiology and other behaviours. I measured problem solving using five food-baited puzzles (matchbox and cylinder in the home cage, and activity board with pillars to push, tiles to slide and levers to lift in an open field), and an escape-motivated obstruction task in a light/dark box. Faecal samples were collected from individuals during routine cage cleaning. Adrenocortical activity was evaluated non-invasively by measuring faecal corticosterone metabolites using an enzyme immunoassay, which was biochemically and biologically validated. Despite varying over time, adrenocortical activity was not significantly related to problem solving success or time spent interacting for any task.

However, as adrenocortical activity is reflective of multiple physiological processes, including stress and metabolism, future studies should consider how other measures of physiology are also linked to problem solving.

## Introduction

Throughout an animal's life, it will experience changes in its immediate environment. As it grows and develops, a cascade of physiological changes will influence how it responds to its environment (Malishev & Kramer-Schadt, 2021). Likewise, when the animal disperses from its natal territory, it will experience a suite of novel challenges, including increased competition and predation risk. To cope with these challenges, animals can rapidly adjust their behavioural (e.g. exploration) and cognitive (e.g. learning) responses, which are both underpinned by the animal's adrenocortical activity (Wilson et al., 2019).

Adrenocortical activity is the change in an animal's glucocorticoid (e.g. cortisol and corticosterone) concentrations (Palme, 2019). These physiological changes could be a marker for an animal's metabolism, which is an animal's energetic state (Malishev & Kramer-Schadt, 2021). Adrenocortical activity can therefore influence how much energy and/or time an animal can invest in simply growing and maintaining its own condition (Nagy, 2000), foraging, defending territory, migrating, or mating (Malishev & Kramer-Schadt, 2021). Adrenocortical activity could also indicate an animal's stress levels, as glucocorticoids are released after various stressors (Wingfield, 2013). Consequently, an individual's adrenocortical activity can impact its behavioural (Stöwe et al., 2010) and cognitive outputs (Lupien et al., 2009). For example, glucocorticoids mobilise glucose (Wingfield et al., 1998), providing energy for appropriate behavioural (e.g. increased foraging; Schommer et al., 2003) and cognitive (e.g. rapid learning; Sandi & Rose, 1994) responses to threats (Tsigos & Chrousos, 2002). However, the level of individual variation in adrenocortical activity is not well known for many species. This variation could contribute to differences in how individuals cope with environmental challenges, such as the ability to solve problems (Bókony et al., 2014).

Simply defined, problem solving is an animal's ability to overcome an obstacle to obtain a reward (Chow et al., 2017). Problem solving can be innovative, where an animal uses a new behaviour, or an existing behaviour in a new context, to solve the problem (Reader & Laland, 2003), or can rely on forms of learning, such as trial-and-error (Thornton & Samson, 2012) or imitating other individuals (Heyes, 1993). Individual variation in problem solving is well documented in many species, often due to underlying individual differences in motor skills, personality and/or cognitive ability (Chapter 2; Rowell et al., 2021). However, physiological responses, such as adrenocortical activity, could also contribute to individual differences in problem solving (Laland & Reader, 1999). For example, problem solving success in a foraging task presented to pheasant chicks *Phasianus colchicus* was affected by differences in motivation (van Horik & Madden, 2016), which is regulated by the neurotransmitter dopamine (Wise, 2006). However, the direct links between physiology and problem solving performance are poorly studied.

Currently, studies relating adrenocortical activity to problem solving ability show mixed results. For example, Bókony et al. (2014) found that house sparrows *Passer domesticus* with lower corticosterone concentrations solved complex problems faster than birds with higher corticosterone concentrations. However, horses *Equus callabus* that were capable of innovating had significantly higher corticosterone concentrations than horses that did not innovate (Esch et al., 2019), and blood glucose and ketone concentrations were not related to problem solving in African striped mice *Rhabdomys pumilio* (Rochais et al., 2021). This suggests that the relationship between adrenocortical activity and problem solving may be species-specific, and that the methods of measuring this response could impact the results.

Therefore, I investigated whether adrenocortical activity, assessed using corticosterone metabolite concentration, was related to problem solving performance in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*. Mosaic-tailed rats are medium-sized (72.9 ± 12 g) murid rodents found in forests along the eastern coast of Australia (Callaway et al., 2018). These habitats are complex, showing spatial and temporal variation in food availability, indicating that mosaic-tailed rats likely experience variations in metabolic demand. Furthermore, these habitats often experience high levels of disturbance, yet mosaic-tailed rats also thrive in these conditions, indicating a good capacity for problem solving. In support of this, mosaic-tailed rats are capable innovators (Chapter 3; Rowell & Rymer, 2020b). Previous studies have found that more exploratory mosaic-tailed rats are better problem solvers than avoidant individuals (Chapter 7; Rowell & Rymer, 2021a). Mosaic-tailed rat personality has also been linked to some physiological measures (glucose and testosterone concentrations, Turner, 2015), suggesting a potential for adrenocortical effects on problem solving. I measured problem solving performance using six problem types of different complexities in different contexts, and I collected faecal samples from each individual outside of these contexts to assess corticosterone metabolite concentrations, and therefore, adrenocortical activity levels. As adrenocortical activity could reflect variations in metabolism (Sandi & Rose, 1994) or stress (Tsigos & Chrousos, 2002), both of which are known to impact behaviour (Careau et al., 2008; Lupien et al., 2009) and cognition (Hoyer & Lannert, 2008), I predicted that individual variation in adrenocortical activity would reflect individual variation in problem solving ability, but due to mixed results (e.g. Bókony et al., 2014; Esch et al., 2019), I made no *a priori* predictions about the direction of this relationship.

## Methods

### *Ethical Note*

The research complied with the ABS/ASAB guidelines for the ethical treatment of animals (Bee et al., 2020) and the Australian Code for the Care and Use of Animals for Scientific Purposes (National Health and Medical Research Council, 2013). The study was approved by the Animal Ethics Screening Committee of James Cook University (clearance number: A2539). I observed all animals daily, and animals were weighed every two weeks to monitor condition. No animals exhibited signs of extreme stress (e.g. prolonged vocalisation, seizures, sudden weight loss) during testing or after testing. Individuals were returned to their home cages following testing and were monitored for any abnormal behaviours (of which none were observed).

### *Husbandry*

Animals used in this study were 25 wild-caught individuals from a free-living population (14 male and 11 female) and 29 F1 or F2 captive-born (15 male and 14 female) individuals from the mosaic-tailed rat breeding colony at James Cook University, Cairns, Australia. F1 individuals were individuals born in captivity to 11 wild-caught females, while F2 individuals were born to F1 females in captivity. This represents a larger sample size (n = 54) than some other studies examining the relationship between problem solving and glucocorticoid concentrations (e.g. 16 individuals in Esch et al. (2019); 23 individuals in Pfeffer et al. (2002)). All individuals were tested as adults (i.e. sexually mature; range: 7 months to > 2 years of age at first test). Mosaic-tailed rats were kept under partially controlled environmental conditions (natural lighting from a large window; 22-26 °C; 50-65% relative humidity) in a laboratory for at least 7 months before being tested.

As mosaic-tailed rats are solitary (Rader & Krockenberger, 2006), they were individually housed in wire frame cages (34.5 x 28 x 38 cm) with deep plastic bases (34.5 x 28 x 11 cm) containing ± 10 cm of wood shavings. Individuals were each given a cylindrical plastic nest box (11 x 11 x 20 cm), a handful of pasture hay and two pieces of paper towel for nesting material. A cardboard roll was provided for enrichment. As mosaic-tailed rates are semi-arboreal (Rader & Krockenberger, 2006), cages were equipped to enable climbing, with a wire platform near the top of the cage and sticks from the base to the top of the cage. Approximately 5 g of mixed seed and rodent chow (Rodent Origins, Vetafarm, Wagga Wagga, Australia) and 5 g of vegetable/fruit (e.g. sweet potato, apple) were given to each individual daily. Average animal mass during the testing period was 91.05 ± 1.28 g. On days of problem solving testing, food was only given to the animals once testing was completed to motivate animals to participate in the test. All individuals were therefore deprived of food for approximately 24 hours prior to testing. Water was available *ad libitum*.

### ***Problem Solving Tests***

Tests were conducted between August 2018 and August 2020. Individuals were tested in a random order, and received the different problem tasks in a random order, except for the Trixie dog activity board, which was presented last due to its complexity and the need to habituate animals first to the novel arena in which it was presented (see below). Individuals were rested for at least 24 hours between each test. Testing occurred during the peak period of mosaic-tailed rat activity (between 18h00 and 22h00, Wood, 1971) under red light (except for the obstruction test), which does not affect mosaic-tailed rat behaviour (Paulling et al., 2019). Tests were recorded with a Sony HDR-CX405 Camcorder from above. Behavioural data were then extracted from videos using the video analysis software BORIS (version 7.9.6, Friard & Gamba, 2016). Mosaic-tailed rats were tested individually and returned to their home cage and fed immediately after testing.

To gain a comprehensive measure of the problem solving abilities of individuals, I assessed problem solving using five foraging-motivated problem-solving tests and one escape-motivated problem-solving test. These problems differed in complexity across three contexts (home cage, open field arena, or light/dark box). Animals were not trained in any test, and were only presented with each test once, as I were interested in the natural problem solving abilities of individuals. The methods are fully outlined in Chapter 3 (Rowell & Rymer, 2020b). If testing occurred outside of the home cage (i.e. the Trixie Dog Activity Board Level 2 and the obstruction task), mosaic-tailed rats were removed from their cage by gently guiding them into a plastic cup using a piece of cardboard. The individual was then released into the testing arena on the side opposite the problem. The individual was returned to its home cage after testing in the same manner. For all tests, I measured the latency to solve the puzzle once the individual began interacting with it, the time spent interacting with the puzzle, and whether the puzzle was successfully solved.

### *Problem Solving in the Home Cage*

Briefly, I presented mosaic-tailed rats with two food-baited puzzle boxes in their home cages (presented on separate nights). The matchbox task consisted of a cardboard matchbox (solved by pushing or pulling the box out the sleeve, or chewing through the sleeve) and the cylinder task was a plastic cylinder (solved by pulling or pushing through the open end that was covered with tinfoil). 2 g of fruit (e.g. banana) was used as a reward in these tests.

### *Problem Solving in an Open Field*

I also presented mosaic-tailed rats with three simultaneous problems on a food-baited Trixie Dog Activity Board Level 2 (two pillars to push, two tiles to slide and two levers to lift) placed in an open field arena. Two sunflower seeds were placed under each task on this board, as fruit could have become lodged in the mechanisms. Although presented at the same time, as they were located on the same board, these tasks required different methodologies to solve and differed in complexity. Mosaic-tailed rats were given 30 minutes to interact with and solve the puzzles (they only had to solve one of each type (e.g. one pillar) to be classified as a successful solver of that task).

### *Problem Solving in the Light/Dark Box*

I also used an obstruction task to measure escape-motivated problem solving in a light/dark box. Mosaic-tailed rats had to either push or pull a crumpled piece of paper out of a doorway to escape to the dark compartment. This was presented to the mosaic-tailed rats for three, 3-minute rounds in a single testing session to increase the chance of participation, as this was a stressful test because of a bright LED light trained on the light compartment of the box (Chapter 3; Rowell & Rymer, 2020b). In terms of complexity, the pillar task was the easiest to solve, followed by the cylinder, matchbox, obstruction, tile, and lever tasks (Chapter 3; Rowell & Rymer, 2020b).

### *Faecal Sample Collection and Hormone Metabolite Extraction*

Faecal samples were collected from individuals between September 2019 and June 2020 during routine cage cleaning. Some individuals (n = 42) had two sets of samples collected and analysed (one from 2019 and one from 2020). Faecal samples were only collected once individuals had experienced all problem solving tests. Mosaic-tailed rats were placed in a plastic tub while the cage was cleaned (maximum 20 minute process) and any faecal boli excreted during this time (that were uncontaminated by urine) were collected. Cages were cleaned between 9h00 and 11h00 once per fortnight. At least two sessions of cleaning were required to collect sufficient faecal boli for each individual (I required at least 1 g of faeces per individual). Although the gut retention time of mosaic-tailed rats is unknown, collection of faeces in the morning likely corresponded with their main activity period (night time). Faecal samples were stored in a plastic Eppendorf tube at -20°C. I used several faecal samples collected during multiple routine cage cleaning episodes as these would likely provide a better representative of general adrenocortical activity, rather than a stress response to the problem solving tests. Due to the gut passage time, sampling during cage cleaning was not expected to significantly impact hormone concentrations.

To biologically validate faecal corticosterone metabolite measurements in this species, I collected faecal samples from some of the individuals (n = 11) while they were undergoing repeated sessions of behavioural and cognitive testing for another study that will be published separately. These tests were conducted outside of the home cage exposing individuals to novel objects in a novel arena and were thus considered to be stressful for the individuals. Testing occurred at the beginning of the dark cycle (i.e. between 18h00 and 19h00). Individuals received multiple tests approximately 24 hours apart and had at least two faecal samples collected. Fresh faecal samples were collected immediately following the testing sessions.

Faecal samples were prepared according to Murray et al. (2013). Briefly, samples were flash-frozen for 15 minutes at -80 °C, and then dried overnight in a ScanSpeed 40 speed vacuum concentrator spun at 1000 rpm and connected to a Scanvac CoolSafe condenser at ~100°C. Samples were then weighed to the nearest 0.01 mg. An 80% ethanol

(100% ethanol: distilled water) solution was added to each sample so that the sample was at a 1:10 concentration. Faecal boli were physically broken down into small pieces by using tweezers to push the boli against the sample tube walls. Tweezers were thoroughly wiped with ethanol in between each sample to avoid cross-contamination. Samples were vortexed and placed on a rotator overnight. Samples were then centrifuged at 15000 rpm for 15 minutes. I created a dilution by pipetting 2 µl of the 80% ethanol solution from each sample into 998 µl of hormone kit assay buffer with a final sample dilution of 1:500. All samples were then vortexed again.

### *Faecal Corticosterone Metabolite Quantification*

I used a corticosterone enzyme-linked immunosorbent assay (ELISA) kits (ADI-900-097, Enzo Life Sciences, Farmingdale, New York, NY, USA), following the manufacturer's instructions, to analyse faecal corticosterone metabolites in each sample. Samples were plated in duplicate to measure intra-assay variation (average 11.4%). A single sample was repeated across plates to measure inter-assay variation (2.2% coefficient of variation). The cross-reactivities of corticosterone antibodies are reported in detail in previous studies (Sullivan et al., 2019). Sample concentrations were multiplied by 500 to account for the dilution.

As per the ELISA kit instructions, plates were read on a POLARstar Omega (BMG Labtech, Ortenberg, Germany) plate reader to measure the optical density of each well. I used Omega software v5.11 (BMG Labtech) and MARS Data Analysis software v3.20 R2 (BMG Labtech) to compare the optical densities to the standard curve. One individual was excluded from all statistical analyses (see below) due to an extremely high (173 x more than the group average) corticosterone metabolite concentration, suggesting an error during the plating process. Despite the high corticosterone concentration, the problem solving abilities of this individual were similar to other animals included in the study (solved 3 of the 6 tasks, average 130 s latency to solve 3 tasks).

### *Statistics*

Statistical analyses were performed using RStudio (version 1.0.153; https://www.rproject.org; R version 4.0.2, https://cran.rstudio.com, 22 June 2020). The model-level significance was set at $\alpha = 0.05$. Data and model residuals were tested for normality (Shapiro-Wilk test). The descdist function ('fitdistrplus' package, Delignette-

Muller & Dutang, 2015) was used to find the distribution of best fit for each response variable used in the regression models. In all models, animal birth origin (captive born vs. wild caught) and sex were included as fixed factors. Body mass and 2020 faecal corticosterone metabolite concentrations (non-transformed, unless otherwise stated) were included as continuous predictors. Linear models were checked for homoscedasticity of residuals using the gqtest function ('lmtest' package, Hothorn et al., 2015) and for a linear relationship with continuous predictors. The emmeans function ('emmeans' package, Lenth et al., 2020) was used to calculate the means and standard errors of variables included as dependent variables in the models.

I used a paired t-test to test the biological validity of faecal metabolite measurement in this species. I compared the two measures of non-transformed faecal corticosterone metabolite concentrations between the samples collected after undergoing a stressor and samples collected during cage cleaning from the same individuals.

I then considered the intra-individual variation in corticosterone metabolite concentration using a test of repeatability ('rptR' package, Stoffel et al., 2017) to analyse whether the corticosterone metabolite concentration of individuals (n = 42) significantly changed from 2019 to 2020. I also considered inter-individual variation of the 2020 samples, as this was the larger sample size (n = 53). I used a linear model with 2020 corticosterone metabolite concentration (log-transformed) as the dependent variable, and individual mass, sex, and birth origin as independent variables.

I ran separate Cox's proportional hazards models for each year of physiological sampling to analyse the relationship between problem solving latency and the corticosterone metabolite concentrations (2019 and 2020) across all six solving tasks ('survival' package, Therneau & Lumley, 2014; 'survminer' package, Kassambara et al., 2017). I report the hazard ratios (differences between groups in the limit of the number of events per time/number at risk; $e^b$) with confidence intervals and p values for these models (as per Bókony et al., 2014). For the puzzles presented in the open field arena (the pillar, tile and lever tasks on the Trixie Dog Activity Board), I used the latency to solve the first of each puzzle type, as puzzles were given in duplicate (e.g. whichever tile was slid open first). The maximum value was given if an individual did not solve a task (i.e. 1800 s; Liker & Bókony, 2009) or did not participate in the test (i.e. did not interact with the task; cylinder = 1 individual, matchbox = 2 individuals, obstruction = 11 individuals). The maximum latencies were treated as censored data in the Cox's proportional hazards models.

The data for time spent interacting were not normally distributed. Therefore, the 2020 data were transformed using the orderNorm function (‘bestNormalize’ package, Peterson, 2021). The data were then analysed using a linear model with a Gaussian distribution (‘lme4’ package, Bates et al., 2007). The 2020 corticosterone metabolite concentration was included as a continuous predictor, and problem type was included as a fixed factor. The 2019 data could not be transformed, and so a separate beta regression model (‘betareg’ package, Cribari-Neto & Zeileis, 2010) was conducted with the proportional time interacting, with the 2019 corticosterone metabolite concentration included as a continuous predictor, and problem type as a fixed factor. If two replicas of the same puzzle were presented to the mosaic-tailed rats (e.g. pillar, tile, lever and obstruction tasks), I used the average time spent interacting between the replicates.

As per the descdist function, I used a general linear model (‘nlme’ package, Pinheiro et al., 2020) with a Poisson distribution to assess the effect of 2020 corticosterone concentration on overall problem solving performance (i.e. the total number of puzzle types solved). The model was tested for overdispersion using the dispersiontest function (‘AER’ package, Kleiber et al., 2020). Individuals were considered to have solved a puzzle if at least one repeat (e.g. one of two tiles) was solved. There were six types of puzzles that could be solved (matchbox, cylinder, obstruction, pillar, tile, lever).

## Results

### *Biological Validation of the Assay to Measure Faecal Corticosterone Metabolites*

Behavioural and cognitive testing resulted in a significant increase in adrenocortical activity in mosaic-tailed rats ($t_{10} = 4.26$, $p = 0.002$, stressed = 137.47 ± 28.12 ng/g faeces, control = 64.81 ± 13.63 ng/g faeces), with faecal corticosterone metabolite concentration being 2.1 x higher when individuals were undergoing testing than when they were not (Fig. 6.1).

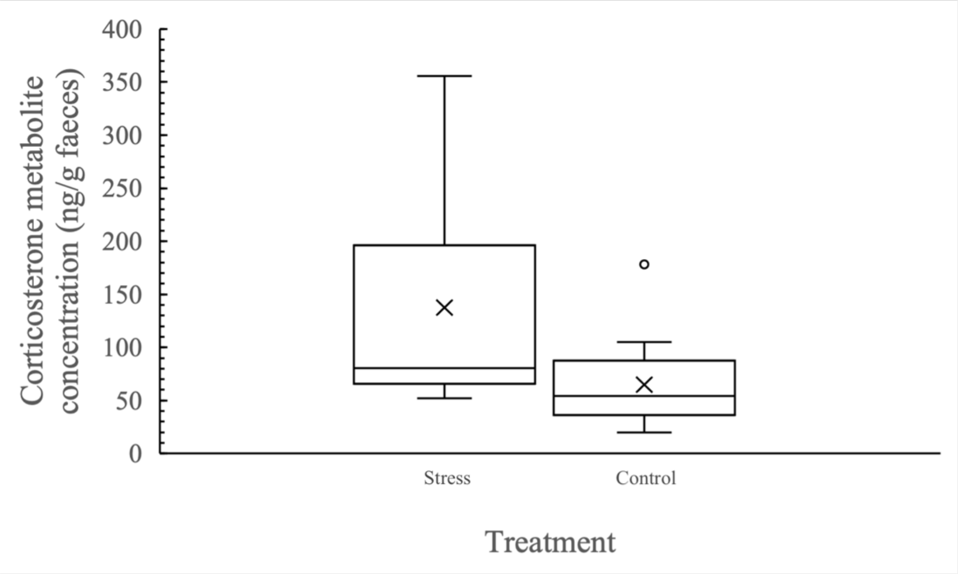

**Figure 6.1.** Boxplot graphs of faecal corticosterone metabolite concentrations (ng/g faeces) of individual fawn-footed mosaic-tailed rats *Melomys cervinipes* when undergoing testing (Stressed) and when not being tested (Control). The mean for each group is indicated by X.

### *Individual Variation in Corticosterone Metabolite Concentration*

Individual corticosterone metabolite concentrations (measured from faecal samples collected during cage cleaning) were not repeatable between 2019 and 2020 ($R = 0.09$, $p = 0.281$). The average faecal corticosterone metabolite concentration was 138.30 ± 21.82 ng/g faeces for mosaic-tailed rats sampled in 2019, and 79.86 ± 12.26 ng/g faeces for mosaic-tailed rats sampled in 2020. Individual concentrations ranged between 11.58 and 494.25 ng/g faeces. Faecal corticosterone metabolite concentrations were similar between individuals of different sexes ($F_{1,53} = 0.05$, $p = 0.826$; male = 82.31 ± 17.69 ng/g faeces, females = 67.52 ± 9.50 ng/g faeces), birth origins ($F_{1,53} = 0.06$, $p = 0.813$; captive born = 79.94 ± 8.20 ng/g faeces, wild caught = 70.17 ± 10.59 ng/g faeces), and mass ($F_{1,53} = 0.34$, $p = 0.562$).

### *Latency to Solve Problems*

Regardless of the year of sampling, the latency to solve the six problems was not significantly related to corticosterone metabolite concentration (2019: $e^b = 0.99$ [0.99, 1.00], $p = 0.380$; 2020: $e^b = 0.99$ [0.99, 1.00], $p = 0.397$), sex (2019: $e^b = 0.92$ [0.64, 1.84], $p = 0.929$; 2020: $e^b = 1.03$ [0.59, 1.77], $p = 0.795$), birth origin (2019: $e^b = 1.10$ [0.61, 1.96], $p = 0.758$; 2020: $e^b = 0.95$ [0.61, 1.49], $p = 0.822$), mass (2019: $e^b = 0.99$ [0.95, 1.03], $p = 0.584$; 2020: $e^b = 1..00$ [0.97, 1.03], $p = 0.991$) or problem type (2019: $e^b = 1.12$ [0.15, 8.85], $p = 0.912$; 2020: $e^b = 0.98$ [0.30, 3.22], $p = 0.977$).

### *Time Spent Interacting with Problems*

Time spent interacting with the tasks was significantly related to the problem type (2019: $\chi^2_5 = 65.29$, $p < 0.001$; 2020: $F_{1,5} = 40.01$, $p < 0.001$), with individuals interacting significantly less with the pillar and tile tasks than all other tasks (Fig, 6.2). Corticosterone metabolite concentration (2019: $\chi^2_1 = 1.81$, $p = 0.178$; 2020: $F_{1,318} = 0.50$, $p = 0.482$), birth origin (2019: $\chi^2_1 = 3.36$, $p = 0.067$; 2020: $F_{1,318} < 0.01$, $p = 0.950$), mass (2019: $\chi^2_1 = 0.09$, $p = 0.762$; 2020: $F_{1,318} = 3.89$, $p = 0.050$), and sex (2019: $\chi^2_1 = 2.62$, $p = 0.106$; 2020: $F_{1,318} = 3.65$, $p = 0.057$) were not significantly related to how much time the mosaic-tailed rats spent interacting with the problems.

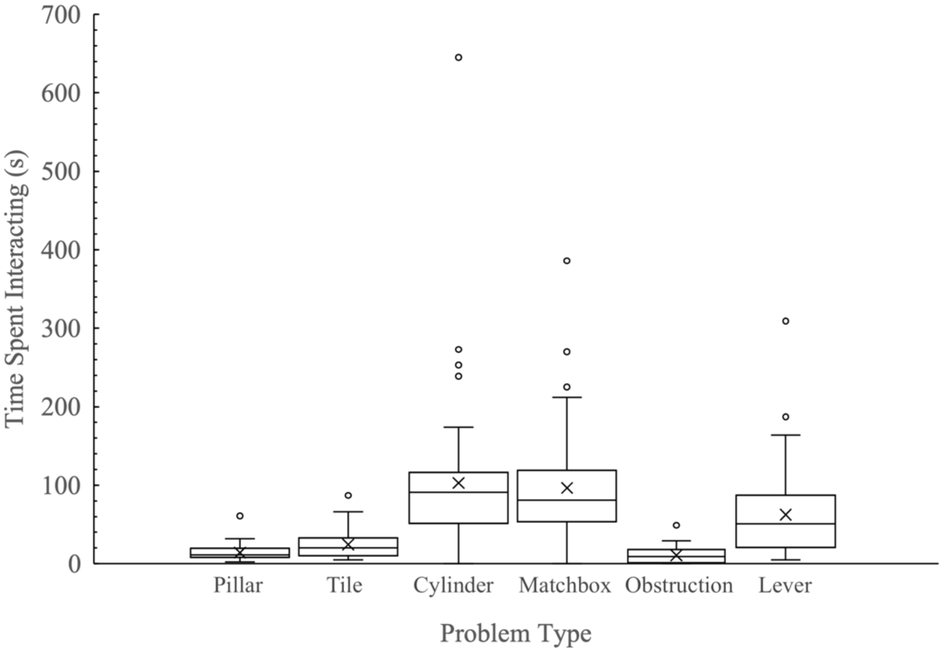

**Figure 6.2.** Boxplot graphs of the relationship between problem type and time spent interacting (s) with the tasks of fawn-footed mosaic-tailed rats *Melomys cervinipes*. The mean for each group is indicated by X.

### Overall Solving Ability

The total number of problems solved was not significantly related to corticosterone metabolite concentration ($\chi^2_1 = 0.43$, $p = 0.512$), sex (male = 1.42 ± 0.11, female = 1.33 ± 0.10; $\chi^2_1 = 0.13$, $p = 0.720$), birth origin (captive born = 1.41 ± 0.10, wild caught = 1.34 ± 0.11; $\chi^2_1 = 0.65$, $p = 0.420$) or mass ($\chi^2_1 = 0.04$, $p = 0.837$).

## Discussion

In this study, I explored the relationships between adrenocortical activity (corticosterone metabolite concentration) and problem solving in a native Australian rodent. I found that individuals varied in their adrenocortical activity over time, possibly due to seasonal variation (e.g. house sparrows, Romero et al., 2006), age effects (e.g. chickens *Gallus gallus domesticus*, Schmeling & Nockels, 1978), variation in sex hormones (e.g. Wistar rats *Rattus norvegicus*, Atkinson & Waddell, 1997), or unintended methodological variation. Despite these intra-individual differences, there was no significant variation in adrenocortical activity between individuals of different birth origin, sex, or mass. While I found a difference in metabolite concentrations between stressed and control animals, and I did not find an effect of yearly corticosterone variation on problem solving, I must express some caution. The collection time for the stressed and control samples differed due to behavioural testing being conducted at the beginning of the dark phase and cages being cleaned (and control samples collected) at the start of the light phase. A circadian rhythm influenced faecal corticosterone metabolite levels in laboratory rats, and metabolite levels peaked towards the end of the dark phase, and were lowest at the beginning of the light phase (Lepschy et al., 2007). Therefore, I would expect methodological differences to reflect either (1) no variation between samples, as the interaction between stressful condition and circadian rhythm would “cancel” each other out or (2) that the samples collected during routine cage cleaning would show higher concentrations, reflecting the peak circadian rhythm activity period (the night before). However, my results indicate the opposite pattern (i.e. higher concentrations collected during the testing phase), indicating that the difference in metabolite levels between stressed and control groups most likely reflects the response to the testing stressor. While blood samples collected from this species during the dark phase show a similar increase in corticosterone concentrations due to stress (Turner, 2015), I recommend that future studies should collect faecal samples during all phases. For both 2019 and 2020 sampling points, faecal sample collection periods varied between individuals, as the number of faecal boli individuals produced varied, with some individuals producing more in each sampling session than others. Variation in adrenocortical activity between samples could therefore also reflect seasonal variation (Romero et al., 2006) or differences in other physiological cycles (e.g. oestrous cycle, Atkinson & Waddell, 1997). Future studies should consider adjusting the sampling period for all individuals to minimize these possible influences.

Contrary to expectations, adrenocortical activity was not related to the latency to solve problems or the total number of problems solved. For the simple problems, these results are consistent with Bókony et al. (2014), who also found corticosterone concentration was not related to the latency to solve simple tasks in house sparrows. This could suggest that these tasks may not solely rely on cognitive processes (e.g. trial-and-error learning) to solve, which are known to be impacted by adrenocortical activity (e.g. metabolism, Careau et al., 2008). Instead, the successful solving of simple or moderate tasks may have relied on individuals being motivated and persistent (Griffin & Guez, 2014), which is related to other physiological processes (e.g. dopamine release, Laszy et al., 2005).

However, my results for the more complex problems were not supported by previous work. Other studies have found that adrenocortical activity was related to problem solving performance in complex problems, with higher corticosterone concentrations increasing problem solving performance in some species (e.g. greylag geese *Anser anser*, Pfeffer et al., 2002; horses, Esch et al., 2019) and decreasing performance in others (e.g. house sparrows, Bókony et al., 2014). However, problem solving in African striped mice was not related to physiological measures, including glucose and ketone concentrations as a measure of metabolism (Rochais et al., 2021). The lack of relationship between adrenocortical activity and complex problem solving performance in mosaic-tailed rats could indicate that, as for simple tasks, problem solving might be more reliant on other physiological processes.

This lack of consistency in results could also be due to the complex effects that corticosterone may have on an animal's physiology and behaviour, as well as a misunderstanding of what these measures represent (MacDougall-Shackleton et al., 2019). While higher corticosterone concentration can indicate a heightened metabolic response (MacDougall-Shackleton et al., 2019), it may also be indicative of heightened stress (Johnstone et al., 2012) or eustress (i.e. stimulation or arousal, Edgar et al., 2012; McCullough et al., 2018). As such, using only corticosterone concentration as a physiological measure may not be adequate to fully determine an animal's adrenocortical activity level (e.g. metabolic condition or stress level, MacDougall-Shackleton et al., 2019). Future studies should, therefore, consider measuring other physiological measures (e.g. oxidative stress and parasite load as indicators of a negative state, Bókony et al., 2014; salivary proteins as indicators of a positive state, Boissy et al., 2007), and how these relate to problem solving performance.

Similar to what has been found in other studies (Chapter 3; Rowell & Rymer, 2020b), mosaic-tailed rats differed in the amount of time spent interacting with different types of problems. Individuals spent significantly less time interacting with two of the problems in the open field (the pillar and tile tasks) than in the home cage (matchbox and cylinder) and light/dark box (obstruction) problems. The difference in interacting behaviour is likely a function of test context and complexity. Individuals may have been more active and less stressed in their home cages (Tang et al., 2002), leading to higher times interacting with these problems. In contrast, individuals may have been more motivated to solve and escape the stressful conditions of the obstruction task (Ben Abdallah et al., 2011) than in the open field, also leading to higher times spent interacting with these problems. Within the open field, the lever task was the most complex task, and individuals needed to interact with it more to solve it (Chapter 3; Rowell & Rymer, 2020b), resulting in the time interacting being similar between this task and the tasks in the other contexts.

Overall, I found that adrenocortical activity, as measured using corticosterone metabolite concentrations, was not significantly related to the latency to solve problems or time spent interacting with problems by fawn-footed mosaic-tailed rats. This could indicate that adrenocortical activity, possibly indicating stress, eustress, or metabolism, does not interfere with the capacity to problem solve in mosaic-tailed rats. Due to the complex nature of adrenocortical processes, future studies should consider including other markers of physiology (e.g. oxidative stress or positive state) when comparing physiology to behaviour and cognition in this species.

# Chapter 7: Exploration influences problem solving in the fawn-footed mosaic-tailed rat *Melomys cervinipes*

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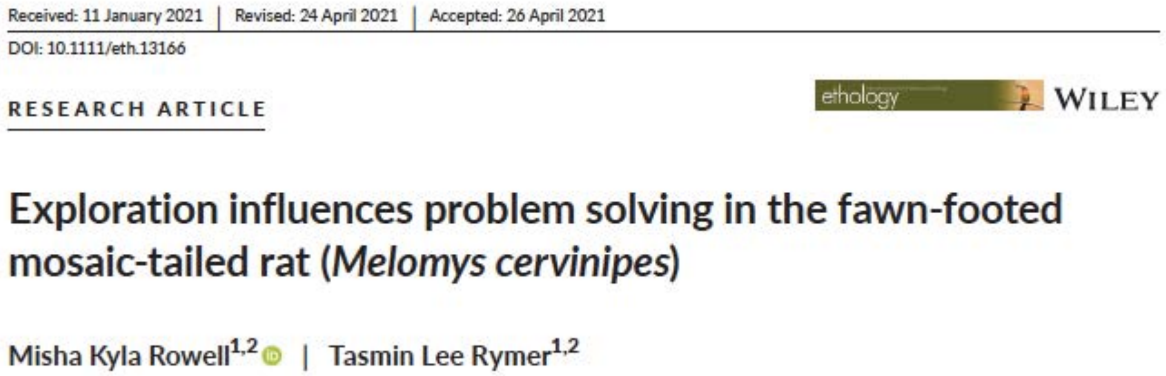

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RESEARCH ARTICLE

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## Exploration influences problem solving in the fawn-footed mosaic-tailed rat (*Melomys cervinipes*)

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## Abstract

The relationship between an animal’s personality and its problem solving ability has become a popular topic of investigation. However, results are conflicting, suggesting that these relationships may be species-specific. I investigated these relationships in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*. I predicted that more exploratory and less anxious mosaic-tailed rats would be better problem solvers (e.g. faster to solve the problem) as they would interact with the puzzles more and would be more willing to engage with the task. I assessed personality across two contexts (exploration in an open field and novel object test, and anxiety under simulated predation risk in a light/dark box) and over time (three repetitions). I measured problem solving using two food-baited puzzle boxes (matchbox and cylinder), a Trixie Dog Activity Board with three problems (pillars, tiles, and levers) and an obstruction task. Individual mosaic-tailed rats showed consistent individual differences in personality, but not problem solving ability. Furthermore, I found a positive relationship between personality and problem solving ability, with more exploratory individuals solving more problems, and solving problems faster, than less exploratory individuals. Exploratory individuals could be better problem solvers because they are more willing to interact with objects and are less neophobic than less exploratory individuals. However, less exploratory individuals still persist in the population, possibly due to differences in cognitive abilities, such as discrimination or recognition, that allow them to compensate for poorer problem solving abilities.

# Introduction

To survive, an animal must explore its environment and forage for resources. However, it risks predation or injury each time it does so. Therefore, animals must trade-off gaining resources against avoiding predation (Sih et al., 2004a). Animals can mitigate the risk of predation using problem solving. For example, laboratory mice could push an obstacle out of the way to escape to a hide (Ben Abdallah et al., 2011). Similarly, animals can use their problem solving abilities to access food resources. For example, many species of carnivorous mammals are capable of solving food-baited puzzle boxes (Benson-Amram et al., 2016). While there are many definitions of problem solving (e.g. Scheerer, 1963; Heppner & Krauskopf, 1987), problem solving (in the context of foraging or anti-predator behaviour) requires an animal to move itself or an object to overcome a barrier to either access food (solve a physical problem, Chow et al., 2017) or escape from a predator (solve a situational problem, Ben Abdallah et al., 2011).

An individual's problem solving ability does not occur independently of other behavioural and cognitive tendencies (Amici et al., 2019), as many of these are required for accurate problem solving (Griffin & Guez, 2014). In particular, persistence and behavioural flexibility (i.e. trying multiple behaviours and/or adjusting behaviours when strategies are not working, Griffin & Guez, 2014) are important for problem solving in multiple species (Griffin & Guez, 2014; Thornton & Samson, 2012). Problem solving is, therefore, not likely to require higher-order cognitive processes, such as insight (Thornton & Samson, 2012), whereas individual variation (Cole et al., 2011), particularly related to personality, could be more important.

Personality in animals refers to an individual's behavioural responses that are consistent over time and across different contexts (e.g. foraging or predation, Sih et al., 2004a). Personality is often assessed along five behavioural axes (e.g. shyness-boldness: reaction to a risky situation; exploration-avoidance: reaction to a new situation; activity: general level of activity; aggressiveness: reaction to conspecifics, and sociality: reaction to presence/absence of conspecifics, other than aggression, Réale et al., 2007) that are often positively or negatively correlated (Coppens et al., 2010; Koolhaas et al., 1999). An animal's personality can also affect how an animal responds to perceived predatory threats or how it approaches new food resources. For example, bolder individuals are often more exploratory and active, are attracted to new objects (neophillic, Biondi et al., 2010), and are more willing to take risks than shy individuals (Koolhaas et al., 1999; Réale et al., 2010). In addition, an animal's personality may also affect how it approaches and interacts with problems, which may ultimately affect how the animal solves a particular problem.

The relationship between personality and problem solving has been studied in many taxa (see Griffin & Guez, 2014), but inconsistency in personality terminology can make these results difficult to compare. Studies have found that less neophobic or more bold individuals are better problem solvers than more neophobic or less bold ones, either solving problems faster (e.g. callitrichid monkeys, Day et al., 2003) or having higher success rates (e.g. spotted hyenas *Crocutta crocutta*, Benson-Amram & Holekamp, 2012; guinea pigs *Cavia porcellus*, Guenther & Brust, 2017). However, neophobia and boldness were measured using a novel object test in these studies, which measures exploration according to the criteria set out in Réale et al. (2007). Exploratory individuals could be better problem solvers because, by being more willing to explore than less exploratory individuals, they are more likely to interact with problems and ultimately solve them (Griffin & Guez, 2014; Guenther & Brust, 2017). Similarly, individuals that are less stressed or anxious are better problem solvers due to increased persistence (e.g. house sparrows *Passer domesticus*, Bókony et al., 2014; dogs *Canis familiaris*, Bray et al., 2017; horses *Equus caballus*, Esch et al., 2019). However, less exploratory individuals could be better problem solvers than exploratory ones, as exploratory individuals may dominate easily accessible resources (Huntingford et al., 2012), forcing less exploratory individuals to solve problems to access alternative resources (e.g. exploration of novel area in common mynas *Acridotheres tristis*, Lermite et al., 2017). Finally, other studies have failed to find a relationship between personality and problem solving. For example, less exploratory wild-caught adult Chimango caracaras *Milvago chimango* did not have higher solving success than exploratory birds, possibly because some individuals may have experienced the novel objects in the past (Biondi et al., 2010). Similarly, while juvenile meerkats *Suricata suricatta* were less neophobic (measured in a novel object test) than adult meerkats, they were less efficient solvers, possibly due to their smaller size and/or lack of dexterity (Thornton & Samson, 2012). The equivocal nature of these results suggests that relationships between personality and problem solving may be species-specific (Griffin & Guez, 2014).

However, the inconsistencies observed in these relationships could also be a consequence of different methods used to assess personality (but see Dingemanse & Wright, 2020 for suggested analyses). For example, of two studies that have assessed personality (either neophobia or exploration) in common mynas, Griffin et al. (2014) assessed personality as the latency to approach a novel object, while Lermite et al. (2017)

assessed exploration of a novel environment. Furthermore, studies looking for a relationship between personality and problem solving generally only measure the behavioural type, using one neophobia/exploration trial, without measuring the effect of personality on problem solving across time (Biondi et al., 2010; Griffin et al., 2014) or context (Webster & Lefebvre, 2001; Thornton & Samson, 2012), thereby failing to take into account potential repeatability of the behavioural response. Even fewer studies have assessed whether problem solving itself is consistent over time (Shaw, 2017), despite this being important for estimating the fitness benefits of problem solving (Thornton et al., 2014).

To gain a better understanding of these complex relationships, I assessed the relationship between personality and problem solving ability within and across different behavioural axes in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes.* Personality was established by measuring exploratory (investigation of a novel arena and objects) and anxiety-like (response to a novel risky situation) behaviour across three tests. The behaviour of many Australian rodents is poorly studied, or only studied over short periods of time (e.g. Cremona et al., 2015; Jolly et al., 2019). This study represents one of the first to explore these longer-term relationships in a native Australian rodent. These medium-sized rodents (72.9 ± 12g, Callaway et al. 2018) are abundant in multiple forest types along the eastern coast of Australia (Moore et al., 2008), and are also found in disturbed forest edges and fragments (Goosem & Marsh, 1997). This suggests that while living in a structurally and biologically complex environment, and utilising 3-dimensional vertical space, mosaic-tailed rats regularly encounter novel conditions and environmental challenges, and should therefore rely on high levels of exploration to be capable problem solvers. Associated with this, there should be selection for reduced neophobia and anxiety in these environments, because of the associated energetic costs (Sih et al., 2004b). I hypothesised that personality, as measured by exploration and anxiety, would impact the problem solving abilities of mosaic-tailed rats. I predicted that more exploratory and less anxious mosaic-tailed rats would be better problem solvers (e.g. faster to solve the problem) as they would interact with the puzzles more and would be more willing to engage with the task (Guenther & Brust, 2017).

## Methods

### *Ethical Note*

The research complied with the ABS/ASAB guidelines for the ethical treatment of animals (Bee et al., 2020) and 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). All individuals were observed daily, weighed every two weeks to monitor health, and received behavioural enrichment (seeds scattered to stimulate foraging, sticks and platforms for climbing, cardboard rolls, and occasional wooden blocks for chewing). There were no negative effects of testing on the animals, as no animals exhibited signs of extreme stress (e.g. seizures, prolonged vocalisations, sudden weight loss). Mosaic-tailed rats were returned to their home cages following testing and immediately resumed foraging when presented with food. All other behaviours appeared normal. Mosaic-tailed rats were returned to the colony following completion of testing to be used in future studies and for breeding purposes.

### *Husbandry*

Subjects used in this study were 19 wild-caught (14 male and 5 female) and 15 F1 captive-born (9 male and 6 female) individuals that originated from the mosaic-tailed rat breeding colony at James Cook University, Cairns, Australia. Wild-caught individuals were trapped using Elliott traps on the James Cook University Cairns campus, and adjoining Smithfield Conservation Park (16°49’1.938”, 145°41’12.1884”) from 2016 – 2017 (permit numbers WISP14530814 and WITK14530914). F1 individuals were the first generation offspring of the wild-caught female mosaic-tailed rats. All individuals were tested for personality and problem solving ability as adults (i.e. sexually mature; 1 year - > 2 years of age at first test) at least 10 months after capture. Mosaic-tailed rats were kept under partially controlled environmental conditions (natural lighting from a large window; 22-26 °C; 50-65% relative humidity).

As this species is solitary (Rader & Krockenberger, 2006), mosaic-tailed rats were individually housed in wire frame cages (34.5 x 28 x 38 cm) with deep plastic bases (34.5 x 28 x 11 cm) containing ± 10 cm of wood shavings. A cylindrical plastic nest box (11 x 11 x 20 cm), a handful of pasture hay and two pieces of paper towel were provided for nesting material. A wire platform was provided near the top of the cage, and a cardboard roll and sticks were provided for behavioural enrichment, as mosaic-tailed rats are semi-arboreal (Rader & Krockenberger, 2006). Approximately 5 g of mixed seed and rodent chow (Vetafarm Origins) and 5 g of vegetable/fruit (e.g. sweet potato, apple) were given to each individual daily. Average animal mass during the testing period was 97.44 ± 0.55 g. On days of problem solving testing, food was only given to the animals once testing was completed to motivate them to participate in the test. Water was available *ad libitum*. Individuals were also given an electrolyte solution (Hydralyte) once a month to supplement any vitamins or minerals that might be missing from the captive diet, as suggested by a wildlife veterinarian. Animals were weighed every two weeks, and visually inspected daily.

## *Experimental Design*

The intention was to obtain repeated behavioural measurements for personality assessment of each individual in a series of tests, with all individuals (n = 34) experiencing three rounds of testing (see below). Rats experienced personality tests in random order on consecutive nights, except for the novel object test, which always immediately followed the open field test. To reduce the effects of learning on problem solving performance, mosaic-tailed rats were only presented with each of the problem solving tasks once in a random order, except for the Trixie Dog Activity Board, which was presented last due to its complexity and multiple tasks present. However, the context of the problems (foraging within a familiar environment (matchbox and cylinder in the home cage) vs. foraging in an unfamiliar environment for the Trixie Dog Activity Board) was repeated across the tests. Problem solving tests were presented one to five months after completion of the personality tests.

Testing occurred between 18h00 and 22h00 during the peak period of mosaic-tailed rat activity (Wood, 1971) under red light (except for the light/dark box and obstruction tests; see below), which does not affect mosaic-tailed rat behaviour (Paulling et al., 2019). When tests were conducted outside of the home cage, mosaic-tailed rats were gently ushered into a plastic cup in their home cage using a soft piece of cardboard. This cardboard was used to cover the cup while individuals were transferred from their cage to the testing arena. Animals were habituated to this handling technique as it was also used to move animals into and out of cages during routine husbandry. Behaviours were recorded from above with a GoPro Hero5 or Sony HDR-CX405 Camcorder. Behavioural data were collected from videos using the video analysis software BORIS v. 7.9.6 (Friard & Gamba, 2016). Mosaic-tailed rats were tested individually and returned to their home cage immediately after testing.

## *Personality Tests*

I assessed personality by measuring behaviour of each individual across three tests: 1) exploration in the open field test (Carola et al., 2002); 2) exploration in the novel object test (Guenther & Brust, 2017); and 3) anxiety in the light/dark box test (Guenther & Brust, 2017; Supplementary Table 7.1). Individuals experienced each test three times (replicates), at least four weeks apart, to assess repeatability of behaviour (Guenther & Brust, 2017). Measuring personality over different contexts and over time gives a robust understanding of its ecological and evolutionary significance (Guenther & Brust, 2017).

### *Open Field and Novel Object Tests*

The open field test was a coloured plastic storage container (56.5 x 40 x 32.5 cm) with a 3.5 cm perimeter (edge) marked (Figure 7.1a). An individual mosaic-tailed rat was placed in the centre of the open field and left for 10 minutes. I 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.

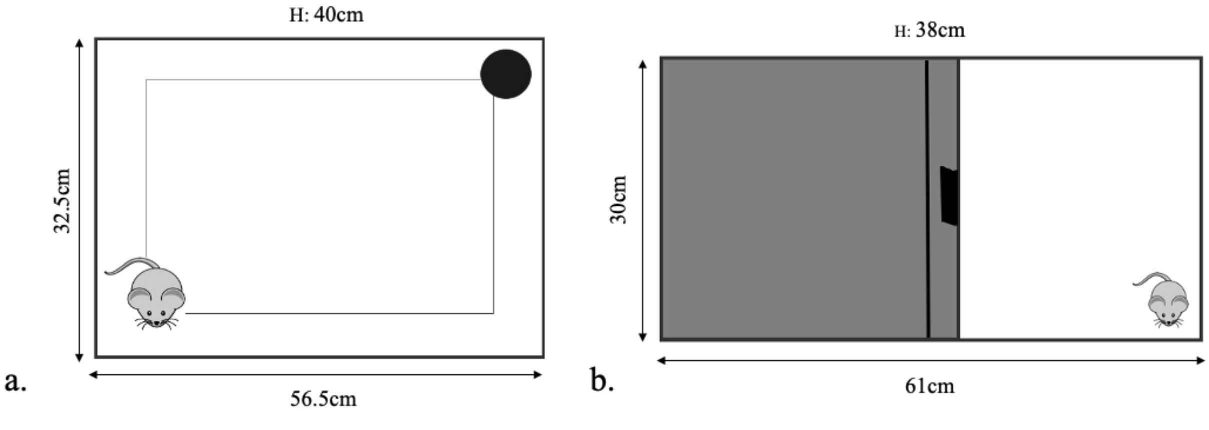


**Figure 7.1.** Testing conditions used to measure personality in fawn-footed mosaic-tailed rats *Melomys cervinipes*. a) Container used for open field and novel object tests with novel object placed (dark circle). b) Light/dark box set up.

At the end of the 10-minute period, a novel object was placed in the container at the end opposite to the subject (Figure 7.1a). If the animal suddenly moved while I was lowering the novel object into the testing arena, I quickly adjusted the object placement to put it as far away from the animal as possible. Different objects were used for each round of testing to ensure the object was novel to the animals. For the first round of personality testing, the novel object was a small tennis ball glued to a PVC pipe base (to prevent it from rolling, 8.3 x 6.5 x 6.5 cm). In the second round of testing, the novel object was a seal-shaped pencil eraser (3.5 x 7.5 x 12 cm), and in the third round of testing, the novel object was a coloured plastic clothes peg (0.9 x 2.8 x 7 cm). The individual's behaviour was recorded for the 10-minute test period. I 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, the frequency of crosses between the centre and periphery of the arena, and the duration of time spent active in the centre.

### *Light/Dark Box Test*

The light/dark box consisted of a glass tank (61 x 38 x 30 cm) divided in half with a plastic barrier (Figure 7.1b). The barrier had a small doorway (10 x 10 cm) to allow the rat to move freely between sections. One section (including the barrier) was painted 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). A mosaic-tailed rat was placed in the light compartment. I measured the latency to enter the dark compartment from this point. The individual was then allowed to explore for 10 minutes after it entered the dark compartment. All individuals moved into the dark compartment and participated in this test. I also 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.

## ***Problem Solving Tests***

I assessed problem solving across six tasks as described in Rowell & Rymer (2020b; Chapter 3). Animals were not trained in each test prior to experimentation, as I was interested in the natural problem solving abilities of individuals. Briefly, I tested problem solving in a foraging context by presenting mosaic-tailed rats with two food-baited puzzle boxes in their home cages, namely a cardboard matchbox (rats had to either push or pull out from the sleeve, or chew through the box; Figure 7.2a) and plastic cylinder (rats had to pull or push through the open end that was covered with tinfoil; Figure 7.2b). I also tested problem solving in a foraging context using a food-baited Trixie Dog Activity Board Level 2 (two pillars to push, two tiles to slide, and two levers to pull; Figure 7.2c) placed in an open field arena. Rats were given 30 minutes to interact with and solve the puzzles. I also measured problem solving in an escape-motivated context by placing the rats in the light/dark box where they had to either push or pull a crumpled piece of paper out of the doorway to escape to the dark compartment (Figure 7.2d). This was presented to the rats for three, 3-minute rounds in a single testing session to increase the chance of participation, as this was a stressful test (Chapter 3; Rowell & Rymer, 2020b). For all tests, I measured the latency to solve the puzzle, the time spent interacting with each puzzle, and the number of interactions with each puzzle.

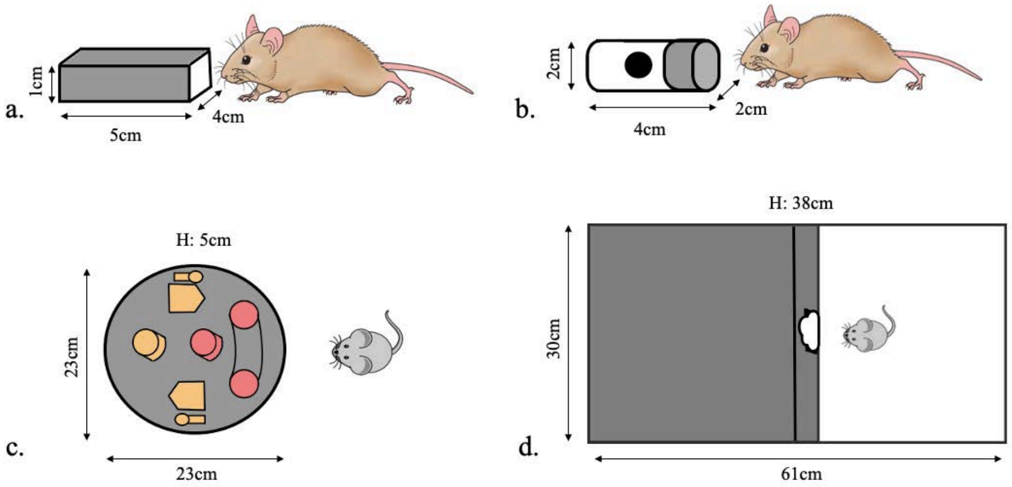


**Figure 7.2.** Problem solving tasks given to fawn-footed mosaic-tailed rats *Melomys cervinipes*. a) Matchbox task; b) Cylinder task with food (black circle) inside and tinfoil over one end; c) Trixie dog activity board with pillar, tile and lever tasks; and d) Obstruction task with a piece of crumpled paper blocking the entrance.

### *Statistics*

Statistical analyses were performed using R version 3.5.0 (R Core Team, 2020). The model-level significance was set at $\alpha = 0.05$. Data and models were tested for normality (Shapiro-Wilk test), and all data were tested for homogeneity of variance (Levene's test). In all original models, animal birth origin (captive born vs. wild caught), average body mass and sex were included as fixed factors, and individual ID was included as a random factor (unless stated otherwise below). Thereafter, I ran multiple models excluding non-significant factors, and compared model Akaike information criteria (AICs) to help determine models of best fit (Supplementary Table 7.2). I report only the statistics from these best models. Individual effects on problem solving measures were calculated using the ranova function (lmerTest package, Kuznetsova et al., 2017). I report Cliff's delta effect sizes with lower and upper confidence intervals (presented in square brackets) for all models. Significant differences in the main effects were identified using Tukey's *post hoc* tests (emmeans package, Lenth et al., 2020).

### *Personality*

Personality was assessed using each individual's behaviours from the three tests (open field and novel object = exploration; light/dark box test = anxiety). For each behaviour within each test, I ran repeatability analyses across the three replicates (rptR package, Stoffel et al., 2017). Repeatability (R) was calculated by dividing the group-level variance by the sum of the group-level and data-level variance (Stoffel et al., 2017). Repeatability estimate confidence intervals were calculated 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. Data were transformed and Gaussian distributions were used. Model residuals were checked using the lmerTest package (Kuznetsova et al., 2017). For each behaviour that was repeatable (Table 1), I calculated the average over the three replicates.

Considering the two personality axes being studied, I then ran two separate principal component analyses (PCAs; corrplot package, Wei et al., 2017). In the first PCA, I included the averaged values for each repeatable open field/novel object behaviour. In the second PCA, I included the averaged values for each repeatable light/dark box behaviour. I followed this protocol to reduce the number of predictor variables (Dingemanse and Wright, 2020). Data were not scaled before the PCA was conducted. I included principal components (PC) in the final analyses only if the eigen values were above 1, and if the PCs explained close to 70% of the variance (combined or alone). For the open field/novel object PCA, the first PC (hereafter PC_Exploration) explained 70.5% of the variance and comprised of eight behaviours (99.9% of that variation; Supplementary Table 7.2). For the light/dark box PCA, the first PC (hereafter PC_Anxiety) explained 67.7% of the variance and was comprised of four behaviours (100% of that variation; Table 1). High scores for PC_Exploration indicated that individuals were more exploratory (i.e. spent more time in the arena centre, made more arena crosses, and interacted with the novel object faster, for longer, and more frequently), while high scores for PC_Anxiety indicated that individuals were more anxious (i.e. spent less time in the light compartment, was less active in the light compartment, made fewer crosses into the light compartment, and had a longer latency to re-enter the light compartment).

I used separate linear models for each personality measure. I first added 200 to the PC_Anxiety score values (to make all values positive) and then the data were square-root transformed. PC_Exploration or the transformed PC_Anxiety scores were the dependent variables. Mass, sex, and birth origin were independent variables. The other personality measure (PC_Anxiety or PC_Exploration, whichever was not the dependent variable), was also included as an independent variable to explore the relationship between the personality axes (e.g. in model 1, where PC_Exploration was the dependent variable, PC_Anxiety was included as an independent variable).

### *Problem Solving Ability*

I first assessed the repeatability of problem solving ability using proportional solving latency (latency to solve task/maximum test duration). This was done using the function rptProportion with a Gaussian distribution (Stoffel et al., 2017). This analysed repeatability of problem solving within contexts (i.e. between tests in the foraging context) and across contexts (i.e. between foraging- and escape-motivated tests). I ran repeatability analyses on solving latency, with individual identity and task type included as random factors, and sex and birth origin included as fixed factors.

I examined latency to solve a puzzle after making first contact. For the Trixie dog activity board, I used the latency to solve the first task for each puzzle, as puzzles were given in duplicate (e.g. whichever pillar was knocked over first). Individuals that did not solve the tasks were given the maximum value (Liker & Bókony, 2009).

Finally, I tested whether the duration of time spent interacting with puzzles and the number of interactions with puzzles influenced solving latency of the individuals. Problems in the activity board and trials in the obstruction task were not independent (i.e. presented at the same time or in the same session), so interaction measures were averaged for each problem within each test (e.g. pillar 1 and 2 in the activity board).

I used a linear mixed effects model (lmerTest package, Kuznetsova et al., 2017; Pinheiro et al., 2020) to analyse the influence of the interaction measures (duration and frequency) or average interaction measures (duration and frequency of interaction in obstruction, pillar, lever and tile tasks) on solving latency (dependent variable).

### *Personality and Problem Solving Comparisons*

I used a linear model to assess the effect of personality on overall problem solving ability. The total number of puzzle types solved was used as an indication of overall solving ability. Individuals were considered to have solved a puzzle if at least one repeat (e.g. one of three obstruction trials or one of two pillars) was solved. There were six types of puzzles that could be solved (matchbox, cylinder, obstruction, pillar, lever, tile). Exploration and anxiety scores were included as continuous predictors.

I also used a linear mixed effects model to assess the relationship between the latency (square-root transformed) to solve a problem and personality. Latency to solve each test was the dependent variable, exploration score was included as a continuous predictor, and individual identity was included as a random effect. Problem solving task type was included as a fixed factor. Birth origin, body mass, sex, anxiety score, and the interaction between problem type and exploration score were not included in the model (they did not have a significant effect on latency to solve a problem).

I also used separate linear models to assess the relationship between personality and interacting measures. The duration of time spent interacting (cube-root transformed) and number of interactions (log-transformed) with each task were the dependent variables. The relationship between personality and the frequency of interactions was assessed using a linear model. For both models, exploration was included as a continuous predictor, problem type was included as a fixed factor, and individual identity was included as a random factor. The interaction between problem type and exploration score was included in the linear model.

## Results

### Personality

In the open field test, all behaviours, except for the latency to return to the centre after reaching the edge, were repeatable over testing sessions (Table 7.1). All behaviours were repeatable in the novel object test over testing sessions (Table 7.1). These behaviours were used to generate the exploration PCA score. In the light/dark test, all behaviours, except for the latency to enter the dark compartment, were repeatable over testing sessions (Table 7.1), and these behaviours were used for the anxiety PCA score.

Exploration score was not significantly impacted by anxiety score ($F_{1, 34} = 0.59$, $p = 0.449$), mass ($F_{1, 34} = 1.77$, $p = 0.194$), sex ($F_{1, 34} = 0.43$, $p = 0.518$) or birth origin ($F_{1, 34} = 4.13$, $p = 0.051$). However, anxiety score was significantly affected by mass ($F_{1, 34} = 6.84$, $p = 0.014$), with heavier individuals being less anxious than lighter individuals (Figure 7.3). Anxiety score was not significantly affected by exploration score ($F_{1, 34} = 0.43$, $p = 0.519$), sex ($F_{1, 34} < 0.01$, $p = 0.981$) or birth origin ($F_{1, 34} = 0.08$, $p = 0.785$).

**Table 7.1.** 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). Behaviours were considered repeatable if the $p$ value was significant, and if the confidence intervals did not overlap 0. Significant values are indicated in bold.

| Test | Behaviour | Repeatability Output | Mean ± SE | Confidence Intervals | Loadings |
|---|---|---|---|---|---|
| Open field (exploration) | Latency to return to centre | R = 0.07, $p$ = 0.443 | 65.45 ± 13.34 | 0.0, 0.33 | N/A |
| | Time in open field centre | **R = 0.42, $p$ < 0.001** | 162.10 ± 16.93 | 0.18, 0.63 | +8.1% |
| | Time active in open field centre | **R = 0.32, $p$ = 0.003** | 82.14 ± 8.60 | 0.08, 0.55 | +11.9% |
| | Open field crosses | **R = 0.43, $p$ < 0.001** | 16.07 ± 1.40 | 0.19, 0.65 | +13.8% |
| Novel object (exploration) | Novel object approach latency | **R = 0.30, $p$ = 0.008** | 317.86 ± 30.27 | 0.09, 0.52 | +15.3% |
| | Time interacting with novel object | **R = 0.24, $p$ = 0.040** | 61.36 ± 10.14 | 0.02, 0.45 | +10.8% |
| | Number of novel object interactions | **R = 0.40, $p$ < 0.001** | 5.79 ± 0.97 | 0.18, 0.62 | +14.2% |
| | Time active in centre of novel object arena | **R = 0.23, $p$ = 0.036** | 96.61 ± 12.25 | 0.08, 0.53 | +12% |
| | Novel object test arena crosses | **R = 0.48, $p$ < 0.001** | 6.48 ± 1.08 | 0.27, 0.67 | +13.8% |
| Light/dark box (anxiety) | Latency to enter dark compartment | R = 0.19, $p$ = 0.072 | 15.76 ± 9.49 | 0.0, 0.41 | N/A |
| | Latency to re-enter the light compartment | **R = 0.26, $p$ = 0.023** | 115.04 ± 20.24 | 0.05, 0.50 | +21.4% |
| | Total time in light compartment | **R = 0.42, $p$ < 0.001** | 87.06 ± 13.00 | 0.19, 0.63 | +24.9% |
| | Time active in light compartment | **R = 0.38, $p$ < 0.001** | 68.16 ± 8.21 | 0.16, 0.60 | +30.9% |
| | The number of crosses made in the light compartment | **R = 0.26, $p$ = 0.019** | 5.42 ± 0.47 | 0.01, 0.50 | +22.8% |

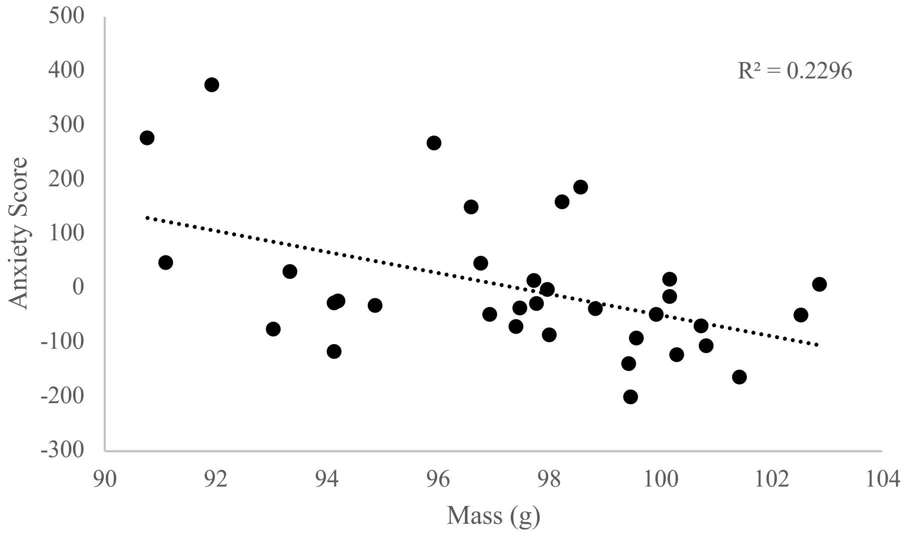


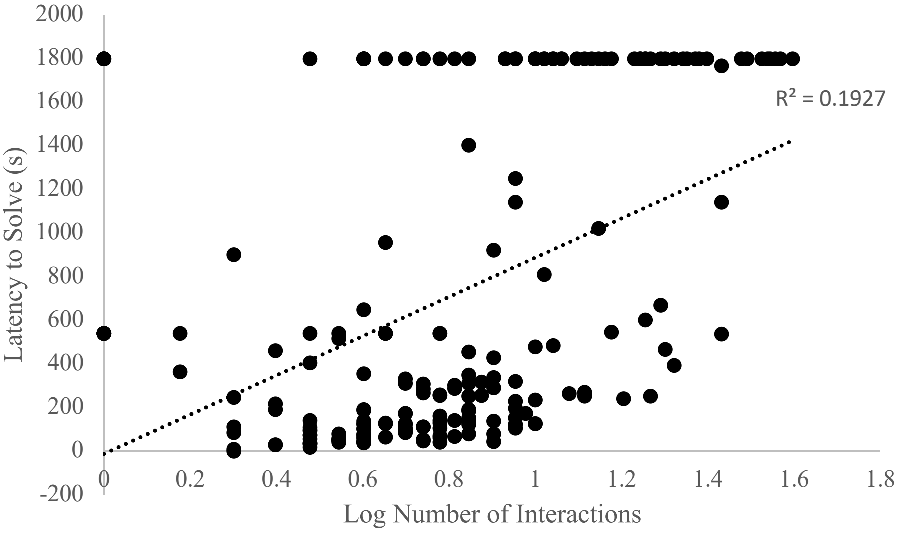
**Figure 7.3.** The relationship between mass (g) and PC_Anxiety score (from the light/dark box) in mosaic-tailed rats *Melomys cervinipes* in a linear model. Individual data points (n=34) are plotted as closed circles.

## *Problem Solving Ability*

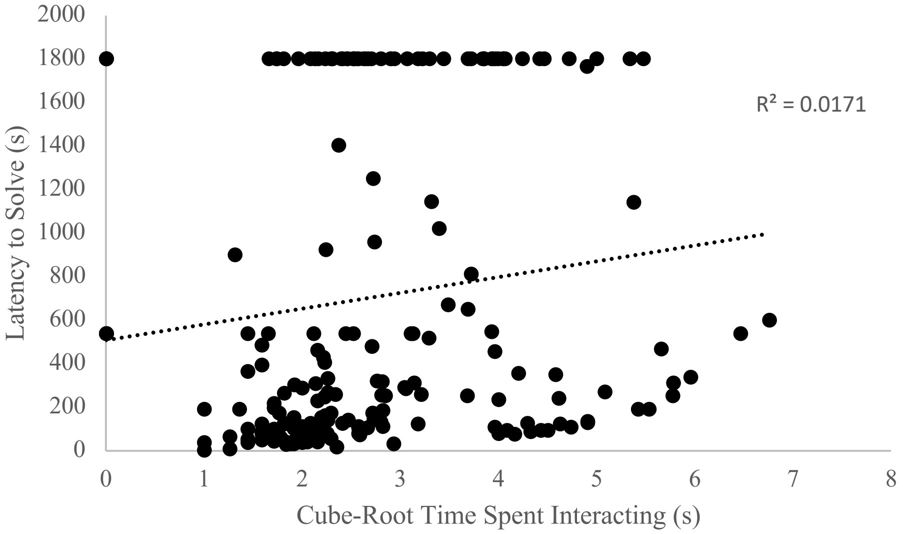
Individual mosaic-tailed rats were all capable of solving at least one type of task. Most individuals were successful in the simpler tasks, with 32 individuals solving the pillar task (94%), 30 individuals solving the cylinder task (88%), and 26 individuals solving the matchbox task (76%). There was more variation in solving abilities of the more complex tasks, with only 21 individuals solving the obstruction task (62%), 19 individuals solving the tile task (56%), and only 6 individuals solving the lever task (18%). Although solving latency as a proportion of test duration was repeatable across tasks (R = 0.112, $p = 0.011$), repeatability was very low.

## *Number and Duration of Interactions during Problem Solving Tests*

The number of interactions with the puzzles ($\chi^2_1 = 17.03$, $p < 0.001$; effect size = 0.70; [-0.21; 0.96]; mean ± SE: 0.80 ± 0.02) and the duration of interactions ($\chi^2_1 = 10.93$, $p < 0.001$; effect size = 1.0; [0.84; 1.0]; mean ± SE: 0.03 ± 0.003) were significant predictors of the latency to solve the problems, with faster solvers making fewer interactions (Figure 7.4a), and spending less time interacting (Figure 7.4b), than slower solvers or non-solvers. The latency to solve tasks was also significantly predicted by problem type ($\chi^2_5 = 105.16$, $p < 0.001$; effect size = 0.85; [-0.94; -0.66]), with the tiles (mean ± SE: 1028.52 ± 126.45) and levers (mean ± SE: 1622.17 ± 77.01) taking significantly longer to solve than the other tasks. Body mass also significantly affected latency to solve ($\chi^2_1 = 5.93$, $p = 0.015$; effect size = -0.08; [-0.62; 0.51]), with heavier individuals being faster solvers. Birth origin ($\chi^2_1 = 3.40$, $p = 0.065$; effect size = -0.13; [-0.28; 0.03]; mean ± SE: captive born = 605.79 ± 72.06, wild caught = 784.62 ± 73.92) and sex ($\chi^2_1 = 0.69$, $p = 0.408$; effect size = 0.08; [-0.09; 0.25]; mean ± SE: male = 668.73 ± 61.69, female = 783.09 ± 90.17) did not significantly affect solving latency.



a)



b)

**Figure 7.4.** The effect of a) the number of interactions made with puzzles (log-transformed), and b) the time spent interacting with puzzles (cube-root transformed) on the solving latency (s) of mosaic-tailed rats *Melomys cervinipes* in a linear mixed effects model. Individual data points (n = 34) are plotted as closed circles.

### *Personality and Problem Solving Comparisons*

PC_Exploration score (min = -323.107; max = 356.509) was a significant predictor of overall problem solving ability (3.94 ± 0.25), with more exploratory individuals solving significantly more problems than less exploratory individuals ($F_{1,34} = 8.49$, $p = 0.007$; Figure 7.5a). PC_Anxiety score (min = -199.341; max = 374.977) did not significantly affect overall solving ability ($F_{1,34} = 1.53$, $p = 0.227$). Body mass also had a significant effect on overall problem solving ability, with heavier individuals solving significantly more problem types than lighter individuals ($F_{1,34} = 4.92$, $p = 0.035$). Overall problem solving ability was not significantly affected by sex ($F_{1,34} = 0.47$, $p = 0.501$; effect size = 0.01; [-0.43; 0.45]; mean ± SE: males = 3.96 ± 0.28, females = 3.91 ± 0.55) or birth origin ($F_{1,34} = 1.65$, $p = 0.209$; effect size = 0.36; [-0.07; 0.68]; mean ± SE: captive born = 4.47 ± 0.41, wild caught = 3.53 ± 0.29).

PC_Exploration score was also a significant predictor of the latency to solve a problem ($\chi^2_1 = 23.26$, $p < 0.001$; effect size = 0.39; [-0.33; 0.82]; mean ± SE: 705.73 ± 50.93), with more exploratory individuals solving the problems faster than less exploratory individuals (Figure 7.5b). Problem type was also a significant predictor of latency to solve a problem ($\chi^2_5 = 198.95$, $p < 0.001$; effect size = -0.85; [-0.94; -0.66]), with the more complex tasks (i.e. mean ± SE: tiles = 1028.52 ± 126.45; levers = 1622.17 ± 77.01) taking significantly longer to solve than the simpler tasks (i.e. mean ± SE: pillars = 326.13 ± 87.31; cylinders = 341.97 ± 95.42). The interaction between problem type and exploration score did not have a significant impact on the latency to solve the tasks ($\chi^2_5 = 3.79$, $p = 0.580$)**.** However, individual identity ($\sigma^2 = 11.75$; residual $\sigma^2 = 85.41$) had a significant effect on the latency to solve the problems ($\chi^2_1 = 5.49$, $p = 0.019$), with some individuals being significantly faster solvers than others (Supplementary Figure 7.1).

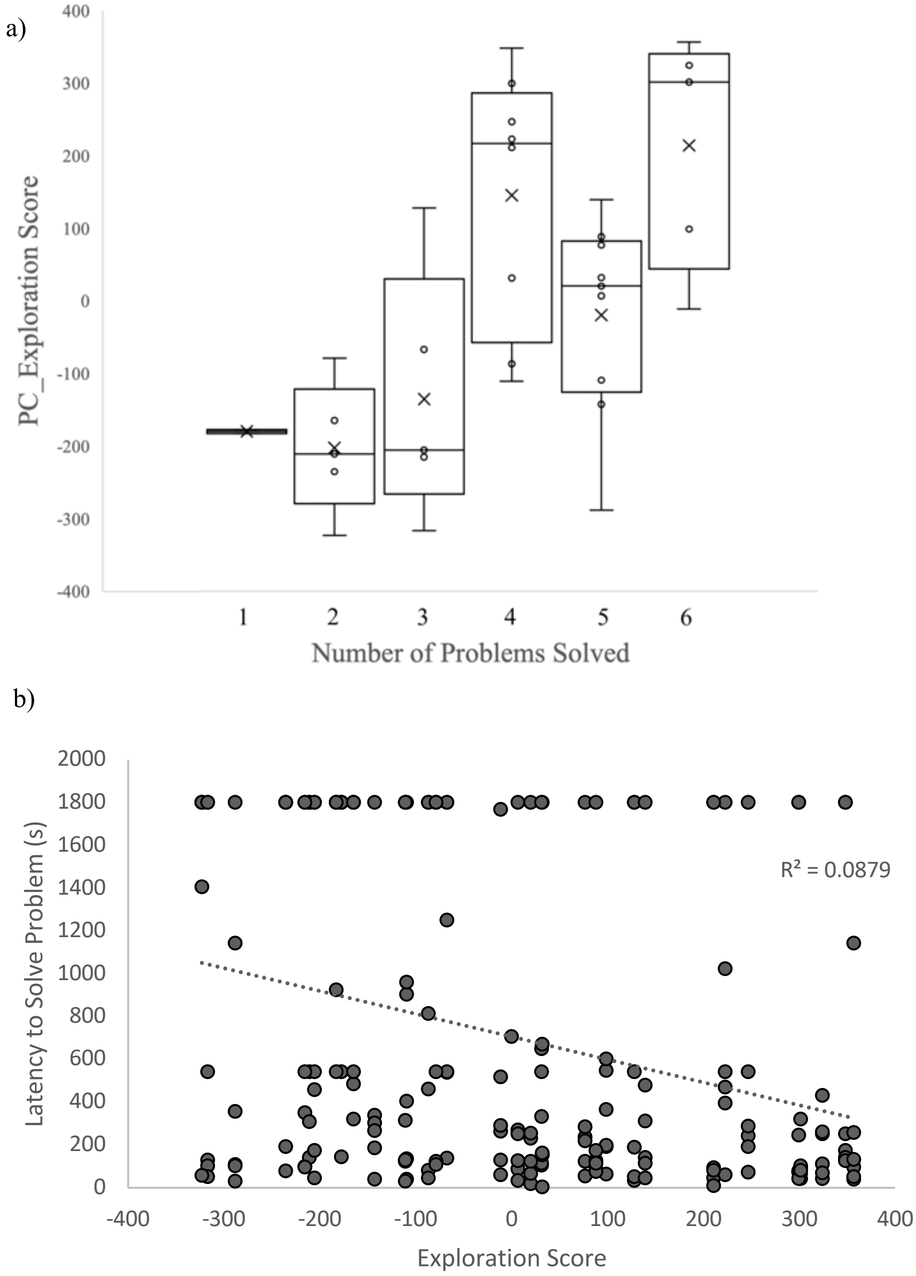


**Figure 7.5.** The relationship between (a) number of problems solved and PC_Exploration score, and b) PC_Exploration score and latency to solve problems by fawn-footed mosaic-tailed rats *Melomys cervinipes* in a linear model and linear mixed effects model, respectively. Individual data points (n = 34) are plotted as closed circles.

The interaction between PC_Exploration and problem type had a significant impact on the time spent interacting with the puzzles ($\chi^2_5 = 13.00$, $p = 0.023$), with all individuals interacting significantly more with the matchbox task, and exploratory individuals interacting significantly more with the levers than any other problem (Figure 7.6). PC_Exploration significantly affected how much time the mosaic-tailed rats spent interacting with the puzzles ($\chi^2_1 = 6.23$, $p = 0.013$; effect size = -0.92; [-0.97; -0.75]). Problem type also had a significant effect on time spent interacting with the tasks ($\chi^2_5 = 184.75$, $p < 0.001$; effect size = -0.06; [-0.63; 0.56]). Mosaic-tailed rats spent a significantly lower amount of time interacting with the cylinder (mean ± SE: 1.77 ± 0.109 s) and obstruction (mean ± SE: 1.94 ± 0.194 s) than the other tasks (Figure 7.6). Individual identity ($\sigma^2 = 0.09$; residual $\sigma^2 = 0.83$) significantly affected the time spent interacting with the problems ($\chi^2_1 = 3.86$, $p = 0.050$; (Supplementary Figure 7.3), with the two individuals that interacted the most being significantly different from the individual that interacted the least.

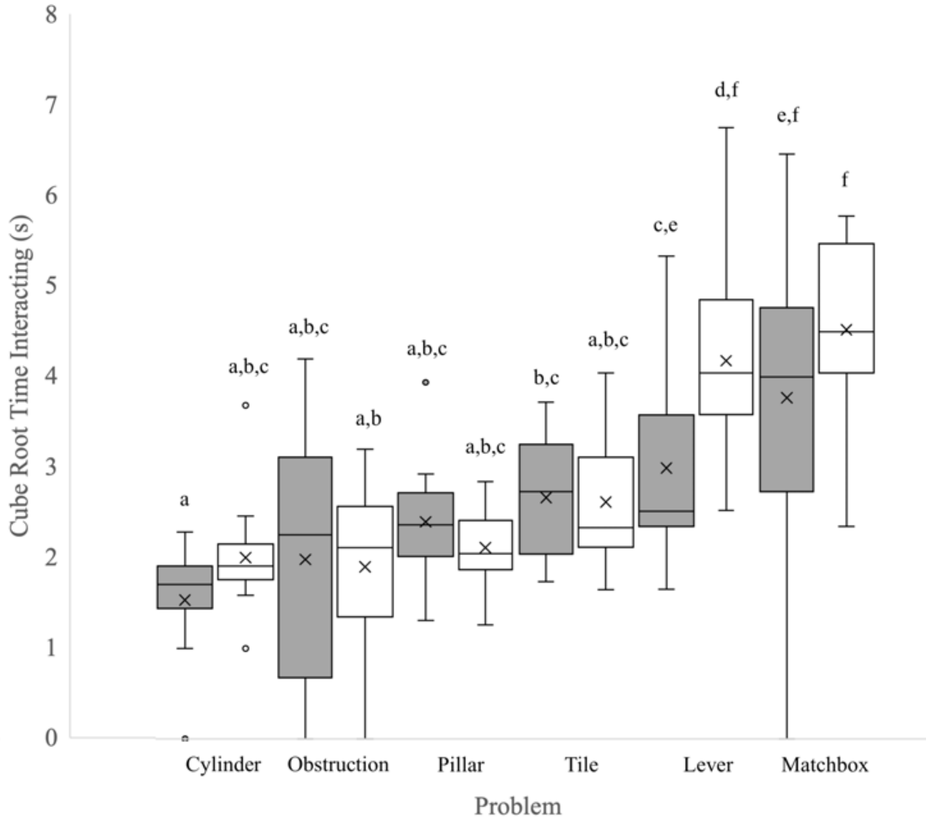


**Figure 7.6.** Mean ± SE time spent interacting (cube-root transformed) by exploratory (white bars) and avoidant (grey bars) individuals with the six problem solving tasks given to fawn-footed mosaic-tailed rats *Melomys cervinipes*. The statistical relationship was assessed using a linear mixed effects model. Bars with the same letters indicate non-significant differences (Tukey's *post hoc* tests).

There was a significant interaction between exploration score and problem type on the number of interactions made with the problem ($\chi^2_5 = 12.43$, $p = 0.029$), with exploratory mosaic-tailed rats interacting significantly more with the lever task than all other tasks (Figure 7.7). PC_Exploration score also significantly predicted the number of interactions with the problems ($\chi^2_1 = 3.93$, $p = 0.047$; effect size = 0.08; [-0.60; 0.70]). The number of interactions also differed significantly between problem types ($\chi^2_5 = 235.08$, $p < 0.001$;

effect size = -0.83; [-0.92; -0.66]), with the mosaic-tailed rats interacting significantly less with the obstruction (mean ± SE: 0.43 ± 0.04), and significantly more with the levers (1.24 ± 0.04), than the other problems. Individual identity ($\sigma^2 = 0.06$; residual $\sigma^2 = 0.57$) did not significantly affect the number of interactions with the problems ($\chi^2_1 = 3.80$, $p = 0.051$; Supplementary Figure 7.3).

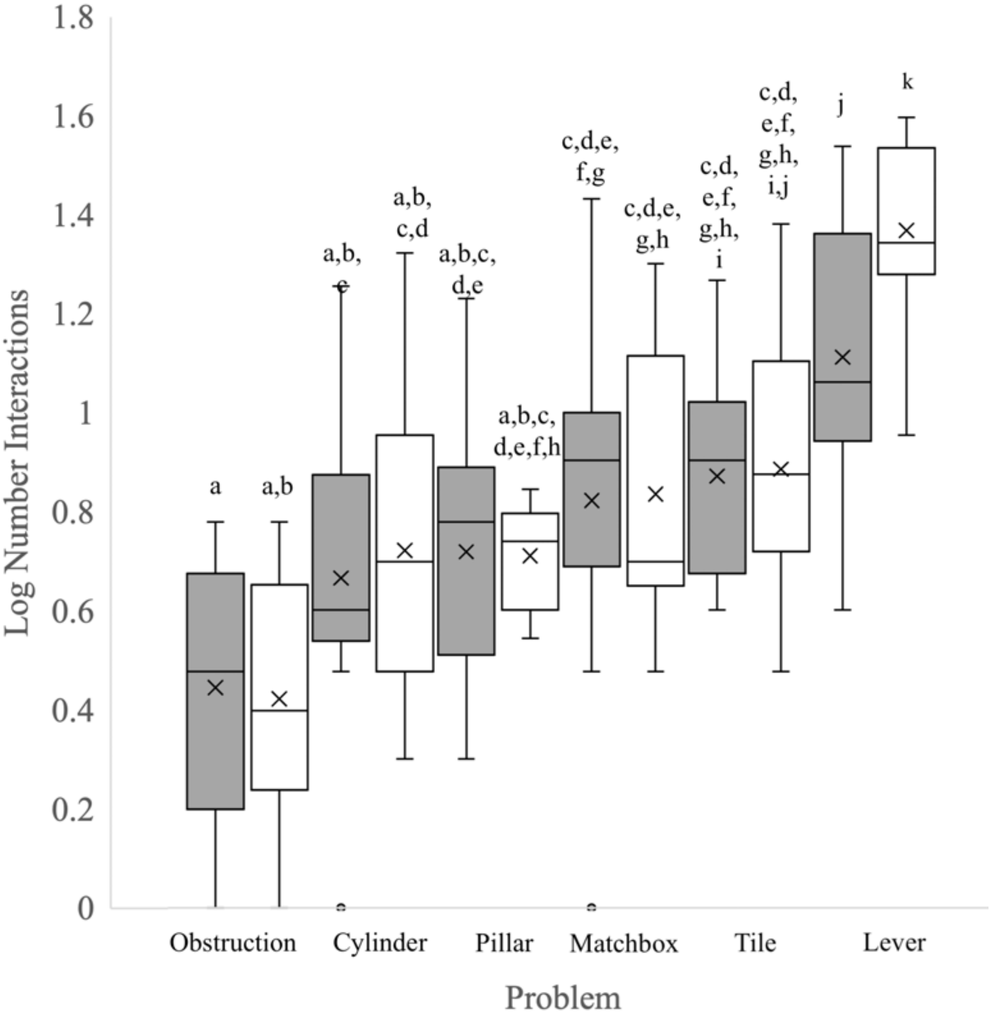


**Figure 7.7.** Mean ± SE log number of interactions by exploratory (white bars) and avoidant (grey bars) individuals with six problem solving tasks presented to fawn-footed mosaic-tailed rats *Melomys cervinipes*. The statistical relationship was assessed using a linear mixed effects model. Bars with the same letters indicate non-significant differences (Tukey's *post hoc* tests).

## Discussion

Fawn-footed mosaic-tailed rats showed consistent individual differences in behaviour, indicative of personalities (Sih et al., 2004a), with some individuals showing exploratory responses to a novel arena and stimuli (high exploration with low neophobia) and others showing avoidant responses (lower exploration and high neophobia). Interestingly, while exploration behaviours were correlated across tests, anxiety-like behaviours were not correlated with exploration behaviours. These results are consistent with those of Guenther et al. (2014) in wild guinea pigs. In a frequently changing environment, it could be energetically costly for animals to continuously gather environmental information and constantly change their behaviour in response to changing conditions (Sih et al., 2004b; Tello-Ramos et al., 2018). Consistent behavioural responses, therefore, enable individuals to avoid these costs (Sih et al., 2004b).

I also found that, despite differences in interaction measures across tasks, an individual's problem solving ability (latency to solve problems and whether the problems were solved) was consistent across tests and contexts (foraging- vs. escape-motivated). While few studies have investigated the consistency of problem solving ability, consistent individual performance has been recorded (e.g. great tits, Cole et al., 2011). However, in my study, the statistical repeatability output was low, and solving latency was largely affected by task complexity (see Rowell & Rymer, 2020b). This suggests that testing conditions (e.g. home cage vs. novel arena) and task complexity might have had a greater influence on mosaic-tailed rat solving abilities than individual characteristics, such as sex or birth origin. Most previous studies of animal problem solving have only measured problem solving ability in one test, or in one context. For example, Biondi et al. (2010) measured the problem solving abilities of Chimango caracaras using a food-baited puzzle box, while O'Connor et al. (2014) used an escape-motivated puzzle box to measure problem solving in C57/BL6J laboratory mice. As such, studies rarely consider whether problem solving is consistent across contexts (Guenther & Brust, 2017). My results suggest that, while problem solving ability is constrained to a degree (as it is repeatable across tests), it is flexible enough to allow for a changes in response to different situations. Future studies should investigate whether other intrinsic (e.g. genetic, physiological) and/or extrinsic (e.g. environment quality, maternal care) factors contribute to an individual's problem solving ability, and whether constraints on problem solving affect fitness.

Mosaic-tailed rats that solved problems more slowly also spent more time interacting with the tasks, and interacted more with the tasks, than individuals that solved the problems faster. Some studies have suggested that interacting with a problem is important for solving it, as it represents a higher level of persistence (Griffin & Guez, 2014), and allows for trial and error learning (Thornton & Samson, 2012). However, persistence can hinder problem solving if individuals repeatedly make errors that they are unable to recognise and learn from, possibly explaining why slower solvers in this study interacted more times, and spent more time interacting, with problems than faster solvers (Van Horik

& Madden, 2016). Successful problem solving may therefore rely on other forms of cognition, such as recognition or discrimination, or other behavioural traits, including exploration and neophobia.

As predicted, more exploratory rats were better problem solvers. Exploratory individuals solved significantly more tasks, and solved problems faster, than less exploratory individuals. This is consistent with Guenther & Brust (2017) who showed that more exploratory and less neophobic guinea pigs were more likely to solve problems than less exploratory and more neophobic individuals. Interestingly, anxiety did not influence problem solving performance of mosaic-tailed rats, as it did not account for significant variation in any model. This suggests that exploration is more important for problem solving performance. The importance of exploration for problem solving in mosaic-tailed rats is consistent with studies on callitrichid monkeys (Day et al., 2003) and Carib grackles *Quiscalus lugubris* (Webster & Lefebvre, 2001). Exploratory behaviours allow animals to investigate novel environments and access novel resources where it may be necessary to problem solve (Guenther & Brust, 2017). However, avoidant individuals are still present in the population, suggesting that these individuals have other strategies (e.g. being behaviourally flexible, and adjusting their behavioural response, van Horik et al., 2017) that allow them to survive and persist.

I also found that heavier mosaic-tailed rats solved problems faster, and solved more problems, than lighter individuals. Body mass affects problem solving ability in other species. For example, in many species of primates, males dominate easily accessible resources as they are larger, which likely forces smaller individuals (i.e. females or subordinates) to problem solve to find other sources of food (Reader & Laland, 2001). Heavier mosaic-tailed rats could have been better problem solvers because they were more food-motivated than lighter individuals, making them more willing to engage with tasks, as suggested for pheasant chicks *Phasianus colchicus* (van Horik et al., 2017). Alternatively, heavier individuals may be better problem solvers because they have the physical strength to manipulate the task (Papp et al., 2015). Here, all the puzzles given to the mosaic-tailed rats were of a similar size, but some required different motor skills to solve (e.g. pushing of tiles vs. pulling of the lever). This might have led to body mass, and thereby strength, affecting solving performance in some tasks. Further investigation on the problem solving performance of mosaic-tailed rats in the wild would help to show whether the body mass effects I found here are also present under natural foraging conditions.

My study represents one of the first to investigate the relationship between personality and problem-solving ability in a native Australian rodent. While mosaic-tailed rats are commonly found in disturbed areas (Goosem & Marsh, 1997), my study suggests that less exploratory mosaic-tailed rats are not as capable problem solvers as exploratory individuals. Future studies should explore the relative reproductive success and fitness of exploratory and avoidant individuals to ascertain whether avoidant individuals are compromised by a lower problem solving ability.

**Supplementary Table 7.1.** Personality axes and behaviours measured in personality tests given to fawn-footed mosaic-tailed rats *Melomys cervinipes*

| **Test** | **Personality Axis** | **Behaviours measured** |
|---|---|---|
| Open field | Exploration of a novel environment (Réale et al. 2007) | Latency to return to centre<br>Time spent in centre of arena<br>Time spent active in centre<br>Number of arena crosses |
| Novel object | Exploration of a novel object (Réale et al. 2007) | Time spent active in centre<br>Number of arena crosses<br>Number of interactions with object<br>Total time investigating with object<br>Latency to approach novel object |
| Light/dark box | Anxiety while emerging from shelter in a novel environment (Roche et al. 2015) | Latency to enter dark compartment<br>Latency to re-enter light compartment<br>Time spent in light compartment<br>Time spent active in light compartment<br>Number of crosses between light and dark compartments |

**Supplementary Table 7.2**. Alternative models that were compared for personality and problem solving analyses with AIC values shown[†]

| **Analyses Area** | **Final Model** | **Model Comparisons** |
|---|---|---|
| Personality | Model = lm(Exploration ~ Anxiety + Weight + Sex + Birth) | Model = lm(Exploration ~ Anxiety + Weight + Sex + Birth)<br>AIC(model) = 462.5618<br>model1 = lm(Exploration ~ Anxiety + Weight + Sex)<br>AIC(model1) = 465.0871<br>model2 = lm(Exploration ~ Anxiety + Weight + Birth)*<br>AIC(model2) = 461.0599<br>model3 = lm(Exploration ~ Anxiety + Sex + Birth)<br>AIC(model3) = 462.5776 |
| Personality | Model = lm(Anx2 ~ Exploration + Weight + Sex + Birth) | Model = lm(Anx2 ~ Exploration + Weight + Sex + Birth)<br>AIC(model) = 202.2438<br>model1 = lm(Anx2 ~ Exploration + Weight + Sex)<br>AIC(model1) = 200.3323 |

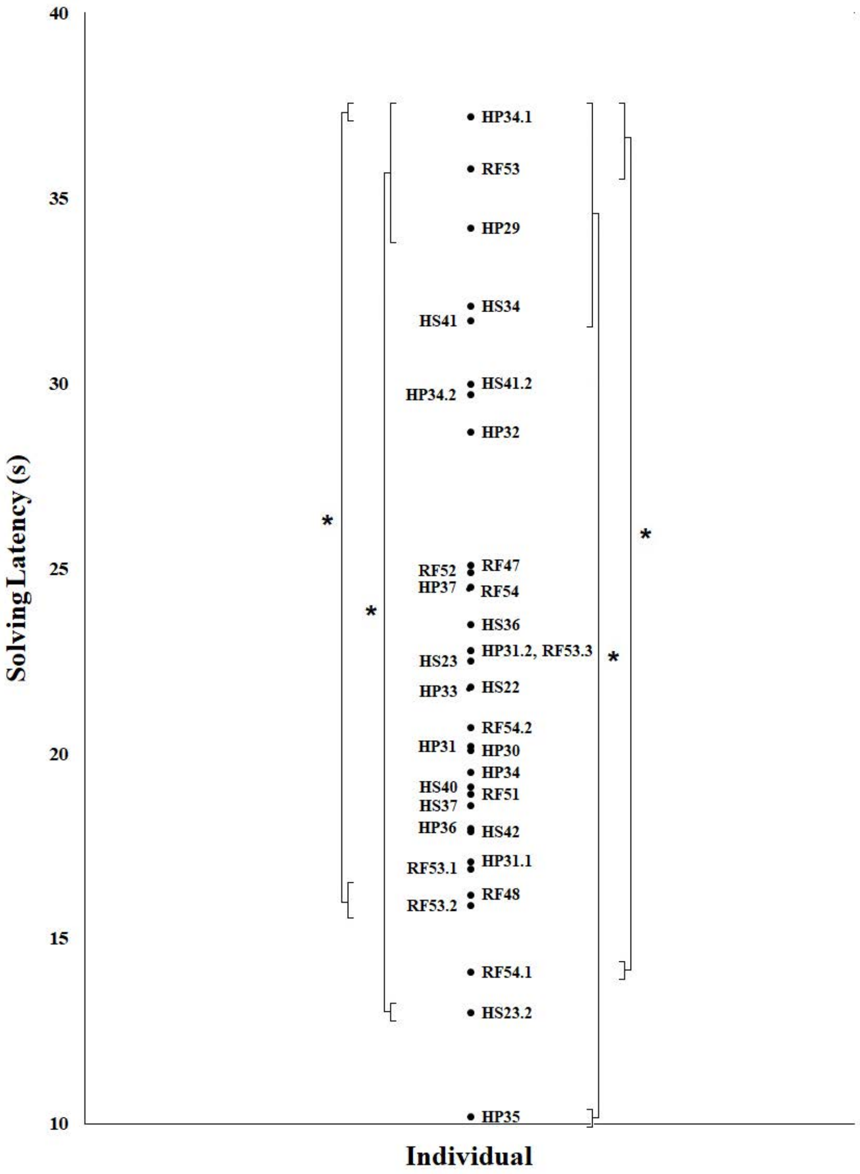
| | | |
|---|---|---|
| | | model2 = lm(Anx2 ~ Exploration + Weight + Birth)*<br>AIC(model2) = 200.2445<br>model3 = lm(Anx2 ~ Exploration + Sex + Birth)<br>AIC(model3) = 207.4444 |
| Interacting on Solving | model=lmer(Sqrt.Latency ~ (1\|ID) + Problem + Cube.Interacting + Freq2 + Birth + Sex + Weight) | Model = lmer(Sqrt.Latency ~ (1\|ID) + Problem + Cube.Interacting + Freq2 + Birth + Sex + Weight)<br>AIC(model) = 1472.112<br>model1 = lmer(Sqrt.Latency ~ (1\|ID) + Problem + Cube.Interacting + Freq2 + Birth + Sex)<br>AIC(model1) = 1491.101<br>model2 = lmer(Sqrt.Latency ~ (1\|ID) + Problem + Cube.Interacting + Freq2 + Birth + Weight)<br>AIC(model2) =1489.972<br>model3 = lmer(Sqrt.Latency ~ (1\|ID) + Problem + Cube.Interacting + Freq2 + Sex + Weight)<br>AIC(model3) = 1492.401 |
| Personality on Solving | model=lm(TotalSolved3 ~ Exploration + Anxiety + Weight + Birth + Sex) | model=lm(TotalSolved3 ~ Exploration + Anxiety + Weight + Birth + Sex)<br>AIC(model) = 115.4255<br>model1=lm(TotalSolved3 ~ Exploration + Anxiety + Weight + Birth)*<br>AIC(model1) = 113.9864<br>model1=lm(TotalSolved3 ~ Exploration + Anxiety + Weight + Sex)<br>AIC(model1) = 115.3778<br>model2=lm(TotalSolved3 ~ Exploration + Anxiety + Birth + Sex)<br>AIC(model2) = 118.929 |
| Personality on Solving | model= lmer(Sqrt.Latency ~ (1\|ID) + Problem + Exploration + Problem*Exploration) | model= lmer(Sqrt.Latency ~ (1\|ID) + Problem + Exploration + Problem*Exploration)<br>AIC(model) = 1552.026<br>model1= lmer(Sqrt.Latency ~ (1\|ID) + Problem + Exploration + Problem*Exploration + Birth + Sex + Weight )*<br>AIC(model1) = 1546.52 |
| Personality on Solving | model= lmer(Cube.Interacting ~ (1\|ID) + Problem + Exploration + Problem*Exploration) | model= lmer(Cube.Interacting ~ (1\|ID) + Problem + Exploration + Problem*Exploration) |

| | | |
|---|---|---|
| | | AIC(model) = 658.9776<br>model1= lmer(Cube.Interacting ~ (1\|ID) + Problem + Exploration + Problem*Exploration + Birth + Weight + Sex)<br>AIC(model1) = 671.6612 |
| Personality on Solving | Model = lmer(Freq2 ~ (1\|ID) + Problem +Exploration + Problem*Exploration) | model= lmer(Freq2 ~ (1\|ID) + Problem + Exploration + Problem*Exploration)<br>AIC(model) = 586.3609<br>model1= lmer(Freq2 ~ (1\|ID) + Problem + Exploration + Problem*Exploration + Birth + Weight + Sex)<br>AIC(model1) = 599.2259 |

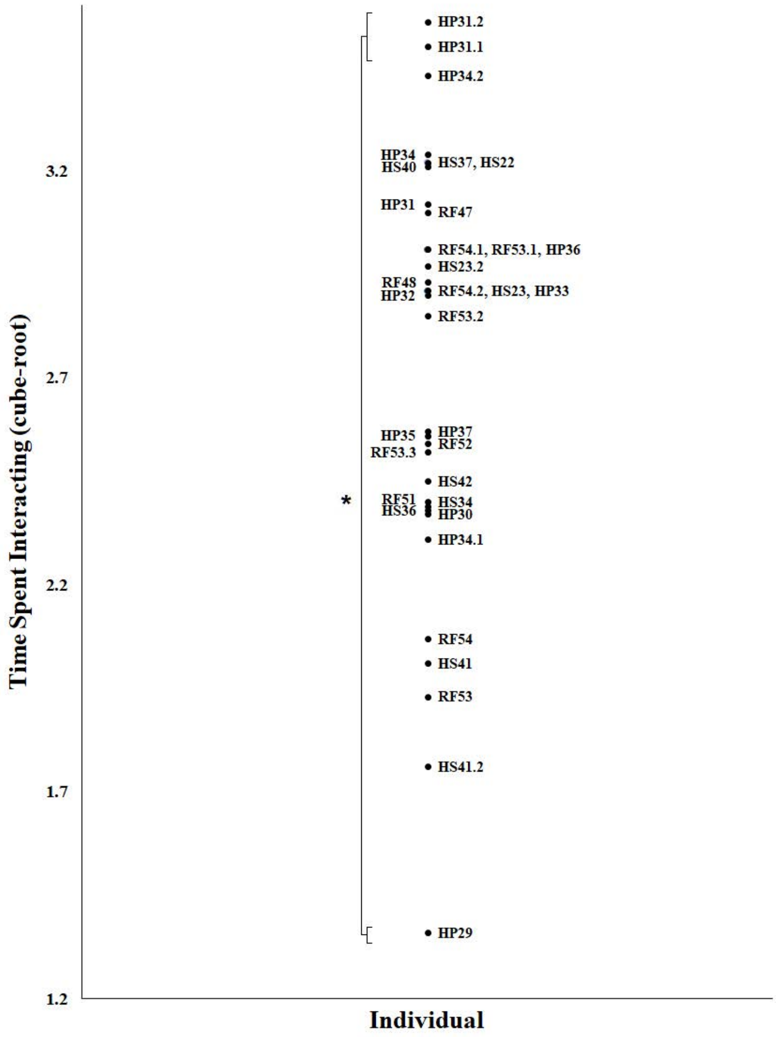
[†] In some instances, I elected to use models with higher AICs to investigate the effect of all factors on the dependent variables, or excluded factors to minimise repetition. The models with the lowest AICs that were not used have been marked in the table with an asterisk.

**Supplementary Table 7.3**. Repeatability outputs and principal component loadings of fawn-footed mosaic-tailed rat *Melomys cervinipes* behaviours measured in the personality tests (open field test, novel object test and light/dark box). Significant values are bolded.

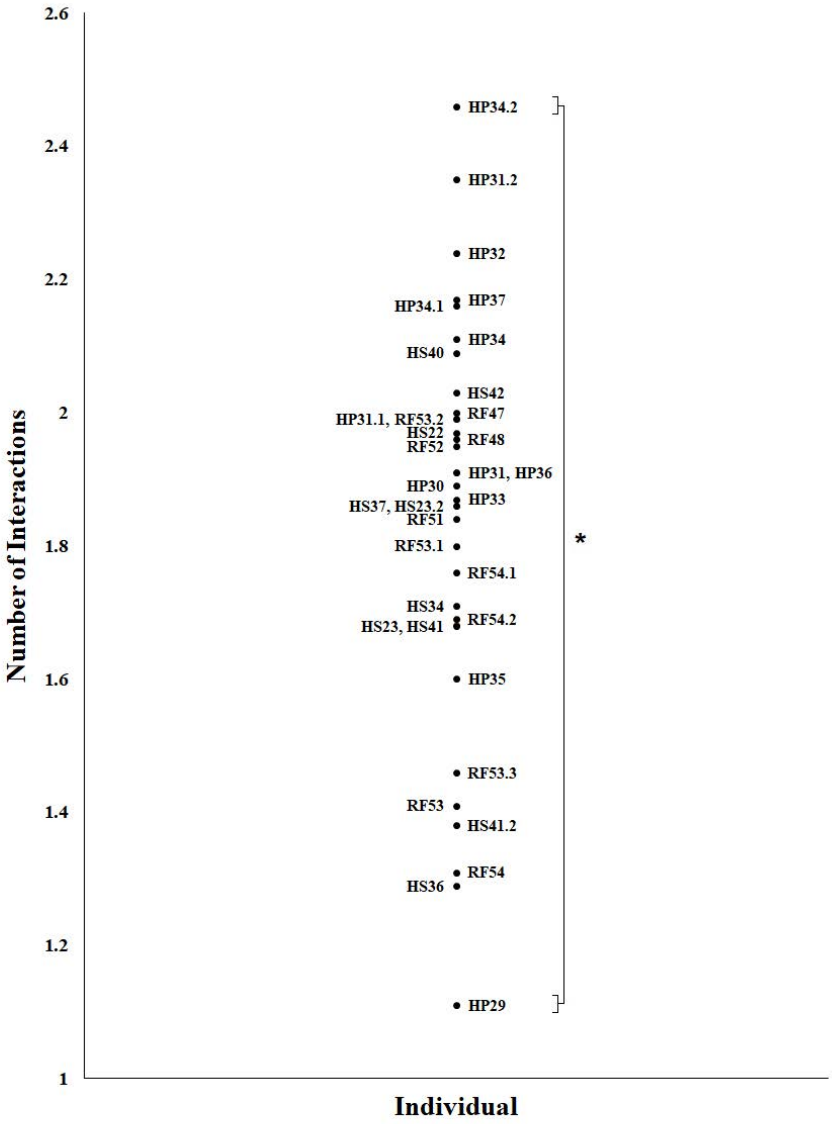
| **Test** | **Behaviour** | **Repeatability Output** | **Mean ± SE** | **Loading** |
|---|---|---|---|---|
| Open field (exploration) | Latency to return to centre | R = 0.07, p = 0.443 | 65.45 ± 13.34 | N/A |
| | Time in open field centre | **R = 0.42, p < 0.001** | 162.10 ± 16.93 | +8.1% |
| | Time active in open field centre | **R = 0.32, p = 0.003** | 82.14 ± 8.60 | +11.9% |
| | Open field crosses | **R = 0.43, p < 0.001** | 16.07 ± 1.40 | +13.8% |
| Novel object (exploration) | Novel object approach latency | **R = 0.30, p = 0.008** | 317.86 ± 30.27 | +15.3% |
| | Time interacting with novel object | **R = 0.24, p = 0.04** | 61.36 ± 10.14 | +10.8% |
| | Number of novel object interactions | **R = 0.40, p < 0.001** | 5.79 ± 0.97 | +14.2% |
| | Time active in centre of novel object arena | **R = 0.23, p = 0.036** | 96.61 ± 12.25 | +12% |
| | Novel object test arena crosses | **R = 0.48, p < 0.001** | 6.48 ± 1.08 | +13.8% |
| Light/dark box (anxiety) | Latency to enter dark compartment | R = 0.19, p = 0.072 | 15.76 ± 9.49 | N/A |
| | Latency to re-enter the light compartment | **R = 0.26, p = 0.023** | 115.04 ± 20.24 | +21.4% |
| | Total time in light compartment | **R = 0.42, p < 0.001** | 87.06 ± 13.00 | +24.9% |
| | Time active in light compartment | **R = 0.38, p < 0.001** | 68.16 ± 8.21 | +30.9% |
| | The number of crosses made in the light compartment | **R = 0.26, p = 0.019** | 5.42 ± 0.47 | +22.8% |



**Supplementary Figure 7.1**. Individual differences in the problem solving latencies of fawn-footed mosaic-tailed rats *Melomys cervinipes*. Lines denote significant differences between individuals.



**Supplementary Figure 7.2**. Individual differences in the time spent interacting with puzzles (cube-root transformed) in fawn-footed mosaic-tailed rats *Melomys cervinipes*. Lines denote significant differences between individuals.



**Supplementary Figure 7.3**. Individual differences in the number of interactions made with puzzles (log-transformed) in fawn-footed mosaic-tailed rats *Melomys cervinipes*. Lines denote significant differences between individuals.

# Chapter 8: Memory enhances problem solving in the fawn-footed mosaic-tailed rat *Melomys cervinipes*

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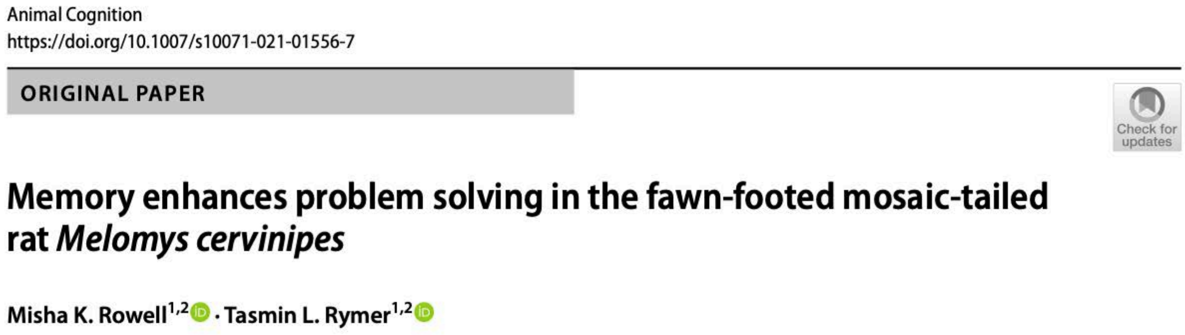

Animal Cognition
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**ORIGINAL PAPER**

## Memory enhances problem solving in the fawn-footed mosaic-tailed rat *Melomys cervinipes*

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## Abstract

Problem solving is important for survival, allowing animals to access novel food resources or escape from predators. It was originally thought to rely on an animal's intelligence; however, studies examining the relationship between individual cognitive ability and problem solving performance show mixed results, and studies are often restricted to only one cognitive and one problem solving task. I investigated the relationship between general cognitive ability and problem solving across multiple tasks in the fawn-footed mosaic-tailed rat *Melomys cervinipes*. I measured general cognitive ability across different domains (memory in an odour learning association task, recognition in a novel object recognition task, size discrimination using different sized pieces of food, and learning across multiple presentations of a food-baited activity board). I also measured problem solving across different contexts (food-baited puzzle boxes in home cage, obstruction task, and food-baited activity board in a novel arena). Mosaic-tailed rats showed a general cognitive ability, with average problem solving latency, memory ability, and learning in the tile task being correlated. As such, individuals that were able to remember an association and learned to solve the tile task solved the problems faster than individuals that could not remember or learn. My results suggest that problem solving in mosaic-tailed rats likely relies on some forms of simple cognition, particularly memory, but could also depend on other traits, such as an individual's persistence.

## Introduction

Cognition is an animal's ability to process environmental information by acquiring and storing it, and then retrieving and using it to select appropriate behaviours in response to a specific situation (Rowe & Healy, 2014; Shettleworth, 2010). Many cognitive processes (e.g. maintaining attention, goal-directed learning, consolidating memories) are predominantly controlled by two brain regions—the hippocampus and prefrontal cortex (Euston et al., 2012).. These regions, or homologous structures, are found in many taxa, including insects (Giurfa, 2013), fish (Rodriguez et al., 2005), reptiles (Day et al., 2001), birds (Shettleworth, 2003), and mammals (Gasbarri et al., 2014). It is, therefore, assumed that, due to these regions being responsible for multiple cognitive functions, different types of cognition are related (Burkart et al., 2017).

Some species have been found to have a "general cognitive ability" (often referred to as "g", Crawford et al., 2020), where an individual's abilities across different types of cognition tests are all correlated (Crawford et al., 2020). In these studies, multiple facets of cognition (Table 1) are measured across different tests and compared. For example, laboratory mice *Mus musculus* (Matzel et al., 2003), various captive primate species (chimpanzees *Pan troglodytes*, Hopkins et al., 2014; orangutans *Pongo abelii* and *P. pygmaeus*, Damerius et al., 2019; cotton-top tamarin monkeys *Saguinus oedipus*, Banerjee et al., 2009), and some wild bird species (song sparrows *Melospiza melodia*, Boogert et al., 2011; spotted bowerbirds *Ptilonorhynchus maculatus*, Isden et al., 2013; New Zealand robins *Petroica longipes*, Shaw et al., 2015) show positive correlations across different cognitive tests, indicating a general cognitive ability.

However, while cognition is driven by particular brain structures, other factors interact with neural processes to affect cognition at the individual, population and species levels. Within species, individuals vary in their cognitive abilities (Coleman et al., 2005; Cussen, 2017) due to ontogeny (Fuster, 2002), maternal effects (Liu et al., 2000), environmental effects (Salvanes et al., 2013), physiology (McLay et al., 1998), and past experience (Gelfo et al., 2018). Individuals can differ in how quickly they learn information, and in their ability to remember this information (Mazza et al., 2018). Consequently, individual differences in cognition could lead to differences in individual fitness (Rowe & Healy, 2014). For example, colonies of bumble bees *Bombus terrestris* that were fast learners in a colour discrimination task were more successful at foraging in the wild than slow-learning colonies, possibly because faster learners are able to assess and track differences in floral cues (Raine & Chittka, 2008). Similarly, individuals of multiple animal species across many taxa that were trained to avoid aversive predator stimuli before being released into the wild had a higher survival rate than untrained individuals, as the trained individuals had already learned to avoid negative stimuli (Morand-Ferron, 2017).

The significance of an individual's cognitive ability, such as its fitness benefits, is often measured by considering an individual's problem solving ability (Cauchard et al., 2013; Cole et al., 2012). Problem solving is an animal's ability to manipulate an object, or move itself around an object, to reach a goal (e.g. a food reward, Chow et al., 2017). This can be innovative, where individuals produce a new behaviour, or use an existing behaviour in a new context, to solve the problem (Reader & Laland, 2001), or based on experience (Griffin and Guez, 2014). In addition, problem solving encompasses not only cognitive ability, but also relies heavily on an individual's motivation, persistence, and behavioural flexibility (Griffin and Guez, 2014).

However, what cognitive abilities are actually required for problem solving is not well understood. To solve a problem, animals theoretically need to perceive the object to begin interacting with it (Greggor et al., 2015). Recognition may follow, allowing them to respond appropriately (e.g. start looking for food in a food-baited puzzle box) and/or to alter a tactic if they are not successful (Thornton and Samson, 2012). Finally, animals could need to learn what tactics solved the problem, and remember this information to solve the problem again in the future (Griffin and Guez, 2014). As such, food-extraction problem solving has been found to be significantly impacted by learning (e.g. feral pigeons *Columba livia*, Bouchard et al., 2007; European starlings *Sturnus vulgaris*, Boogert et al., 2008; meerkats *Suricata suricatta*, Thornton and Samson, 2012) and memory (Eastern grey squirrels *Sciurus carolinensis*, Chow et al., 2017) in some species. For example, grey squirrels learned and remembered how they solved food-extraction problems, allowing them to solve the same problem efficiently for up to 22 months (Chow et al., 2017). However, this is not always the case. For example, despite woodpecker finches *Camarhynchus pallidus* and small tree finches *C. parvulus* having similar learning abilities in a reversal learning task, their problem solving abilities were not the same, with woodpecker finches outperforming small tree finches in a foraging problem solving task (Tebbich et al., 2010). Furthermore, most studies only compare problem solving performance to one cognitive domain (normally learning) and rarely consider the relative impacts that multiple forms of cognition have on problem solving.

**Table 8.1**: Definitions and examples of methods for common types of cognition measured in general cognition ability testing paradigms

| **Cognition Type** | **Definition** | **Test Example** |
|---|---|---|
| Spatial cognition | The process of using localization, sensory imagery, and decision-making to successfully navigate through environments (Arleo and Gerstner 2000) | Learn and/or remember the location of a food reward (Hopkins et al. 2014) |
| Physical cognition | An understanding of objects and their spatial, numerical and causal relationships (Krasheninnikova et al. 2019) | Choose between larger or smaller quantities of a reward (Hopkins et al. 2014) |
| Learning | Acquire new information about a stimulus and its outcomes (Dukas 2004) | Learning the association between a colour and food reward (Benerjee et al. 2009) |
| Memory | Storing information for future use (Rowell & Rymer, 2019) | Ability to remember the location of a food reward after a delayed period (Shaw et al. 2015) |
| Recognition | Predictably respond to stimuli based on past interactions with specific, or similar, stimuli (Mendelson, 2015) | Recognise differences between familiar and novel objects (Bevins & Besheer, 2006) |
| Discrimination | Identify that one stimulus is different to another (Rowell & Rymer, 2019) | Identify one odour as different to another (Matzel et al., 2011) |
| Social cognition | An understanding of intentional actions, perceptions, and knowledge states of others (Krasheninnikova et al., 2019) | Indicating knowledge of the intention of a communicated signal (Hopkins et al., 2014) |
| Tool use | The external use of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool (Shumaker et al., 2011) | Fishing honey out of a tube with a tool (Damerius et al., 2019) |
| Inhibitory control | The ability to inhibit a prepotent response (Shaw et al., 2015) | Moving around a detour to access a reward (Shaw et al., 2015) |

Because the presence of a general cognitive ability in wild species is poorly studied, and it is unclear, in general, which cognitive abilities are involved in problem solving (Shaw et al., 2015), I first investigated whether individual fawn-footed mosaic-tailed rats *Melomys cervinipes* had a general cognitive ability. Thereafter, I explored what specific cognitive abilities influenced their problem solving ability. The fawn-footed mosaic-tailed rat is a medium-sized (72.9 ± 12 g, Callaway et al. 2018) native Australian rodent commonly found in forests along Australia's eastern coast (Moore et al., 2008). These forests are structurally complex environments (Goosem and Marsh, 1997), experiencing both temporal and spatial variation in resource availability, which could promote greater problem solving than more homogenous landscapes (Preiszner et al., 2017).

Individual mosaic-tailed rats vary in their food-extraction and escape-motivated problem solving abilities (Chapter 3; Rowell & Rymer, 2020b) and other aspects of cognition (e.g. spatial cognition, Rowell, 2016; recognition, Paulling et al., 2019), possibly due to individual differences in the underlying mechanisms of these processes (e.g. hippocampus or prefrontal cortex structures). Therefore, I hypothesised that individuals would have a general cognitive ability (Matzel et al., 2003) and that cognition would impact problem solving, as individuals with increased general cognitive abilities could use their cognitive skills (e.g. learning, Guenther & Brust, 2017; tool use, Lefebvre et al., 2004) to solve problems. I expected that both learning and memory would be important for solving problems (Griffin and Guez, 2014).

## Methods

### *Ethical Note*

This research was conducted in accordance with the ABS/ASAB guidelines for the ethical care and treatment of animals (Bee et al., 2020) and 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). Animals received behavioural enrichment, were visually inspected daily, and were weighed every two weeks to further monitor health. No incidents of death or injury occurred during the study. Mosaic-tailed rats were maintained in the colony after testing was completed.

## *Husbandry*

Subjects used in this study were 19 wild-caught (14 male and 5 female) and 15 F1 captive-born (9 male and 6 female) individuals from a colony maintained at James Cook University, Cairns, Australia (16° 49′ S, 145° 41′ E). Wild individuals were trapped on or around the James Cook University Nguma-bada campus using Elliott traps baited with balls of rolled oats, peanut butter and honey (permit numbers: WISP14530814 and WITK14530914). Traps were set in the evening and checked the following morning before 7 am. Once in captivity, animals were kept under partially controlled environmental conditions (12:12 h light cycle; 22–26 °C; 50–65% relative humidity). Mosaic-tailed rats showed differences in personality (exploration and anxiety behaviours, Chapter 7; Rowell & Rymer, 2021a). Therefore, this trapping methodology did not likely lead to a bias in the captive population.

Mosaic-tailed rats were kept individually in wire frame cages (34.5 × 28 × 38 cm) with deep plastic bases (34.5 × 28 × 11 cm) containing ± 10 cm of wood shavings. They were provided with nesting material consisting of a cylindrical plastic nest box (11 × 11 × 20 cm), a handful of pasture hay and two pieces of paper towel. As mosaic-tailed rats are semi-arboreal (Rader and Krockenberger, 2006), climbing equipment (a wire platform near the top of the cage and sticks) was provided for behavioural enrichment. A cardboard paper roll was also provided. Individuals were given approximately 5 g of mixed seed and rodent chow (Vetafarm Origins), and 5 g of vegetable/fruit (e.g. sweet potato, apple) each morning, unless they were being tested in a food-related task (see below), in which case the animal was only fed after testing in the evening to encourage participation. Water was available ad libitum. All individuals were tested for cognition and problem solving ability as adults (i.e. sexually mature; 1–2 years of age at first test) after at least 10 months of living in captivity. I was unable to definitively state the ages of wild individuals, but sexual maturity generally occurs around 5–7 months of age (Yom-Tov, 1985; pers. obs.). Individuals had also all been used previously in other behavioural tests occurring in open field arenas (e.g. Chapter 7; Rowell and Rymer, 2021a), with no ill effects observed.

## *General Testing Procedures*

This study was conducted from August 2018 to January 2019. For all tests, mosaic-tailed rats were tested individually. If testing occurred outside of the home cage, the test was presented in the same open field and mosaic-tailed rats were then returned to their home cages after each test was completed. Tests were allocated in a random order (apart from the Trixie dog activity board, see below), and occurred between 18h00 and 22h00, as the rats are crepuscular/nocturnal (Wood, 1971). Tests were performed under a red light (except for the obstruction test, see below), which does not influence mosaic-tailed rat behaviour (Paulling et al., 2019; Chapter 3; Rowell & Rymer, 2020b), and were filmed using a Sony HDR-CX405 Camcorder. The video analysis software BORIS (http://www.boris.unito.it) was used to collect behavioural data (Friard & Gamba, 2016).

## ***Problem Solving Tests***

We assessed the innovative problem solving ability of mosaic-tailed rats in five food-baited puzzles and one escape-motivated puzzle (Figure 1). This study builds on previous work investigating individual variation in innovation in mosaic-tailed rats (Chapter 3; Rowell & Rymer, 2020b), and explicitly explores the relationship between cognitive abilities and problem solving in these same individuals. The methods are fully described in Chapter 3 (Rowell and Rymer, 2020b). For all problems, I measured the latency to solve the task from the first instance of the animal physically interacting with the task. Individuals were considered to have solved the task once they obtained the reward (i.e. food reward or safety). Individuals that did not solve the task were given the maximum latency for the test. As an individual's problem solving latency was repeatable across tasks (Chapter 7; Rowell & Rymer, 2021a), I averaged the solving latency across the tasks.

### *Simple Puzzles in the Home Cage*

Food-baited puzzles included a plastic cylinder puzzle (Figure 1a) and cardboard matchbox (Figure 1b) that were placed in an individual's home cages for 30 min each, one on each consecutive night. These tasks could be solved by animals pulling or pushing the matchbox out of the sleeve, or chewing through it, and by pushing through or pulling off a piece of tinfoil covering the plastic cylinder's opening.

### *Trixie Dog Activity Board (Level 2)*

More complex problem solving was tested using a Trixie Dog Activity Board (Level 2) (Figure 1d). This board contained three types of puzzles (two of each type) of varying complexity—two pillars to knock over (easy), two tiles to slide (medium), and two levers to pull down to lift up flaps (difficult). Individuals were tested with this board in an open field arena. On the first night, individuals were first habituated to the board for 30 min, where two sunflower seeds were placed in or near each open puzzle. Puzzles could not be solved on this night as they were open. Solving ability was then measured on the following night, where two sunflower seeds were placed in each puzzle, and all puzzles were closed. This first night provides a measure of innovative problem solving.

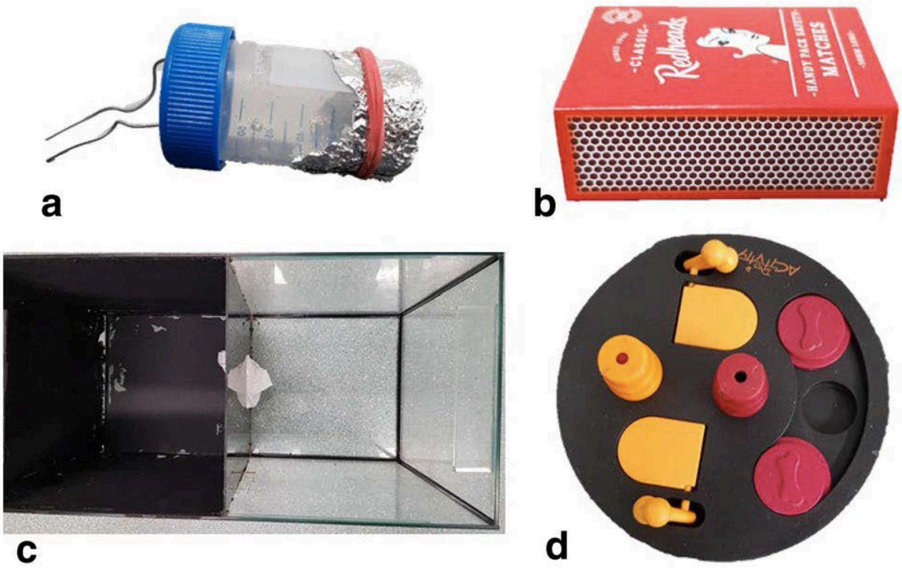

**Figure 8. 1** Problem solving tests given to mosaic-tailed rats *Melomys cervinipes*. a cylinder test: a plastic tube (2 x 4 x 2 cm) with food reward inside, tinfoil on one end and the other secured closed, with small holes poked in the plastic (placed directly in home cage); b matchbox test: Redheads brand (4 x 5 x 1 cm) with food reward inside the cardboard sleeve (placed directly in home cage); c obstruction test: light/dark box: glass tank (61 x 38 x 30 cm) divided in half with a plastic barrier, with one side painted black (dark compartment), the other side left clear (light compartment), a small door (10 x 10 cm) cut in the centre, and a piece of crumpled paper placed in the doorway; d commercial Trixie dog activity board (Level 2), containing three problems (two pillars, two tiles and two levers) of two colours (yellow and red). From Chapter 3 (Rowell and Rymer, 2020b)

### *Obstruction Task*

The escape-motivated puzzle (Figure 1c) was an obstruction task, where an individual was placed in a light–dark box comprised of a glass tank divided in half by a partition with a doorway, with one compartment blacked out and one left clear. An LED lamp illuminated the light compartment. The animal was allowed to habituate to the testing apparatus and move between the light and dark compartments freely for 2 min. Following this, the animal was gently pushed back into the light compartment (if not there already) and the doorway was blocked with a crumpled piece of paper. The animal was then given 3 min to push or pull the paper out of the doorway and escape to the dark compartment. This process was repeated two more times (three trials in total) during the testing session to increase the likelihood of participation, as mosaic-tailed rats are known to sometimes freeze under bright light conditions (Delarue et al., 2020).

## ***Cognition Tests***

I assessed general cognitive ability across multiple contexts to test whether it was consistent (i.e. to ascertain whether a 'smart' individual is always 'smart', Guenther and Brust, 2017).

### *Associative Memory Test*

I measured the ability of mosaic-tailed rats to remember an association between an odour and a food reward over four days (following Tronel & Sara, 2002). Two nights of pre-training occurred first. On Night 1, an individual was placed in an open field arena for 20 min with access to a food reward (chocolate-flavoured breakfast cereal) scattered throughout the arena. This allowed for habituation to the arena and the food. Three individuals did not eat the chocolate cereal during pre-training nights, so sunflower seeds were used instead. On Night 2, the individual was again placed in the arena for 20 min. Ten minutes occurred as previously with the food reward. The remaining 10 min occurred with three pieces of sponge (approximately 6 cm long x 3.5 cm wide x 1 cm high) placed in separate corners of the arena, away from the food. This allowed for habituation to the sponges. All individuals had eaten the food by this stage.

Individuals were given the opportunity to form an association on Night 3 over five 5-min trials (up to 25 min of testing). Three pieces of sponge, each scented with a different odour (vanilla, lemon, or peppermint), were placed in different corners of the arena (one in each corner), with location chosen at random. No scent was in the same location for more than two trials to ensure that location was not the cue being learnt. Sponges were scented by pipetting 20 μL of the essence on each corner of the sponges. One of the three scents was chosen at random to be the association scent for the individual. Four chocolate cereal pieces/sunflower seeds were placed in a small hole (approximately 1 x 1 x 1 cm) cut in the corresponding sponge. For the first trial only, a piece of chocolate cereal/seed was also placed on each corner of the sponge. The individual was then placed in the arena and left to locate the food. The location of the sponges was randomised over each trial to prevent individuals from associating the food with a specific location. Each trial ended when the food had been located and consumed, or when 5 min had elapsed. The animal was then confined for 30 s in a plastic cup outside of the arena, while the sponges were relocated to new areas in the arena and the target sponge rebaited. The remaining trials occurred in a similar manner. If an animal did not try to locate the food within the trial time, it was considered to have not participated, but was continued on to the next trial. If an animal did not participate in 3 of the 5 trials, it was excluded from the study (n = 4).

On Night 4, the individual was tested once with the scented sponges as for Night 3 to assess memory retention. However, in this test, the sponge was not baited with food. During this test, I measured the number of errors made (poke attempts to incorrect sponges), with fewer errors being made indicating the ability to remember the association. I also recorded the latency to find the sponge the individual was trained to as a measure of memory ability, with shorter latencies being indicative of better memory performance. While mosaic-tailed rats were learning this association on Night 3, I did not measure their learning ability in this test, as the repeated trials may have caused stress and elevated stress hormone concentrations, which are known to interfere with learning (Joëls et al., 2006). I, therefore, only focussed on memory performance on Night 4.

### *Recognition Memory Test*

I also assessed cognition using the novel object recognition task following Bevins and Besheer (2006), which relies on visual recognition and discrimination. Mosaic-tailed rats were initially put through a familiarisation round in an open field arena (same arena as previous tests). Here, two identical novel objects (either 1 x 2 x 4 cm toy cars, or 5 x 3 x 4 cm plaster birds) were placed near both corners of one side of the open field arena. An individual rat was then placed on the opposite side of the arena, facing away from the objects, and left to explore for 10 min. The animal was then returned to its home cage and rested for 1 h during which time the arena and objects were cleaned and wiped down with a 70% ethanol solution.

I then placed one of the previous objects from the familiarisation round and a new novel object (either a toy car or bird ornament—whichever had not been used previously) in each corner of one side of the open arena. The individual was again placed on the opposite side of the arena, facing away from the objects, and was then observed for 2 min, as habituation was likely to occur if a longer testing time was used (Bevins and Besheer, 2006). The objects were randomised, so that half of the animals had the bird ornaments in the familiar round, and the other half had toy cars as familiar objects. In the novel testing round, I measured the difference in the time individuals spent investigating the novel and familiar objects, with more time interacting with the novel object signifying that the individual recognised it as being novel (Bevins and Besheer, 2006).

### *Learning in Food-Extraction Test*

I also measured learning performance over repeated presentations of the Trixie Dog Activity Board (Level 2). Individuals were tested over five consecutive nights, with the first night being indicative of innovative problem solving (see above), and the following nights reflective of learning performance. Testing conditions were the same as described for the first night. I measured the latency to solve each task type (pillar, tile, lever) each night and recorded the difference between Night 5 and Night 1 as a measure of learning ability. Successful learning was established if the individual improved in the number of puzzle tasks solved from Night 1 to Night 5, as well as the latency to solve them.

### *Discrimination Test*

I measured visual size discrimination for each individual over five trials on a single night in their home cage. Two pieces of sweet potato (a favoured food of the mosaic-tailed rats) of the same weight (4 g) were cut into different sized pieces: one large (4 x 4 x 0.1 cm) and one small (2 x 2 x 2 cm). Both pieces were presented to each individual simultaneously, with the largest side of the food being shown to the animals. Individuals were used to being hand fed, and approached the front of the cage readily. Both pieces of sweet potato were held directly in front of the animal (outside the cage to prevent the individual accessing the food directly) for 5 s. The position of the pieces was then swapped to the opposite side, and each piece then moved to the sides of the cage to prevent the animals forming a side bias. The individual had 1 min to make a decision (i.e. move towards the piece it wanted at the side of the cage). I then returned both pieces to the front of the cage and repeated the trial, randomising the side that the large piece went to. I recorded which piece the individual first chose for each trial (i.e. which piece the individual moved towards). I did not measure the time spent investigating the sweet potato pieces as the round ended as soon as the animal made its choice. Size discrimination was considered to have occurred if mosaic-tailed rats chose either the bigger or smaller piece at least 80% of the time (i.e. at least 4 out of 5 trials).

## *Statistics*

Statistical analyses were conducted using RStudio (version 1.0.153; https://www.rproject.org; R version 3.5.0, https://cranrstudio.com). The model-level significance was set at $\alpha \leq 0.05$. All variables were assessed for normality using a Shapiro–Wilk test. Four individuals (males = 2, females = 2; wild caught = 1, captive born = 3) did not participate in the memory task and so were removed from all statistical analyses to keep the number of data points consistent between variables. Animal birth origin (captive born or wild caught) and sex were included as categorical fixed factors, and animal mass was included as a continuous predictor.

### *Cognitive Ability*

Within each cognition test (memory, recognition, learning, and discrimination), I recorded if the individual successfully completed the task (no = 0, yes = 1). An individual was considered to have completed the task if they performed positively in the test (i.e. remembered the scent association, recognised the novel object, improved at problem solving in the pillar/tile/lever, and discriminated between sizes). I used this binary success value here due to the difficulty of the raw data (e.g. containing negative variables or being zero-inflated), and the inability to transform it. I used a general linear mixed effect model (GLMER) with a binomial distribution and logit link function (lmerTest packages, Kuznetsova et al., 2015) to assess the impact of cognitive task type, birth origin, mass, and sex (fixed factors) on the ability of mosaic-tailed rats to successfully complete the tasks. I originally included individual identity as a random factor in this model. However, the model returned a singular fit, indicating that the variance of the random factor was close to 0. Model fit was not improved by including the random factor, so I elected to exclude individual identity from this model.

To investigate whether mosaic-tailed rats had a general cognitive ability, I loaded cognitive test measures (difference in pillar task latency, difference in lever task latency, difference in tile task latency, memory test latency, difference in time spent investigating novel and habituated objects in recognition test, and number of times big food piece was chosen in discrimination test) and the average problem solving latency into a principal component analysis (PCA, corrplot package, Wei et al., 2017). I selected principal components (PC) with eigenvalues above 1 (Budaev, 2010) that explained at least 70% of the variance (alone or in combination, Shaw et al., 2015).

*Comparing Cognition Scores and Problem Solving*

I ran a general linear model to investigate which cognition type had the largest impact on solving ability. The average latency to solve the tasks (square root transformed) was the dependent variable, and the cognitive ability (difference in pillar task latency, difference in lever task latency, difference in tile task latency, memory test latency, difference in time spent investigating novel and habituated objects in recognition test, and number of times big food piece was chosen in discrimination test) were the continuous predictors. Mass, sex, and birth origin were also included in the model as fixed factors.

## Results

### Cognitive Performance

Of the 30 mosaic-tailed rats, 21 (70%) remembered the olfactory association, 21 (70%) recognised the novel object, 21 (70%) learned how to solve problems in the Trixie dog activity board task, and 10 (33%) discriminated between food of different sizes. Cognitive test type had a significant effect on whether the test could be completed, with significantly fewer individuals discriminating between food sizes (($\chi^2_3 = 11.86$, $p = 0.008$; mean ± SE: discrimination test = 0.33 ± 0.088; learning in food-extraction test = 0.70 ± 0.086; associative memory Test = 0.70 ± 0.086; recognition memory test = 0.70 ± 0.08; Figure 8.2). Birth origin ($\chi^2_1 = 1.59$, $p = 0.207$), body mass ($\chi^2_1 = 1.64$, $p = 0.200$) and sex ($\chi^2_1 = 1.91$, $p = 0.167$) did not significantly affect whether mosaic-tailed rats were successful in solving the cognitive tasks.

### General Cognitive Ability

For the PCA of general cognitive ability, three principal components were extracted with eigenvalues above 1 (Table 8.2). PC1 comprised the average problem solving latency, Associative Memory test latency, and learning the tile task in the Food-Extraction task, and explained 39.45% of the total variance (Table 8.2). PC2 comprised the Associative Memory test latency, and learning the pillar and lever tasks in the Food-Extraction task, which explained 27.12% of the variance (Table 8.2). Finally, PC3 comprised the Discrimination test performance and Recognition Memory ability, and explained a further 17.75% of the variance (Table 8.2). Collectively, these three PCs explained 84.32% of the variance. Variable loadings are shown in Supplementary Table 8.1.

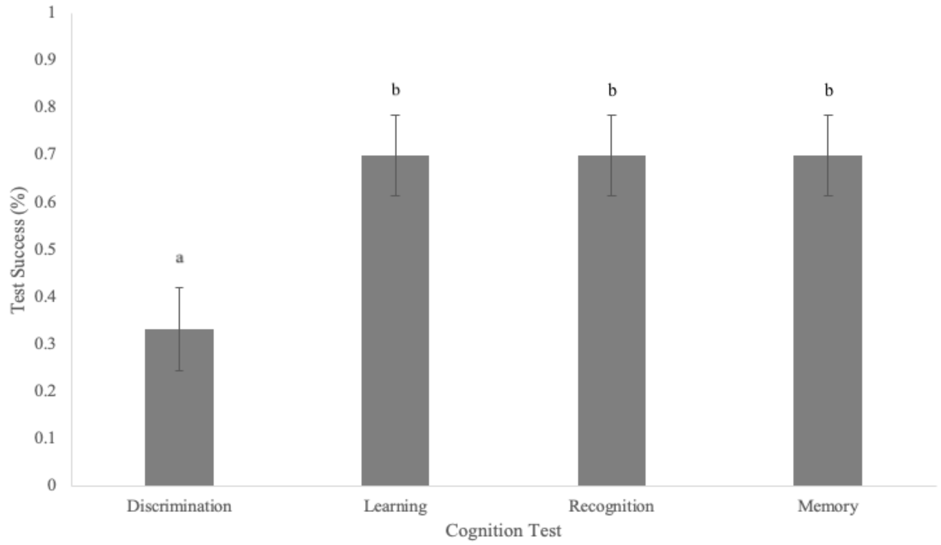

**Figure 8.2**. Mean (± SE) test success of different cognitive tests given to fawn-footed mosaic-tailed rats *Melomys cervinipes*. Bars with the same letters indicate non-significant differences (Tukey's *post hoc* tests).

**Table 8.2.** Results of the principal component analysis for the mosaic-tailed rats that completed all tasks (n = 30). The variables that contributed the most to the PC are in bold.

| Task Measure | PC1 | PC2 | PC3 |
|---|---|---|---|
| Average problem solving latency | **28.60** | 5.68 | 0.02 |
| Associative Memory test latency | **17.84** | **21.56** | 0.04 |
| Learning Pillar task | 9.49 | **18.49** | 5.31 |
| Learning Tile task | **16.46** | 9.32 | 1.07 |
| Learning lever task | 11.50 | **33.09** | 0.01 |
| Discrimination test | 4.36 | 7.23 | **59.00** |
| Recognition Memory test | 11.76 | 4.64 | **34.55** |
| Eigenvalue | 2.76 | 1.90 | 1.24 |
| % Variance explained | 39.45 | 27.12 | 17.75 |

## *Problem Solving Ability*

All mosaic-tailed rats were capable of innovative problem solving in at least one task (Chapter 3; Rowell and Rymer 2020b). Five individuals (16.7%) solved all six tasks, nine individuals (30%) solved five tasks, eight individuals (26.7%) solved four tasks, four individuals (13.3%) solved three tasks, three individuals (10%) solved two tasks, and one individual (0.3%) solved only one task. The lever task had the lowest success rate of any task, with only 5 individuals (16.7%) being able to solve it.

### *Comparing Cognition and Problem Solving Abilities*

Performance in the Associative Memory Test (latency to trained sponge) was a significant predictor of average problem solving latency ($F_{1, 30} = 7.41, p = 0.013$), with mosaic-tailed rats with shorter latencies in the Associative Memory Test being significantly faster at solving the problem tasks (Figure 8.3). Learning the tile food-extraction task (difference in solving latency from Night 5 to Night 1) was also a significant predictor of average solving latency ($F_{1, 30} = 6.52, p = 0.019$), with slower solvers being better learners (improving their performance the most) over the repeated sessions (Figure 8.4). Birth origin was also a significant predictor of average problem solving latency ($F_{1, 30} = 22.33, p < 0.001$; mean ± SE: captive born = 689.08 ± 108.84, wild caught = 517.12 ± 65.60), with captive-born individuals solving problems 1.3 times slower than wild-caught animals (Figure 8.5). Performance in the pillar food-extraction task (difference in solving latency from Night 5 to Night 1; $F_{1, 30} = 0.09, p = 0.758$), lever food-extraction task (difference in solving latency from Night 5 to Night 1; $F_{1, 30} = 0.80, p = 0.381$), Recognition Memory test (difference between time interacting with novel and familiar objects; $F_{1, 30} = 0.02, p = 0.902$), and Discrimination test (number of times large piece chosen; $F_{1, 30} = 1.12, p = 0.303$) were not significant predictors of average solving latency. Individual sex ($F_{1, 30} = 1.21, p = 0.285$) or weight ($F_{1, 30} = 2.79, p = 0.110$) did not significantly influence average problem solving latency.

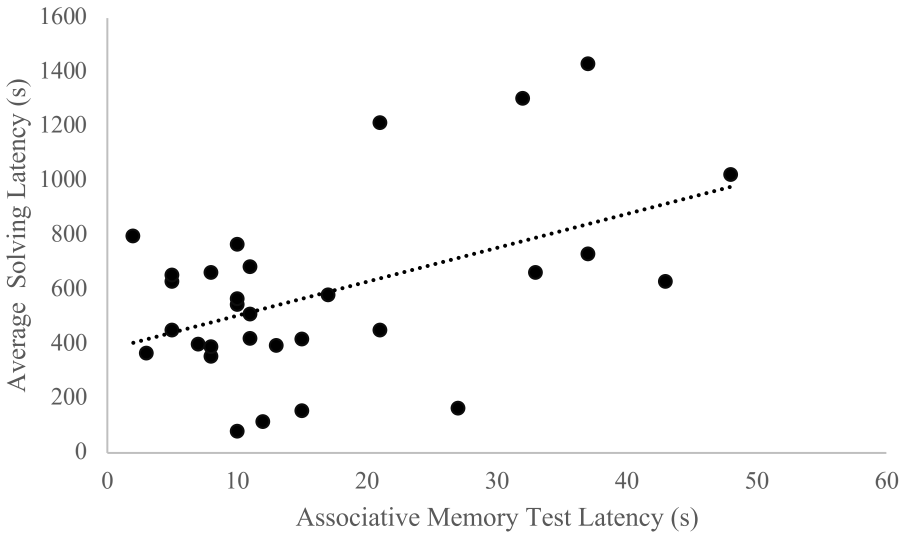

**Figure 8.3.** The relationship between latency (s) in the Associative Memory Test and average problem solving latency (s) in fawn-footed mosaic-tailed rats *Melomys cervinipes*

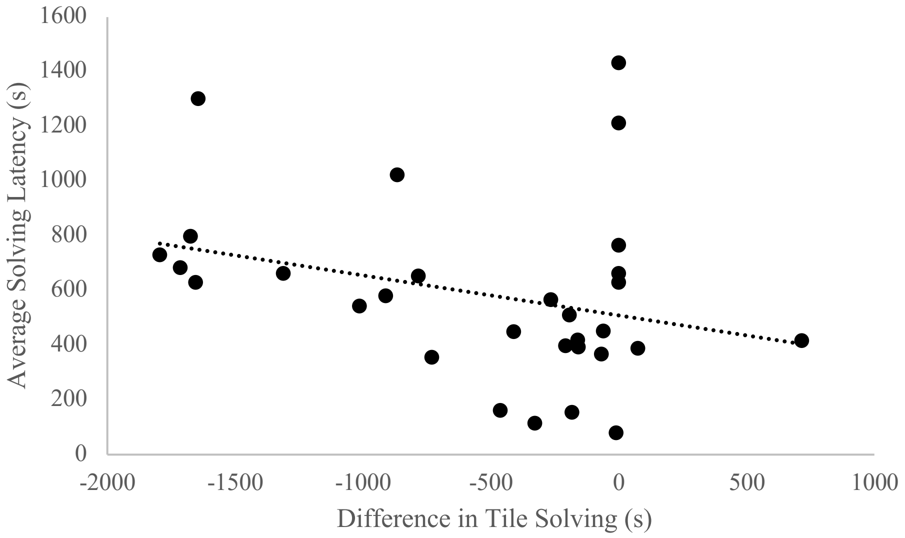

**Figure 8.4.** The relationship between the difference in solving performance (s) in the tile task from Night 1 to Night 5 and average solving latency (s) in fawn-footed mosaic-tailed rats *Melomys cervinipes*

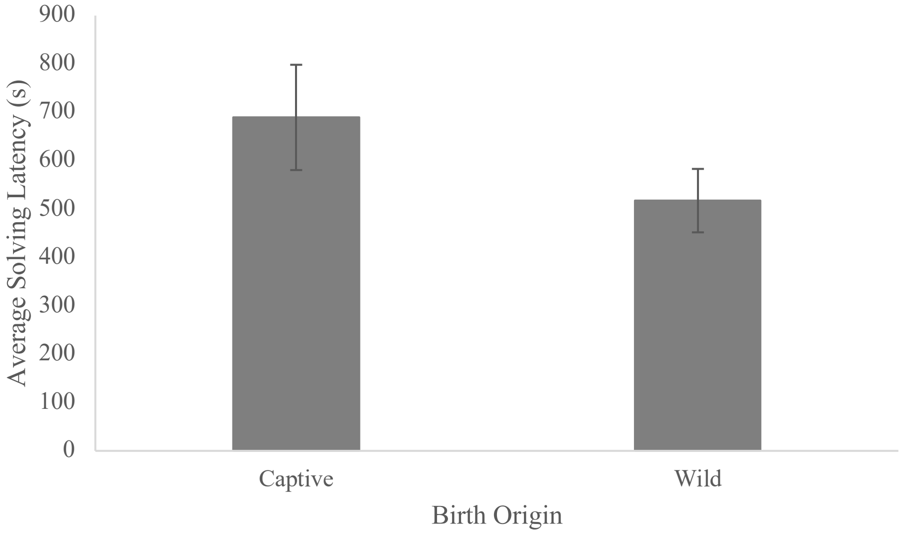

**Figure 8.5.** Mean (± SE) latency (s) to solve problems by captive-born and wild-caught fawn-footed mosaic-tailed rats *Melomys cervinipes*

## Discussion

The cognitive abilities of wild animals, and the relationship between cognition and problem solving ability, are a growing area of interest. However, it is not clear what cognitive abilities are important for successful problem solving. Here, I measured multiple aspects of cognition in mosaic-tailed rats, to generate a general cognitive ability score, and to relate cognitive abilities to problem solving ability.

As expected, mosaic-tailed rats showed a general cognitive ability, intelligence, or "g", as some of the cognitive measures (problem solving, learning, memory, discrimination, and recognition) were correlated with each other. This is consistent with other studies in laboratory mice (Matzel et al., 2003) and some other wild animal species (spotted bowerbirds, Isden et al., 2013; chimpanzees, Hopkins et al., 2014). These cognitive abilities may, therefore, be controlled by the same regions of the brain (Burkart et al., 2017), or may be related to underlying behavioural processes, such as exploration or stress reactivity (Matzel et al., 2011). In a previous study, I found that mosaic-tailed rats that were more exploratory solved the problems faster (Chapter 7; Rowell & Rymer, 2021a), providing some support for a close relationship between personality, cognition and problem solving.

Mosaic-tailed rats were capable of completing several cognitive tasks, demonstrating an ability to recognise objects, remember associations, and learn how to solve problems.

These cognitive abilities have been observed in other species, including guinea pigs (learning, Guenther and Brust 2017), squirrels (memory, Chow et al., 2017), Atlantic salmon *Salmo salar* (recognition, Leduc et al., 2007), and spotted hyaenas *Crocuta crocuta* (discrimination, Benson-Amram et al., 2011). Despite some individuals being successful in the task, most mosaic-tailed rats, in general, were not able to discriminate between different sized pieces of food. As a nocturnal species (Wood, 1971), visual discrimination abilities may not be as important as other cognitive abilities, leading to the low success rate in this task. Alternatively, the visual acuity of mosaic-tailed rats may be limited, and the inability of mosaic-tailed rats to directly interact with the pieces may have limited their ability to discriminate. However, I included this test as it assessed cognition in a different domain.

Few studies have considered multiple cognitive tests when studying wild species (Guenther and Brust, 2017) and, as such, the relative importance of each cognitive aspect for solving problems is poorly understood. When considering the different types of cognition, associative memory ability significantly influenced problem solving performance, as mosaic-tailed rats that were better at remembering an association were faster at solving repeated problems. This has also been found in lions *Panthera leo* (Borrego & Dowling, 2016). Learning in the tile task (a task with intermediate level complexity) also significantly impacted average problem solving ability, with mosaic-tailed rats that could learn the task solving problems faster than those that could not learn. Learning to solve a problem, and remembering the solution to the problem, would be beneficial for successful solving in the future (Chow et al., 2017). Learning and storing information as a memory allows animals to avoid having to repeatedly form the association, thereby conserving energy (Rowell & Rymer, 2019). This was not found with learning the pillar task (most simple task) or learning in the lever task (most complex task). It is possible that individuals could not become more efficient in solving the pillars over time due to the simplicity of the task. The results also suggests that other forms of cognition, such as causal understanding, may be required for complex solving to occur (i.e. solving the levers), resulting in a lower solving success rate among individuals, but this remains to be tested. Future work should consider whether the interactions between learning, memory and problem solving impact fitness in mosaic-tailed rats.

While memory improved problem solving, the latency to solve a problem was not significantly affected by the ability to discriminate or recognise. Isden et al. (2013) found that discrimination abilities were not correlated with problem solving ability in male spotted bowerbirds. Hodges et al. (1999) found that object recognition ability did not impact problem solving performance in humans, suggesting that it was not important to know what the object was to understand how to use it. This suggests that it may not have been important for mosaic-tailed rats to be able to recognise or discriminate between different parts of the puzzles. Overall, these results suggest that innovative problem solving may only have a small cognitive basis in mosaic-tailed rats, with other individual characteristics, such as motivation, possibly being more important, as suggested by van Horik and Madden (2016) for pheasants *Phasianus colchicus*.

Birth origin impacted problem solving ability. Captive-born mosaic-tailed rats solved the tasks significantly slower than wild-caught individuals. This is surprising, as captive individuals are often better solvers as they are less neophobic of man-made items (spotted hyaenas, Benson-Amram et al., 2013). However, wild-caught mosaic-tailed rats used in this study had been in captivity for at least 10 months at the time of testing, which should have been sufficient time for them to become familiar with captivity and man-made objects (Griffin et al., 2013). Therefore, it is possible that experience of problems during an early life in the wild (i.e. overcoming challenges in a changing environment), rather than experiences during adulthood, may be more important for successful problem solving (Aisner & Terkel, 1992). Currently, very few studies have reported whether cognitive ability is repeatable in non-human animals (Cauchoix et al., 2018). Therefore, future studies should investigate whether cognitive ability is consistent across an animal's lifetime in more species and, whether the relationship between cognition and problem solving is affected by an individual's development (Rowe and Healy, 2014). While it is important to understand what cognitive abilities a species (as a whole) is capable of, individual variation in cognitive ability can lead to individual variation in fitness (Rowe and Healy, 2014). This suggests that it is, therefore, also important to consider variation in these abilities at the individual level.

Overall, I found that mosaic-tailed rats showed a general intelligence, where cognitive abilities were likely underpinned by the same neural processes. I also found that the ability to remember and learn in the tile task were important for solving tasks. My findings suggest that some basic cognitive functions are necessary for problem solving, but that individual differences in other factors, such as persistence, could also be important for successfully completing problem solving tests. Alternatively, developmental effects may shape cognitive ability and problem solving ability early in life, suggesting that the early environment may be critical for determining adult responses to novel problems.

**Supplementary Table 8.1.** Variable loadings of the principal component analysis for the mosaic-tailed rats that completed all tasks (n = 30).

| **Task Measure** | **PC1** | **PC2** | **PC3** |
|---|---|---|---|
| Average problem solving latency | -0.53 | -0.24 | -0.01 |
| Associative Memory test latency | -0.42 | 0.46 | -0.02 |
| Learning Pillar task | -0.31 | 0.43 | -0.23 |
| Learning Tile task | 0.41 | -0.31 | -0.10 |
| Learning lever task | -0.34 | -0.58 | 0.01 |
| Discrimination test | 0.21 | 0.27 | 0.77 |
| Recognition Memory test | 0.34 | 0.22 | -0.59 |

# Chapter 9: General Discussion

Innovative problem solving in animals has become a popular area of research over recent decades, with this ability being observed across all vertebrate taxa, both in captive and wild populations (Chapter 2; Rowell et al., 2021). Problem solving ability is often measured using a foraging-extraction task, such as a puzzle box (Griffin & Guez, 2017). However, animals can also use problem solving to move around their environment more efficiently (e.g. move an obstruction out of a path or detour around a barrier; Munteanu et al., 2016). Consequently, it has been suggested that problem solving is important for an animal's survival and reproductive success, with some studies showing that good problem solvers are more likely to survive harsh conditions (Kozlovsky et al., 2015) or produce more offspring (Cole et al., 2012).

Despite its suggested importance, variation in problem solving ability has been recorded between species (Benson-Amram et al., 2016), within populations of the same species (Cook et al., 2017), and even between conspecific individuals (Thornton & Samson, 2012). While differences in problem solving abilities between species could be due to morphological differences, and differences in solving ability between populations could be due to environmental effects (Chapter 2; Rowell et al., 2021), differences in problem solving abilities between individuals in the same population, exposed to similar environmental conditions, are more likely to be due to ontogenetic differences (Chapter 2; Rowell et al., 2021).

Initially, I identified that both intrinsic and extrinsic factors are capable of influencing an individual's problem solving ability (Chapter 2; Rowell et al., 2021). As an individual develops, it undergoes a series of physiological, morphological, and cognitive changes (Ryan & Wilczynski, 2011; Stamps, 2003) that are often affected by the environmental conditions that the individual is exposed to (Groothuis & Trillmich, 2011). These changes could be governed, to a degree, by underlying genetic architecture, and/or influenced by epigenetic effects during early life, leading to variations in the expression of adult problem solving. In addition, these physiological, morphological, and cognitive changes have been found to influence an individual's behaviour, including personality (Guenther et al., 2014), as well as its cognitive ability (e.g. learning, Brown & Kraemer, 1997), which can feedback to further affect problem solving.

The objective of my study was to investigate the development of problem solving. To do this, I used fawn-footed mosaic-tailed rats *Melomys cervinipes*, as this species is abundant (Moore et al., 2008), and found in complex and degraded habitats (Laurance, 1994), which may present them with a variety of environmental challenges. I first assessed the relative feasibility of this species for studying problem solving and its development by presenting adults with six innovative problems that varied in complexity (the pillar, cylinder, matchbox, obstruction, tile, and lever tasks).

After finding that adult mosaic-tailed rats were capable of solving problems, and that individuals varied in their solving abilities (Chapter 3; Rowell & Rymer, 2020b), my study had two broad aims. The first aim was to investigate what factors could influence how problem solving developed in an individual. I used a series of experiments to isolate the effects of different developmental factors, namely maternal genetic and non-genetic (care) effects, and age and experience on problem solving ability across different life stages. I found that there was no significant genetic relationship of problem solving down the matriline (Chapter 4), and no significant effects of non-genetic factors (i.e. maternal care during early postnatal development) on offspring problem solving abilities Chapter 4). I also found that, while juvenile mosaic-tailed rats became more proficient at solving problems as they gained experience, problem solving during early life was not affected by the age of the individual (Chapter 5). However, naïve adults were more likely to solve a problem, and were faster at solving problems, than juveniles, further suggesting that experience more broadly (handling and mechanical dexterity in general) is important for problem solving.

The second aim of my study was to investigate which factors could influence the expression of problem solving in adult mosaic-tailed rats. Unlike in horses *Equus callabus* (Esch et al., 2019), problem solving in adults was not related to their adrenocortical activity, as measured by faecal corticosterone metabolite concentrations (Chapter 6). However, problem solving was related to an individual's personality, with more exploratory individuals being better solvers than avoidant individuals (Chapter 7; Rowell & Rymer, 2021a). This is consistent with other studies (e.g. Guenther & Brust, 2017). Furthermore, problem solving was related to some aspects of the individual's cognitive ability, particularly learning and memory (Chapter 8; Rowell & Rymer, 2021b), which again is consistent with previous work (e.g. Borrego & Dowling, 2016).

## Early Life and the Development of Problem Solving (Chapters 4 and 5)

How individuals change in their problem solving ability across different life stages has rarely been measured, because finding and tracking wild animals over long periods of time is difficult (Chapter 2; Rowell et al., 2021). Previous studies have therefore used different cohorts of individuals to study the influence of age on solving ability (e.g. Biondi et al., 2010). This is problematic, as it does not properly account for how individual variation in other factors (e.g. exploration, learning ability) may influence an individual's problem solving performance. Furthermore, the behaviour and environmental conditions of pre-weaned juveniles is rarely considered due to the difficulty of accessing juveniles in the wild (Griffin & Guez, 2014). Consequently, juveniles are typically studied after they already have experience manipulating objects and feeding, and it is not clear how problem solving initially develops as an individual becomes an independent forager. It is currently unclear as to what individual factors (e.g. motivation, exploration) are important for problem solving to initially emerge, and which individuals would be capable of solving problems as adults. I used a novel experimental design to 1) isolate and control for the effects of age and experience independently, as well as to study their interactions; and 2) measure solving abilities of individuals before and after they were weaned.

The solving abilities of offspring were not significantly correlated to the performance of mothers, suggesting that, while there appears to be some heritability for problem solving, this is small, and is most likely a consequence of heritability for other traits involved with problem solving, particularly exploration and learning. An individual is therefore not constrained in its solving ability based on its genetics, allowing its problem solving to change over its lifetime in response to other influences. Furthermore, the amount of tactile care (licking, grooming and huddling) received from the mother across early stages of development did not significantly influence how quickly offspring solved puzzles as juveniles and adults. This suggests that maternal care does not have a large organising effect on problem solving, and that this ability is likely influenced more by other individual factors, such as personality and cognition. My innovative experimental design showed that age was less important than experience for problem solving. Mosaic-tailed rats become more successful at solving puzzles as they gain more information and experience. This suggests that improved dexterity and experience in manipulating objects may allow individuals to solve problems, irrespective of age and the state of neurological development.

Overall, the results from these early life studies suggest that problem solving in mosaic-tailed rats is flexible, with individuals adjusting their behavioural and cognitive responses to problems over their development. This flexibility allows for appropriate responses to form as the juveniles disperse and start exploring their environment, which is likely critical for survival (Stamps & Swaisgood, 2007). A flexible solving ability would be beneficial in complex, frequently changing environments (Sol et al., 2005), where conditions experienced in early life may differ substantially from those experienced as an adult. This would suggest that the early life environment may not provide relevant information necessary for adult survival (Stamps & Swaisgood, 2007).

## The Expression of Problem Solving in Adults (Chapters 3, 6, 7 and 8)

The complex interactions between physiology, behaviour and cognition are rarely studied in wild species due to the difficulty in repeatedly trapping the same individuals. The ability to keep mosaic-tailed rats in captivity therefore allowed me to thoroughly investigate these relationships. I initially measured innovative problem solving across multiple tasks of varying complexity, which is rarely done (Chapter 3, Rowell & Rymer, 2020b). For example, most studies only present individuals with one foraging task, a food-baited puzzle box (e.g. spotted hyaenas *Crocuta crocuta*, Benson-Amram & Holekamp, 2012; multiple species of Barbados birds, Webster & Lefebvre, 2001; black-throated monitor lizards *Varanus albigularis albigularis*, Manrod et al., 2008). When multiple tasks of varying complexity are presented (e.g. house sparrows *Passer domesticus*, Papp et al., 2015), they are still within the same context (e.g. foraging, Bókony et al., 2014). My work was the first to incorporate multiple tasks of different complexities that crossed contexts (foraging- and escape-motivated).

The relationship between physiology and problem solving has rarely been considered, and this study represents one of the first study to explore this relationship in an Australian species or a wild rodent species. I used faecal corticosterone metabolite concentration to provide an estimate of basal adrenocortical activity. Glucocorticoid hormones, such as corticosterone, control the release of glucose (Sandi & Rose, 1994), the main source of energy for the brain (McNay et al., 2000) and muscles (Westerblad et al., 2010), and are involved in an individual's stress response (Charmandari et al., 2005). Adrenocortical activity could therefore impact cognitive and mechanical performance (Joëls et al., 2006). In contrast to other studies (e.g. Bókony et al., 2014; Esch et al., 2019), I found that problem solving was not significantly influenced by adrenocortical activity. This suggests that, rather than heavily relying on cognitive components (Thornton & Samson, 2012) or mechanical dexterity (Griffin & Guez, 2014), which can be influenced by adrenocortical activity (Lupien et al., 2009; Westerblad et al., 2010) and stress (Joëls et al., 2006), problem solving may instead be impacted by an individual's personality or motivational state (Griffin & Guez, 2014). However, an individual must use stored energy to explore its environment (Malishev & Kramer-Schadt, 2021), and there may thus be some constraints on how exploratory an individual can be based on its adrenocortical activity.

I then assessed exploratory and anxiety behaviours over multiple contexts and repeated over time, unlike previous studies that are mostly based on behaviour at one time point (e.g. Biondi et al., 2010; Griffin & Diquelou, 2015). I found that mosaic-tailed rats showed consistent individual variations in behaviour, indicative of personality along the exploration axis (Sih, Bell, & Johnson, 2004), and that this significantly influenced problem solving ability. Individuals that were more exploratory solved more problems, and solved problems faster, than less exploratory individuals. However, anxiety-like behaviours did not significantly influence problem solving ability, suggesting that this ability may not be impaired by stress compared to other cognitive processes (e.g. outbred CD-1 mice *Mus musculus*, Knapman et al., 2010). For mosaic-tailed rats, it appears that exploration is more important than anxiety for successful problem solving. More exploratory individuals interacted more with the problems than less exploratory individuals and, in general, all individuals also interacted more with complex tasks than simple ones, as the complex tasks took longer to solve. This heightened level of interaction may have allowed individuals to gain information about solving the problem (e.g. through trial-and-error learning, Thornton & Samson, 2012). While exploring the apparatus may facilitate solving, individuals may also require some cognitive abilities to identify, and act upon, the solution (Chapter 8; Rowell et al., 2021b).

Previous studies have typically only considered one aspect of cognition (e.g. learning, Boogert et al., 2006), whereas I measured four aspects of cognition in the same individuals. I found that adult mosaic-tailed rats relied on learning and memory for successful problem solving, measured as the average latency to solve the problems. Importantly, however, average solving ability was only related to learning in the tile task (a moderately complex task) and not the pillar or lever tasks. Learning in the simpler tasks may not have been necessary, as these tasks may have been solved accidentally (e.g. bumping into the pillar and knocking it over). The most complex task, the lever task, had the lowest solving success rate, and this may have been more due to an individual's motivation (Griffin & Guez, 2014) than its learning ability (Chapter 8; Rowell & Rymer, 2021b). The lack of relationship between problem solving and recognition and discrimination ability suggests that mosaic-tailed rats do not need to identify components of the problems (Heinrich & Bugnyar, 2005) to be able to solve them.

Overall, these results suggest that exploration and some forms of cognition are likely more important for successful problem solving than metabolic condition. However, the interplay between exploration, cognition and problem solving likely begins forming during early life, and these interactions require further investigation.

## Combining Life Stages and Future Directions for Study

Individuals develop along independent trajectories, with intrinsic and extrinsic factors, and their interactions, ultimately shaping how individuals respond to their environments. When an individual undergoes early stages of development, it experiences drastic neurological, morphological, and physiological changes. However, these changes are also influenced by what the individual experiences in its environment (e.g. maternal care, Caldji et al., 1998) or its underlying genetic makeup (Dingemanse et al., 2002). Consequently, even by this early life stage, individuals are unique, and this uniqueness only continues to increase over time. As an individual continues to age, it experiences further neural development (Shen et al., 1997). The formation of neural pathways can contribute towards how an individual behaves (Sullivan et al., 2012), including its exploration, foraging and dispersal. This exploration reinforces the growth and maintenance of neurons (Olson et al., 2006), which can then improve the individual's cognition, particularly learning and memory (Nilsson et al., 1999). Personality and cognitive ability are likely controlled by the same underlying mechanisms (e.g. brain regions and neurotransmitters, Carere & Locurto, 2011), and are expected to develop along similar trajectories (Carere & Locurto, 2011). If the individual can learn about features in its environment, this may reinforce exploratory behaviour.

The direct benefits of increased neural development, and the indirect benefits of increased exploration and enhanced cognition, may then enable some individuals to have enhanced problem solving abilities compared to others (Chapter 2; Rowell et al., 2021). While an animal is likely to find resources while it explores its environment, it is also likely to encounter problems (Mettke-Hofmann et al., 2002). Depending on its previous life experience, an individual may explore or avoid a problem (Papp et al., 2015), affecting what information it gains about the problem. Therefore, individuals that are exploratory and capable of learning, are more likely to solve problems than avoidant individuals (Chapter 7; Rowell & Rymer, 2021a), or individuals that have more difficulty learning (Chapter 8; Rowell & Rymer, 2021b). If solving problems gives the individual access to additional resources, or allows the individual to avoid a potential threat, this could enhance its survival (Kozlovsky et al., 2015) and reproductive success (Cole et al., 2012).

Problem solving in mosaic-tailed rats is flexible and primarily influenced by how an individual moves around its environment, the information it learns and remembers, and its previous experience with problems. This thesis comprised the first study of problem solving ability in a native Australian rodent, is one of only a few studies to consider the ontogeny of problem solving in general, and is, to the best of my knowledge, the only study to comprehensively explore multiple factors affecting the ontogeny of problem solving. My studies suggest that some constraints may be present due to maternal effects, and the developmental pathways affecting personality and cognition. Future studies should focus on the ontogeny of personality and cognition in mosaic-tailed rats, including whether they are heritable and how they are influenced by maternal care. This may provide further information on how personality and cognition shape an individual's initial dispersal and territory formation (Stamps & Swaisgood, 2007), which can affect the likelihood of it encountering problems (Mettke-Hofmann et al., 2002). Future work should also consider how personality and cognition interact with each other and problem solving earlier in an individual's lifetime, to explore when they begin to influence problem solving ability.

There are other physiological mechanisms of problem solving that need to be considered. For example, the neurotransmitter dopamine controls motivation, and can then impact behaviour (e.g. exploration, Ikemoto & Panksepp, 1999) and cognition (e.g. learning, Laszy et al., 2005). Dopamine could therefore directly or indirectly affect an animal's problem solving ability. In addition, the measurements of other metabolic factors (e.g. ketones, Rochais et al., 2021) should be incorporated into future studies to gain a better understanding of the energetic costs of solving problems. Integrating these physiological aspects into studies examining individual variation in solving abilities would allow the fitness benefits of solving to be more accurately estimated, ultimately shedding light on the evolution of problem solving.

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