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Problem solving in fawn-footed mosaic-tailed rats *Melomys cervinipes* is not significantly influenced by maternal care or genetic effects

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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. We investigated whether maternal genetic and nongenetic effects influenced problem-solving ability in a native Australian rodent, the fawn-footed mosaic-tailed rat *Melomys cervinipes*. We 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). We 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). We found no relationship between any maternal care measures and problem-solving abilities across multiple tests, suggesting limited (if any) maternal nongenetic effects. We also found that, as shown by low heritability estimates, problem solving only had a small heritable component in some tasks, but this was nonsignificant and 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.

KEYWORDS
development, genetic effects, heritability, innovation, ontogeny

1 | INTRODUCTION

Behavioral 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 behavioral and cognitive traits have a genetic basis (Barlow, 1991). For example, exploratory behavior 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 behavior or cognition in offspring.

The development of behavioral and cognitive traits may be affected by nongenetic effects experienced during early life. In mammals, behavioral 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 behavioral 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 behavior (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 nongenetic parental effects on offspring behavioral and cognitive development have been widely considered (e.g., Francis & Meaney, 1999; Kikusui et al., 2005), little attention has been given to genetic and nongenetic 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). Problem solving is largely dependent on an individual's exploratory behavior and learning ability (Griffin & Guez, 2014), as more exploratory individuals are more likely to interact with and solve problems than shy individuals (Rowell & Rymer, 2021a), and individuals capable of learning solutions are more likely to solve similar problems in the future (Chow et al., 2017). As both exploration and learning 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 nongenetic effects may also impair problem solving. However, maternal feeding behavior in great tits did not significantly affect the problem-solving performance of offspring (Quinn et al., 2016). Therefore, the lack of studies makes broader generalizations challenging. In addition, no studies have investigated both genetic and nongenetic effects simultaneously.

Therefore, we investigated the influence of maternal genetic and nongenetic 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 endemic rodents, and females have up to four 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

Research highlights

- We found no relationship between maternal care and problem solving. Problem solving also only had a small heritable component. Problem solving is unlikely to be constrained by early development and is more likely to be influenced by later factors.

heightened level of maternal care may be present. Furthermore, nipple-clinging suggests there is unlikely to be differential resource allocation within a litter. Mosaic-tailed rats are capable of solving problems, even as juveniles (unpublished 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 bred in captivity and raised by their mothers. We quantified maternal care (grooming, huddling, nesting) given to the pups in each litter. Thereafter, we measured how long it took pups to solve a matchbox task across three trials and compared this to the level of maternal care received. We also tested problem-solving performance of mothers and pups when they reached adulthood 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 nongenetic effects on problem solving, many studies have looked at how these factors influence other behaviors that are known to be important for problem solving (e.g., exploratory behavior, Champagne, 2008; Dingemanse et al., 2002; learning, Liu et al., 2000; Upchurch & Wehner, 1989). We hypothesized that both maternal genetic and nongenetic effects would influence offspring problem-solving performance. We 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 nongenetic maternal effect, as increased care is associated with more exploratory offspring (Champagne, 2008). We 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 behavior (Dingemanse et al., 2002) and learning ability (Upchurch & Wehner, 1989) have heritable components in other species.

2 | MATERIALS AND METHODS

2.1 | 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 vocalizing, sudden weight changes).

2.2 | 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 × 35 × 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 × 11 × 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 behavioral 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 behavioral 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 then removed from the tanks and housed individually in wireframe cages (described below), while 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.

2.3 | General testing procedures

Data collection occurred between August 2018 and March 2021. Tests were conducted during the peak activity period of mosaic-tailed rats (18:00–22:00 h; Wood, 1971) under red light (except for the obstruction test, see below), which does not interfere with mosaic-tailed rat behaviors (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.

2.3.1 | Maternal care

Maternal care was quantified every second night, for a total of six sessions, commencing when pups were 2 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 some of 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. We recorded the mother's behavior for 20 min, including time spent huddling over the pups, time spent licking and grooming pups, and time spent moving the nesting material (paper towel strips) around. We combined the time spent grooming and the time spent huddling over pups across all nights to produce a total direct care measure. We also combined the time spent nesting across all nights to produce a total indirect care value. The total duration of all three behaviors for each night was also added together to produce a total measure of maternal care. As we 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. As there is unlikely to be differential resource allocation within a litter due to nipple-clinging behavior, the average amount is justified.

2.3.2 | 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 × 33 × 40 cm) with two food-baited cardboard matchboxes scaled to body size (small: 4 × 2 × 1, medium: 6 × 3 × 1.5, large: 7 × 5 × 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 min for each testing session. Juveniles were originally divided into two groups, where one group was tested earlier in development (16- to 36-day-old) and the other was tested later in development (36- to 56-day-old). However, as we found no age-effects on solving ability, individuals were combined into one group for the analyses. We recorded the latency to first solve the task across the sessions (i.e., up to 3600 s) to avoid the effects of learning and experience on problem solving.

2.3.3 | Adult problem solving

All mosaic-tailed rats were also tested in six problem-solving tasks (which had previously been presented to different individuals, as

described in Rowell & Rymer, 2020b) as adults (at least 4 months old, Rowell & Rymer, 2020a) to determine the heritability of problem solving and to investigate whether maternal care effects on problem solving were manifested during adulthood. Similar problems have also been presented to other species (e.g., activity board to guinea pigs *Cavia aperea f. porcellus*, Guenther & Brust, 2017). For each problem, we 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. The latency to solve each puzzle was measured as a proportion due to the different amounts of time provided to individuals to solve different puzzle types (e.g., 3 min for the obstruction task, 30 min for the matchbox task). 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), we recorded the latency to solve the first one solved, 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) (a plastic platform containing two pillars to push over, two tiles to slide, and two levers to pull up flaps) given in an open arena (Figure 1). These tasks were presented to animals in a random order, except for the Trixie Dog Activity Board (Level 2) which was given to animals last due to its complex nature. Tasks varied in complexity (assigned based on the amount of sensory information available to the animal and the number of mechanical techniques required to solve the task), with previous work (Rowell & Rymer, 2020b) showing

that the simpler tasks (pillar, cylinder, and matchbox, respectively) were more likely to be solved than the more complex tasks (obstruction, tile and lever task, respectively).

2.4 | 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.

2.4.1 | Maternal care and offspring problem solving

We 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). We 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, we 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.
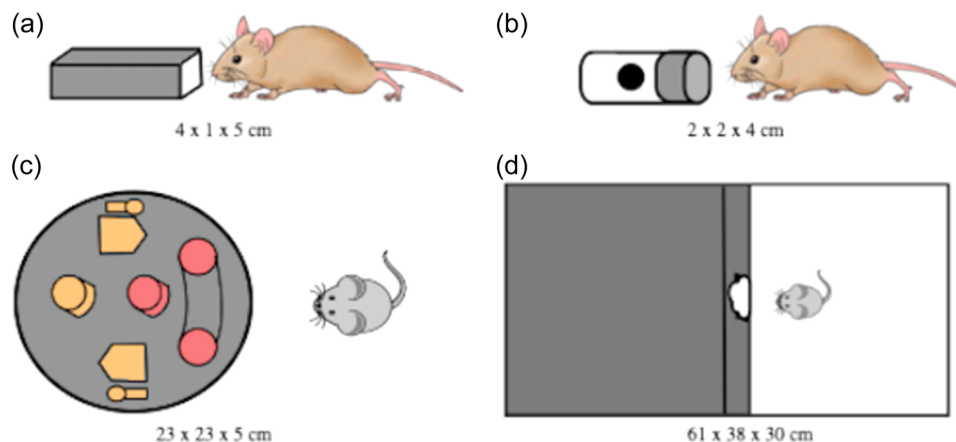

FIGURE 1 Problem-solving tasks given to fawn-footed mosaic-tailed rats (*Melomys cervinipes*). (a) Matchbox task; (b) cylinder task with food (black circle) inside and tinfoil over one end; (c) Trixie dog activity board with pillar, tile, and lever tasks; and (d) obstruction task with a piece of crumpled paper blocking the entrance. From Rowell and Rymer (2021a).

2.4.2 | 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 behavioral measurement, and its heritability is unknown, we 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. We used the scale function to standardize each factor based on its mean and SD, 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.

We 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, we 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.

We 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. We were 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), we could not assume that the maternal genetic contribution represented only ½ h^2. Therefore, as we could not estimate the total heritability values of problem solving, we simply present the maternal h^2 (the beta coefficient). We calculated the correlation of each parent–offspring aggression using $\sqrt{½ h^2}$ (Wray & Visscher, 2008). We assumed that negative heritability estimates were zero (Robinson et al., 1955), but we still present them here, as suggested by Dudley and Moll (1969).

3 | RESULTS

3.1 | 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.

3.2 | 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

TABLE 1 Statistical outputs, power estimates, and R^2 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^2
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	$\chi^2_6 = \mathbf{78.88}$, $\mathbf{p < 0.001}$	-	
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	$\chi^2_6 = \mathbf{78.40}$, $\mathbf{p < 0.001}$	-	
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	$\chi^2_6 = \mathbf{78.07}$, $\mathbf{p < 0.001}$	-	

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 1). However, problem type significantly affected the latency to solve in all models (Table 1), with offspring solving the pillar, cylinder, and matchbox tasks significantly faster than the other problems (Figure 2). The amount of maternal care (direct, indirect, total) received did not significantly affect offspring solving in the remaining tasks (Table 1).

3.3 | Heritability of adult problem solving

We found a trend for heritability of problem solving, albeit it nonsignificant, in the latency to solve the cylinder, tile, and lever tasks (Figure 3 and Table 2). We 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 (Figure 4 and Table 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 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 2).

4 | DISCUSSION

In this study, we investigated genetic and nongenetic maternal effects on offspring problem solving, an area that has received little attention despite several studies showing genetic and
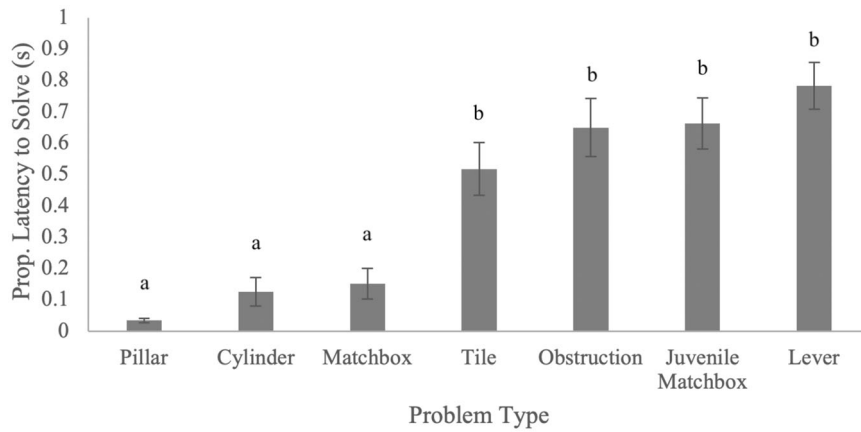
FIGURE 2 The proportional latency to solve (s) of offspring fawn-footed mosaic-tailed rats *Melomys cervinipes* across seven different problem-solving tests.
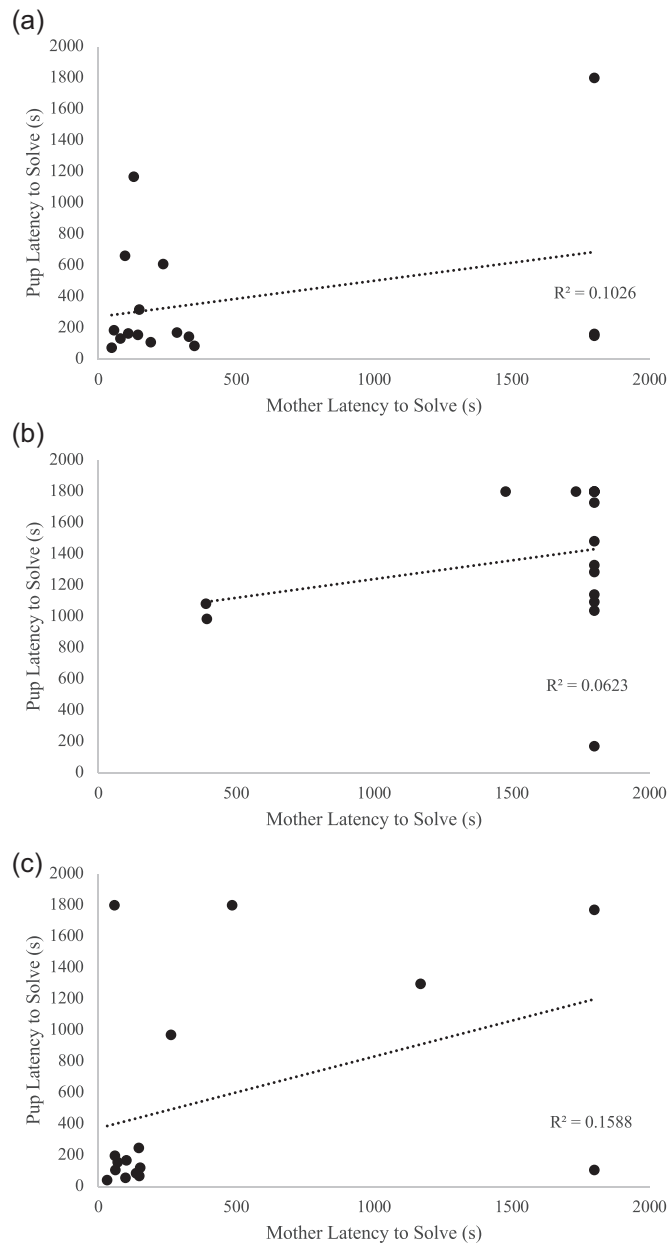

FIGURE 3 The nonsignificant heritability of problem-solving ability between mothers and offspring fawn-footed mosaic-tailed rats *Melomys cervinipes* in (a) the cylinder task, (b) the tile task, and (c) the lever task.

TABLE 2 Narrow sense heritability (h^2) estimates, statistical outputs of parent–offspring regression models of problem solving in adult fawn-footed mosaic-tailed rats *Melomys cervinipes*.

Solving task	Measurement	β ± SE	h^2 ± SE	Statistics	Power	Prop. variation
Matchbox	Latency time interacting	−0.12 ± 0.27 0.21 ± 0.26	−23.88 ± 53.06 41.16 ± 52.30	$F_{(1, 14)}$ = 0.20, p = 0.660 $F_{(1, 14)}$ = 0.62, p = 0.445	0.509 0.652	0.014 0.042
Cylinder	Latency	0.32 ± 0.25	64.07 ± 5.06	$F_{(1, 14)}$ = 1.60, p = 0.226	0.343	0.103
	Time Interacting	0.14 ± 0.26	26.96 ± 52.96	$F_{(1, 14)}$ = 0.26, p = 0.619	0.865	0.018
Obstruction	Latency	−0.28 ± 0.26	−55.87 ± 51.32	$F_{(1, 14)}$ = 1.17, p = 0.295	0.681	0.078
	Time Interacting	0.35 ± 0.25	70.18 ± 50.06	$F_{(1, 14)}$ = 1.965, p = 0.183	0.256	0.123
Pillar	Latency	−0.07 ± 0.27	−14.54 ± 53.32	$F_{(1, 14)}$ = 0.07, p = 0.789	0.733	0.005
	Time Interacting	−0.03 ± 0.27	−5.83 ± 53.42	$F_{(1, 14)}$ = 0.01, p = 0.915	0.839	<0.001
Tile	Latency	0.25 ± 0.26	49.92 ± 51.76	$F_{(1, 14)}$ = 0.93, p = 0.351	0.743	0.062
	Time Interacting	0.25 ± 0.26	50.96 ± 51.68	$F_{(1, 14)}$ = 0.972, p = 0.341	0.806	0.065
Lever	Latency	0.40 ± 0.25	79.7 ± 49.02	$F_{(1, 14)}$ = 2.64, p = 0.126	0.455	0.159
	Time Interacting	0.32 ± 0.25	64.22 ± 50.62	$F_{(1, 14)}$ = 1.61, p = 0.225	0.503	0.103

nongenetic maternal effects on offspring behavioral and cognitive development in general (e.g., Francis & Meaney, 1999; Kikusui et al., 2005). We 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 two 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 (unpublished data) 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).

We found no significant influences of nongenetic maternal care effects on adult problem-solving behavior. While tactile stimulation from mothers is known to improve physiological, behavioral, and cognitive responses in offspring when they reach adulthood in other rodents (Champagne, 2008; Rymer & Pillay, 2011), our 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 behavioral 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).

Our results suggest that there may only be a small heritable component for some problem-solving behaviors (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). Despite not being significant, low heritability estimates demonstrate that genetic heritability contributed a small effect to multiple problem-solving measures. This is similar to the findings of Quinn et al. (2016) for great tits, where problem-solving ability also had low heritability
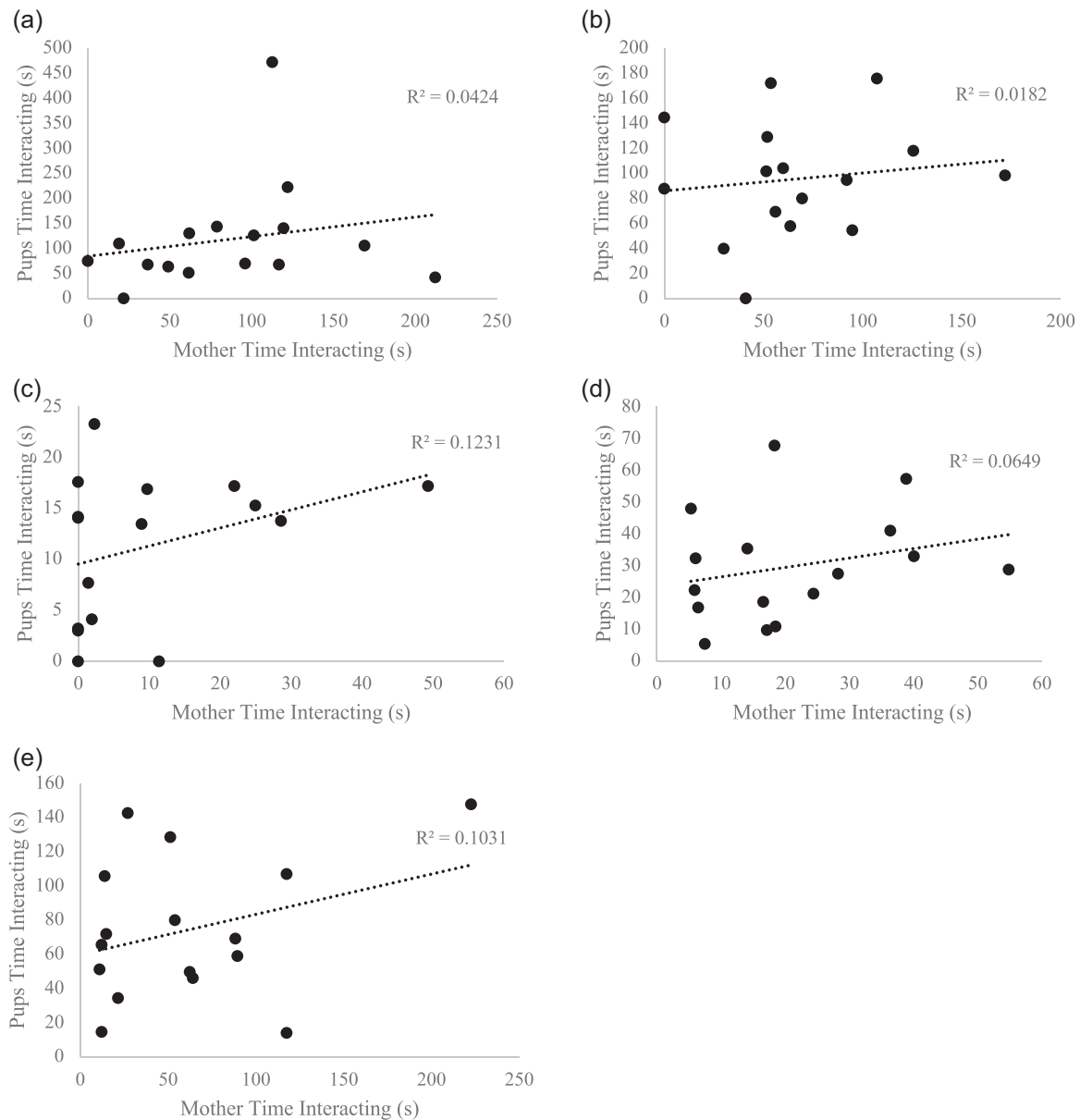
FIGURE 4 The nonsignificant heritability of the time interacting with problems between mothers and offspring fawn-footed mosaic-tailed rats *Melomys cervinipes* in (a) the matchbox task, (b) the cylinder task, (c) the obstruction task, (d) the tile task, and (e) the lever task.

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 behavior, 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 behaviors 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.

5 | CONCLUSION

These results suggest that problem-solving ability in adult mosaic-tailed rats is not largely constrained by genetic effects, most likely because of its multifaceted nature, including its reliance on behavioral and cognitive components, particularly exploration and learning. This complexity could explain why there may be slight genetic effects for some tasks that use these traits, but not others. As such, female mosaic-tailed rats may only have a small organizational effect on the developmental trajectories of their offspring's problem-solving abilities. The development of problem solving 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.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article The data used in this study have been uploaded as a supplementary document.

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