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Experienced problem solvers? The ontogeny of innovation in wild house mice

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Animals frequently encounter challenges requiring innovative problem solving, yet an individual's propensity to innovate is believed to change throughout life. It is still unclear how age and experience interact to shape problem-solving performance over time. Here, we investigate how juvenile and adult wild house mice, *Mus musculus domesticus*, spontaneously engage with and solve novel problems by combining observations from populations living in two conditions, either socially complex seminatural enclosures or in more controlled, laboratory cages. There, we ran experiments to assess (a) the onset of problem-solving behaviours in preweaned mice, (b) spontaneous problem solving across age groups and (c) whether exposure to already solved set-ups improves problem-solving performance. We found that mice interacted with novel problems well before independence, and juveniles began solving problems before reaching sexual maturity. We also observed a contrasting pattern regarding age and performance. Specifically, juveniles and adults performed similarly in spontaneous problem solving when tested alone in standardized cage housing, but adults were more successful in the seminatural enclosures. Individual problem-solving performance remained highly consistent within each housing condition (that is, seminatural enclosures or cages), and exposure to solved set-ups did not help nonsolvers solve novel problems in either condition. In contrast, experience only benefited individuals that were already solvers, allowing them to solve more problems at a later time. Our results suggest that the ability to spontaneously problem solve is an inherent trait in house mice rather than a skill acquired through experience.

In the wild, animals often live under fast-changing conditions and face novel situations they must overcome, often a direct result of human-induced rapid environmental change (Sih et al., 2011). These unpredictable changes can affect the survival of individuals, populations and species (Rymer et al., 2013), but their effects vary across species (Sih et al., 2011). Some species, such as invasive or urban-dwelling ones, have life history, morphological, behavioural or cognitive traits that help them survive and thrive in these fast-changing conditions (Fox et al., 2019; Griffin et al., 2013; Sih et al., 2011; Sol, 2003). Among the many traits influencing species' responses, cognitive and behavioural flexibility, particularly innovation, can be crucial for determining survival and success in novel conditions (Amici et al., 2019; Day et al., 2003; Fox et al., 2019; Nicolakakis et al., 2003; Ramsey et al., 2007; Sol, 2003).

Innovation, the ability to produce new behaviours or apply novel solutions to existing problems or solve problems never encountered before (Kummer & Goodall, 1985; Reader & Laland, 2003), can help animals in establishing themselves in novel environments and withstanding rapid habitat alterations (Ducatez et al., 2020). Innovative behaviours are widespread in the animal kingdom, with a plethora of innovations being recorded in the wild (Fisher, 1949; Klump et al., 2021; Kummer & Goodall, 1985; Lefebvre, 2021). However, recording innovations in the wild is challenging as they are often rare and unpredictable and sometimes difficult to disentangle from the focal species' natural behavioural repertoire (Amici et al., 2019; Rowell et al., 2021). Because studying innovation directly in the wild is impractical, researchers often use problem-solving tasks as proxies to study innovative behaviour, as solving these tasks requires animals to innovate (Morand-Ferron et al., 2011; Overington et al., 2011; Rowell et al., 2021). Problem solving is strongly linked to innovations in the wild (Audet et al., 2024) and is therefore an important measure to understand how individuals (and species)

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innovate. As previous work has pointed out (Griffin & Guez, 2014; Reader & Laland, 2003; Tebbich et al., 2016), what is needed to problem solve is akin to what is needed to innovate; thus, solving a novel problem using any behaviour (innate or novel) is a suitable form of empirical approach to measure an animal's innovative performance.

Since the seminal work of Reader and Laland (2003), research on innovation in wild animals has advanced significantly (Amici et al., 2019; Rowell et al., 2021), from measuring the fitness consequences of innovation (Chen et al., 2019; Johnson-Ulrich et al., 2019) to understanding how innovators thrive in urban and human-altered environments (Klump et al., 2021; Mazza & Guenther, 2021). Despite these recent advances, it remains unclear why individuals, even within the same population, vary in their problem-solving abilities. The two most prominent hypotheses on innovation offer contrasting explanations on why only some individuals solve novel problems. The 'bad competitor' (or 'necessity drives innovation') hypothesis (Amici et al., 2019; Laland & Reader, 1999; Reader & Laland, 2003) suggests that individuals with lower competitive ability seek alternative resources and are therefore more likely to innovate. In contrast, the 'excess of energy' (also 'free time') hypothesis (Amici et al., 2019; Kummer & Goodall, 1985) proposes that individuals with excess energy, time or other resources are the ones better suited to invest in innovation.

Although these hypotheses make clear predictions about which individuals should be more likely to innovate, empirical results are sometimes contradictory. In the context of age, both theories tend to agree that young individuals, often less competitive but with more free time available, should be the most likely to innovate. However, findings seem to be species- and context-specific. For example, adult wild meerkats, *Suricatta suricatta*, were better problem solvers than juveniles (Thornton & Samson, 2012), whereas juvenile kakas, *Nestor meridionalis*, outperformed adults in problem-solving tasks (Loepelt et al., 2016). Similarly, juvenile Chimango caracaras, *Milvago chimango*, solved a puzzle box more quickly and effectively (Biondi et al., 2010), whereas older fawn-footed mosaic-tailed rats, *Melomys cervinipes*, were more likely to explore and eventually solve a novel problem-solving task compared with juveniles (Rowell & Rymer, 2023). In the latter study, the authors were able to explicitly test the effect of experience on problem-solving performance, and indeed more experienced individuals were better problem solvers (Rowell & Rymer, 2023). However, previous experience does not always seem to be beneficial. Dispersal-aged coyotes, *Canis latrans*, that experienced a puzzle box as juveniles were not necessarily better at solving it, but they were more likely to engage with the task later in life (Garcia et al., 2022). Thus, experience may indirectly benefit individuals by improving their chances of engaging with novel opportunities, rather than directly improving their innovative abilities once the opportunity arises.

Noncognitive traits, such as exploration or boldness, may influence how often individuals encounter opportunities to solve novel problems and how persistent they are when innovating (Benson-Amram et al., 2013; van Horik & Madden, 2016; Vezyrakis et al., 2025). These encounters provide opportunities for cognitive traits, such as learning and memory, to potentially improve future problem-solving attempts (Griffin & Guez, 2014). Finally, the presence of more dominant conspecifics can also influence the opportunities to encounter or solve novel problems, as well as having effects on innovative performance itself (Drea & Carter, 2009), thereby leading to contradictory findings across different social contexts (Vezyrakis et al., 2025).

Wild house mice, *Mus musculus domesticus*, are known innovators (Gorshkova et al., 2024; Vezyrakis et al., 2025; Vrbanec et al., 2021), and they are an ideal species to study how age and experience can impact the development of innovation propensity throughout an individual's life. They can be studied in both controlled and seminatural conditions, providing the opportunity to combine observations and experiments to understand problem-solving behaviour in individuals of different ages and experiences. Additionally, the specific characteristics of different life stages of both wild and domesticated house mice have been studied to a great extent (Brust et al., 2015; Prabh et al., 2023), allowing us to precisely estimate how and why individuals of different life stages may engage in innovative behaviours. Briefly, at the age of 12–14 days old, pups develop full sensory perception and begin exploring their surroundings (Brust et al., 2015). Around the age of 30–36 days, juvenile wild house mice are weaned and reach independence from their mother (Prabh et al., 2023). Finally, adulthood is reached at 48–77 days old, with reproduction and the birth of their first litter beginning at around 100 days of age for wild house mice living in seminatural conditions (Darmis et al., 2025). Across these life stages, we aimed to fill the following gaps in our knowledge:

(1) Are there differences in innovative problem solving across ages (that is, across life history stages) in wild house mice living under seminatural conditions?
(2) At what life stage do house mice start showing problem-solving behaviours?
(3) Does experience improve problem-solving performance?

To address these questions, we combined observations from wild house mouse populations living under seminatural conditions and experimental tests conducted in controlled environments. Question (1) was addressed using observations from the seminatural enclosures, which allowed us to monitor spontaneous innovative problem solving across different age groups in a socially and ecologically relevant environment that mimics natural conditions. In these enclosures, mice voluntarily visit and attempt to solve novel problem-solving set-ups, usually alone (in more than 90% of observations) and without facilitation or obstruction by conspecifics (Vezyrakis et al., 2025). Based on these results, there is no indication that, in this setting, mice solve problems via social learning. Therefore, this system allows us to study the problem-solving performance of individuals without the impact of observational learning from others.

In contrast, questions (2) and (3) were addressed in controlled, laboratory conditions. By exposing naïve individuals to problem-solving tasks at different ages and manipulating their prior experience, we could assess the onset of problem-solving behaviour and the effect of experience on performance.

Using both seminatural and controlled conditions was essential and complementary. While the seminatural environment showed how age-related differences in innovative problem solving appear in ecologically relevant conditions, the controlled conditions allowed us to isolate the specific effects of developmental stage and experience on problem solving. To inform the design and interpretation of the experience manipulation in particular, we also conducted a supplementary memory experiment (see Appendix) to determine the timeframe over which learned associations are retained in wild house mice. This enabled us to select intervals at which prior experience would be most likely to influence behaviour. By combining these approaches, we aimed to advance our understanding of how innovative problem solving emerges and develops in house mice, offering insights into both the ontogeny and the ecological relevance of problem-solving abilities.

METHODS

Innovative Problem Solving in Seminatural Enclosures

We set up four replicate seminatural enclosures (19.6 m^2) by releasing adult wild house mice ($N = 35$ individuals in three enclosures, 20 females and 15 males, $N = 34$ individuals in the fourth enclosure, 20 females and 14 males). The founders were descendants of wild-caught mice from the Cologne/Bonn region in Germany. The enclosures were indoors and resembled the natural conditions under which house mice would establish a colony, such as a barn (König et al., 2012). Each enclosure contained woodchip bedding, nesting material (toilet paper and cotton rolls) and 13 nest boxes where the mice could build nests and breed. Food (Altromin 1324, Germany) and water were available ad libitum at nine feeding stations equally distributed in the enclosure. Temperature and light varied naturally but light was supplemented between 0800 and 1700 hours, whereas underfloor heating prevented temperatures dropping below 10 °C. These enclosures are an established system for studying wild house mouse colonies, with close-to-natural population development, and where mice show their natural behaviours. Every 4 weeks, all individuals of an enclosure were caught and weighed, and new individuals ($W > 10$ g) were fitted with radiofrequency identification (RFID) transponders (ISO transponders, PlanetID).

Starting 1 month after establishing the enclosures, we presented four consecutive problem-solving set-ups the mice could voluntarily approach and attempt to solve. The set-ups were presented in the following order: (1) omnidirectional slider, (2) inverted cup, (3) one-directional slider and (4) Petri dish (see Fig. 1). To solve each set-up, the mice were required to perform a simple movement that required minimal force, which enabled all mice to potentially solve them, regardless of their age or physical strength. Although set-ups were not scaled for body size, the weight of individual set-up components did not limit small-bodied individuals from solving them. Set-ups (1) and (2) could be solved by pushing, sliding or pulling the metal lid or plastic cup, respectively, in any direction. Set-up (3) required mice to push or pull the white block in only one direction and set-up (4) required them to lift the lid of the Petri dish. We presented each set-up for 2 h per night for five nights (following a regime of two consecutive testing nights, then a break of five nights, and then three more nights of testing). Between set-ups, there was a minimum gap of 2 weeks, that is, the total testing procedure lasted approximately 16 weeks. For a detailed description of the problem-solving testing protocol see Vezyrakis et al. (2025) and supplementary materials therein. These four problem-solving set-ups, previously used for other small rodents (Mazza & Guenther, 2021) as well as wild house mice (Vrbanec et al., 2021), were baited once, at the start of each trial, with a dried mealworm, *Tenebrio molitor*, larva. This was a novel food source at the start of the experiment and therefore highly attractive for mice.

For each testing night, we placed five testing boxes in predefined locations in each enclosure in the empty space between the nests to minimize the chances any of the boxes would be inside an individual's territory (since mice not belonging to the family would be denied access). The majority of the individuals (93%) visit these problem-solving boxes at least once in their lifetime, usually alone (in more than 90% of observations) and with few competitive interactions with conspecifics (Vezyrakis et al., 2025). The floor of the testing boxes was covered with bedding from the location where they were placed to keep the environment's olfactory cues consistent. Each box had a single entrance that was fitted with an RFID antenna (EuroID, Netherlands) to record the mice that entered or exited the box. For the duration of the 2 h, all activity in the box was video recorded from above (HC–V 180, Panasonic Corporation, Japan).

We recorded when each individual visited the problems using the RFID antenna records at each box's entrance. Specifically, we recorded the number of times each individual visited each set-up they encountered throughout their life and classified those visits depending on whether the problem was already solved or unsolved when they entered the box. We also recorded the identities of the individuals that solved a set-up. Additionally, we recorded whether these individuals belonged to the founding generation (that is, were adults) or were born in the enclosures (being either dependent juveniles or recently independent subadults), as well as their age in each of the above instances. These two distinct generations are further referred to as 'adults' and 'juveniles', respectively.

Controlled Cage Experiments

In all controlled experiments, mice were housed in standard cages (Macrolon Type III; L × W × H: 382 × 220 × 150 mm) filled with woodchip bedding, nesting material and two shelters. Temperature and light conditions varied naturally as in the seminatural

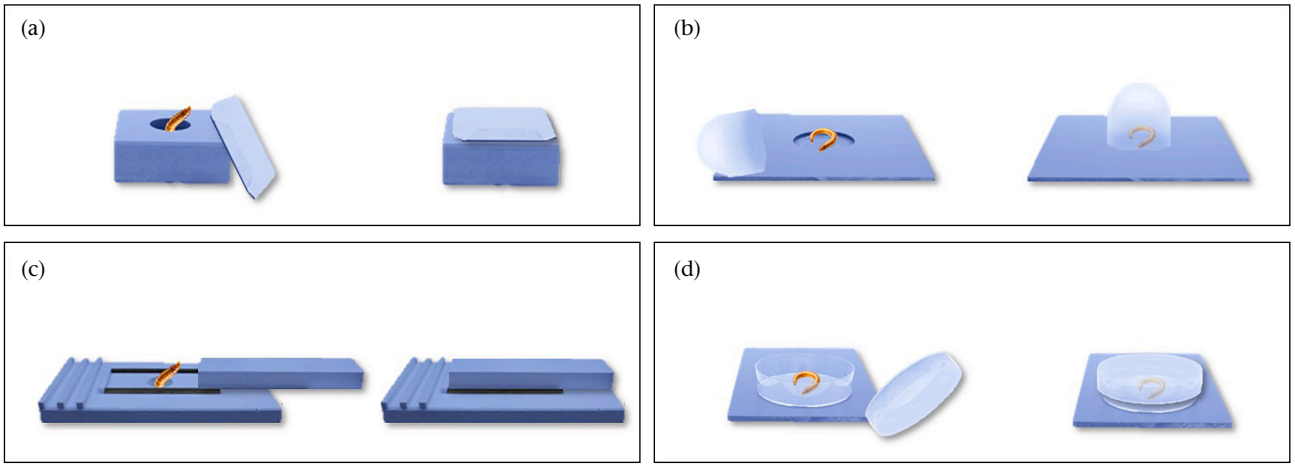

Figure 1. Presentation of the four problem-solving set-ups used in the seminatural enclosures: (a) omnidirectional slider, (b) inverted cup, (c) one-directional slider and (d) Petri dish. The set-ups are shown in their open (solved) configuration on the left and their closed (unsolved) configuration on the right, with a representation of the reward (a mealworm).

enclosures, with supplemental light between 0800 and 1700 hours and underfloor heating keeping temperatures above 10 °C. Food (Altromin 1324, Germany) and water were accessible ad libitum from the cage lid. Unless otherwise mentioned in the following sections, mice were housed in same-sex, usually sibling, pairs. All problem-solving and associative learning tasks (see Appendix) were rewarded with a dried mealworm, *Tenebrio molitor,* larva. None of the mice tested in the controlled experiments participated in the enclosure experiments or vice versa, and each mouse used below participated in only one of the following experiments.

Which Age Marks the Onset of Innovation?

To determine the age at which juvenile house mice begin interacting with problem-solving set-ups, we tested 58 juveniles from 14 different litters, aged 13–20 days. At this stage, young mice are not yet independent but have started feeding on solid food, which could motivate them to engage in an extractive foraging task. Because of their age, the juveniles were not individually tagged, making individual identification impossible, and testing was conducted in their home cages with their mothers present. Each litter was tested once, and the trials lasted 1 h, during which we presented three identical Lego houses (L × W × H: 47 × 48 × 65 mm; Mazza & Guenther, 2021; Vrbanec et al., 2021). To access the reward, the mice needed to open the windows of the set-ups. Trials were video recorded from above (HC–V 180, Panasonic Corporation, Japan), and we recorded whether individuals from each litter interacted or solved any of the problem-solving set-ups. As individual recognition was not possible for mice of this age, we simply report the age at which these juveniles interacted with and possibly solved the set-ups.

Does Exposure to Solved Problems Improve Future Performance?

To investigate how prior experience affects problem-solving performance across different ages, we tested adult (N = 45, aged 12–30 weeks) and weaned juvenile (N = 42, aged 30–36 days) wild house mice. Except for 10 adult males housed alone after aggressive conflicts between siblings, all mice were housed in same-sex sibling pairs as described previously. To familiarize the mice with the rewards, they were provided with sunflower seeds and dried mealworms 2–3 times during the week preceding the experiment.

The mice were tested using two problem-solving set-ups (a Lego house and a slider, see Vrbanec et al., 2021) and a control set-up (a tube filled with bedding, where the reward could be accessed by digging, a natural behaviour for mice). All set-ups, including the control, were baited with one sunflower seed and half a mealworm as rewards. Testing took place in each individual's home cage, and sibling pairs were separated before trials to ensure only one mouse from each pair was tested per day. Siblings were reunited after testing was complete. Based on previous studies, housing conditions (alone or in sibling pairs) as well as brief separation from siblings did not affect motivation or the likelihood to innovate (Vezyrakis et al., 2025). Each trial lasted 1 h and was video recorded from above (HC–V 180, Panasonic Corporation, Japan).

As a first step, we recorded which mice spontaneously solved one or both problem-solving set-ups in the first trial. All mice that solved at least one problem were consequently characterized as 'solvers'. Then, we divided the mice that did not solve any problem into two equally sized 'nonsolver' and 'exposure' groups.

To investigate the effect of exposure on problem solving, the exposure group underwent two sessions with the set-ups in a solved configuration during the interval between the first and second trial. In the first session, the set-ups were fully open, with the rewards readily accessible. In the second session, the set-ups were partially open, requiring minimal action to retrieve the rewards (Fig. 2). Each exposure session lasted 1 h. After these sessions, all individuals from all groups were retested in a second trial.

The interval between the problem-solving trials and exposure sessions was determined based on a pilot associative learning and memory experiment, which demonstrated that wild house mice

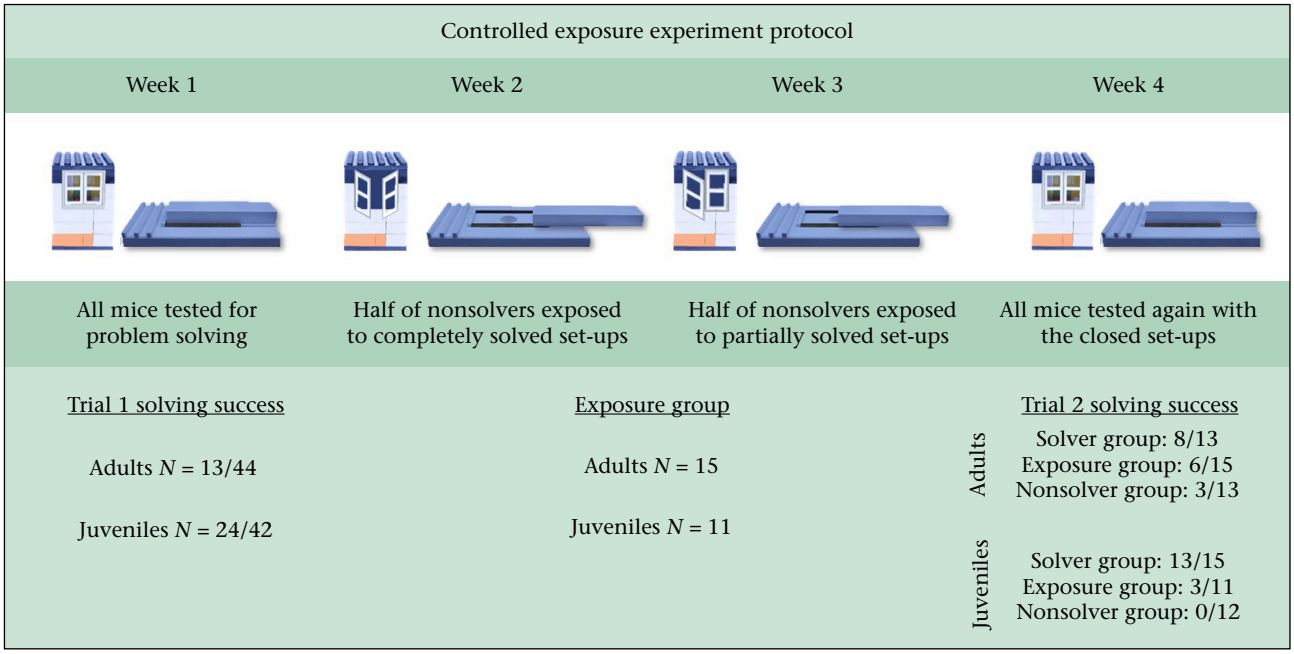

Figure 2. Protocol followed to expose mice to already solved set-ups. In week 1, we tested all individuals (44 adults and 42 juveniles) with two closed problem-solving set-ups. Then, half of the nonsolvers from each age group (15 adults and 11 juveniles) were exposed sequentially to the same set-ups completely open (week 2) and partially open (week 3). Finally, all individuals were tested again using the closed problem-solving set-ups at week 4 and we recorded their problem-solving performance.

can retain learned associations for at least one week (see Appendix). Accordingly, we used this time frame for our experimental design to optimize retention and test outcomes. For a detailed overview of the testing protocol and relevant sample sizes see Fig. 2.

For both problem-solving trials, we recorded each individual's success in solving the set-ups.

Statistical Analyses

All statistical analyses were performed in R 4.4.1 (R Core Team, 2024). Linear mixed effects models were run using the functions of the lme4 (Bates et al., 2015) and glmmTMB (Brooks et al., 2025) packages. Model assumptions were checked using histograms of the residuals and the functions of the DHARMa package (Hartig & Lohse, 2022), and all results are presented using the tab_model function of the sjPlot package (Lüdecke, 2013) in Tables S1–S8. Repeatability estimates were obtained with the rpt function of the rptR package (Nakagawa & Schielzeth, 2010; Stoffel et al., 2017). Repeatability estimates were run using 1000 bootstraps and 1000 permutations, and we report the *P* values estimated from both the likelihood ratio test (LRT) and from permutations.

Problem Solving in Seminatural Enclosures

In all six following generalized linear mixed models (GLMMs), we accounted for enclosure ID by including it as a random factor.

To examine whether different age groups (adults or juveniles) visited the problems at different rates, we ran a negative binomial GLMM (model 1) with the number of visits as the response variable, the interaction of their age group and the problem-solving round as the fixed effects, and the individual ID as a random effect.

To investigate whether individuals visited the problem-solving boxes while the problem was still available to solve or after it was already solved, we ran a generalized linear mixed model (model 2) with a binomial distribution with the 'type' of visit (0: before the problem was solved, 1: after the problem was solved) as the response variable, the age group of the individual as the fixed effect, and the individual ID as a random effect.

To examine whether the solvers changed how often they visited the problem-solving set-ups as the experiment progressed, we ran a generalized mixed model (model 3) with a negative binomial distribution with the number of visits as the response variable, the round number (that is, the four rounds of different set-ups presented) as the fixed effect, and the individual ID as a random effect. For this model, we used the subset of solvers that were present in all four rounds of the experiment. Additionally, to examine whether individual solving performance was consistent throughout the four rounds of the experiment, we ran a binomial repeatability model with the binary solving performance as the response variable, the round number as a fixed effect and the individual ID as a random effect.

Furthermore, we wanted to examine whether individuals of different ages would visit a novel problem at different frequencies, so we ran a generalized linear mixed model (model 4) with a negative binomial distribution, with the number of visits at the first set-up each individual encountered as the response variable, the interaction of the age group with the actual age (in days) at their first visit as the fixed effects and the enclosure ID as the random effect.

To compare the problem-solving performance of the two age groups in the enclosures, we ran a generalized linear mixed model (model 5) with a binomial distribution with the binary solving performance of each individual as the response variable (0: non-solver, 1: solver), their age group as the fixed effect and the enclosure ID as a random effect. Individuals that solved at least one problem were characterized as solvers and repeated solutions of problems did not contribute to this measurement.

Finally, we also ran a generalized linear mixed model (model 6) with a negative binomial distribution to determine whether the solvers from different age groups solved a different number of problems. The model had the number of problems solved as the response variable and the interaction of age group and problem-solving round as the response variable, with the individual ID in addition to the enclosure ID as the random effects.

Does Exposure to Solved Problems Improve Future Performance?

First, we examined the spontaneous problem-solving performance (that is, in the initial trial) of each age group. To do this, we ran a proportion test (χ^2 test) to compare the proportion of adult versus juvenile individuals that solved a problem in their first attempt.

Then, to examine whether individuals performed consistently in the two trials, we ran a binomial repeatability model with the binary solving performance as the response variable, the trial number as a fixed effect and the individual ID as a random effect.

Furthermore, to assess whether the individuals in the 'exposure' group improved between the two trials, we ran a generalized linear model (model 7) with a binomial distribution with the solving success as the response variable and the trial number as a fixed effect. This model was run only on the subset of individuals of the 'exposure' group.

Finally, we specifically examined whether there was a difference in performance between the individuals that were exposed to solve set-ups and the ones that were not. For this, we ran a generalized linear model (model 8) with a binomial distribution with the difference in performance (0: no improvement, 1: improvement) between the two trials as the response variable, with the testing group and the generation as fixed effects. Both models were run on the subset of individuals that did not solve a problem in their first trial and also participated in the second one.

Ethical Note

All experiments conformed to ASAB/ABS guidelines for animal experiments (ASAB Ethical Committee/ABS Animal Care Committee, 2025) and were approved by the Ministerium für Energiewende, Landwirtschaftliche Räume und Umwelt, Kiel (licence V244 - 57612/2022(43-4/19)). Keeping and breeding of mice was approved and is regularly controlled by the Veterinäramt Plön under permit 1401-144/PLÖ-004697.

All animals were descendants of wild-caught individuals, and they were born and raised in the conditions described above. All experiments were performed voluntarily by the animals, and no handling or trapping was involved in the experimental part of the study. Every 4 weeks, all individuals of an enclosure were caught either inside their nests or using clear plastic tubes in the remainder of the enclosure, subsequently weighed and new individuals ($W > 10$ g) were fitted with RFID transponders to control population development and welfare of animals. The transponders were inserted subcutaneously into the loose skin flap at the back of the neck by experienced animal caretakers, in a procedure that takes less than 10 s, causes minimal disturbance, and the wound typically does not bleed and closes within minutes, with no recorded injuries or deaths. The seminatural enclosures are an established system that allow mice to show their natural behaviours (Prabh et al., 2023), and the population size was always kept well under the carrying capacity. In cages, the mice were kept in same-sex sibling pairs whenever possible, and all cages contained

nesting material, shelters, an elevated perch and a running wheel for enrichment. All animals were kept alive after the end of the experiments described here to participate in further studies.

RESULTS

Seminatural Enclosures

Overall, $N = 275$ mice were alive during the problem-solving tests in the enclosures and could voluntarily participate ($N = 128$ adults, $N = 147$ juveniles, mean age difference 165 days). The adults first visited the problems at the age of (mean ± SD) 155 ± 47 days old, whereas the next generation visited for the first time at the age of 39 ± 11 days old.

The different generations visited the problem-solving boxes at different intensities (model 1, GLMM: $\beta = 0.64$, SE ±0.18, $P = 0.001$; see Fig. 3a and Table S1), with juveniles visiting the problem-solving boxes more (as measured by the number of visits per round the individual was alive). The number of visits to the problem-solving boxes did not change as the problem-solving rounds progressed (GLMM: $\beta = 0.04$, SE ±0.04, $P = 0.252$; see Fig. 3a and Table S1), and neither was there an interaction between the age group of the individuals and the problem-solving round (GLMM: $\beta = -0.05$, SE ±0.06, $P = 0.347$; see Fig. 3a and Table S1).

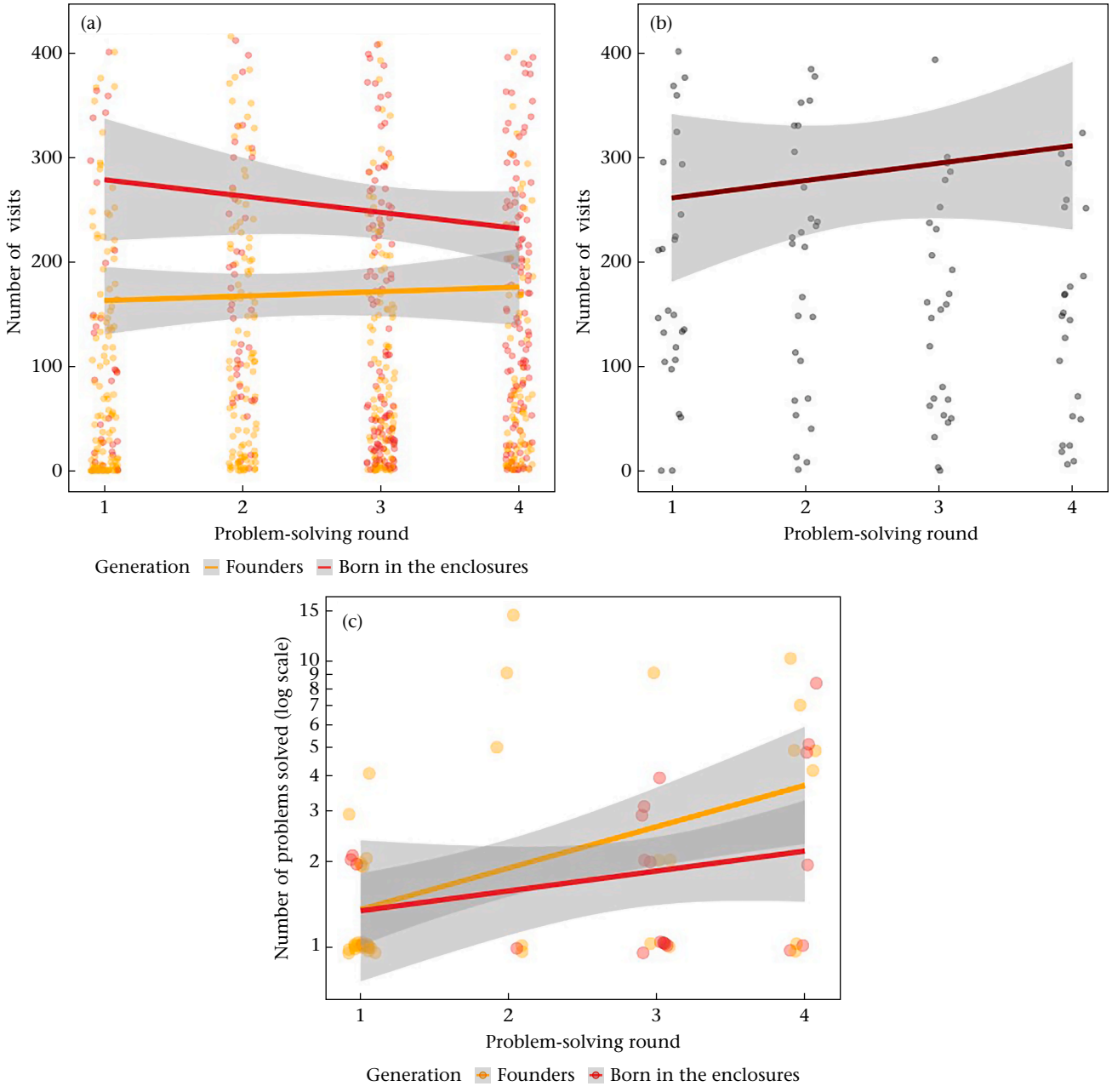

Figure 3. Linear regressions of the number of (a) visits to the problem-solving boxes, (b) visits to the problem-solving boxes only by the solvers that were present in all four rounds and (c) problems solved by the two age groups (orange: founding generation, red: mice born in the enclosures) over the four problem-solving rounds. Shading represents 95% CI. For plotting purposes in (a) and (b), data points of over 400 visits are not shown but are included in the calculation of the regressions (maximum number of visits: 1250). Plots (b) and (c) only include individuals that solved at least one problem. Axis in (c) is in log scale.

We also found that the adults tended to visit the problem-solving boxes more before the problems were solved compared with juveniles, that is, they had more actual chances of solving (model 2, GLMM: $\beta = 0.97$, SE ± 0.16, $P < 0.001$, Table S2). We found, however, that the solvers who were present in all four problem-solving rounds did not change the number of visits they made to the problem-solving boxes (model 3, GLM: $\beta = -0.001$, SE ± 0.063; $P = 0.998$; see Fig. 3b and Table S3). We also saw that individual likelihood to solve was repeatable throughout the four rounds of the experiment (logit-scale repeatability: R = 0.3, SE ± 0.06, $P_{[LRT]} < 0.001$, $P_{[Permutation]} = 0.002$).

Age also affected how mice visited the very first problem they ever encountered. Juveniles tended to visit the first problem they encountered marginally more than adults (mean $\pm$ SD; adults: 157 $\pm$ 203, juveniles: 195 $\pm$ 207; model 4, GLM: $\beta = -0.68$, SE ± 0.41, $P = 0.099$; see Fig. 4 and Table S4). Individuals that were younger when they encountered their first problem visited it significantly more (GLM: $\beta = -0.01$, SE ± 0.001, $P < 0.001$; see Fig. 4 and Table S4), but there was no interaction between age and generation (GLM: $\beta = -0.002$, SE $\pm$ 0.01, $P = 0.830$; see Fig. 4 and Table S4).

Finally, the adults outperformed the juveniles in solving success. Juveniles were less likely to be problem solvers compared with the adults (model 5, GLM: $\beta = -0.78$, SE ± 0.33, $P = 0.019$; see Fig. 5 and Table S5). However, considering only individuals that eventually solved, there was no difference in the number of problems solved by the solvers of each age group (model 6, GLMM: $\beta = -0.38$, SE ± 1.62, $P = 0.813$; see Fig. 3c and Table S6). All solvers, regardless of age, solved more problems in each subsequent round (model 6, GLMM: $\beta = 0.81$, SE ± 0.31, $P = 0.009$; see Fig. 3c and Table S6).

Controlled Experiments

Which age marks the onset of innovation?

In all litters ($N = 14$), juveniles visited and interacted with the problem-solving set-ups starting at the age of 18.7 $\pm$ 1.6 days old. However, no juvenile mouse solved a problem, whereas approximately 43% (6/14) adult mothers successfully solved a problem.

Does exposure to solved problems improve future performance?

Except for one adult that was not motivated to participate in the first trial (that is, did not eat the food reward of the control set-up), a total of 86 individuals participated in the controlled experiments, comprising 44 adults (aged 12–30 weeks) and 42 juveniles (aged 30–36 days). All individuals participated in the initial problem-solving trial, where we found that even though more juveniles (18/42, 42.9%) solved at least one of the problems when compared with adult mice (13/44, 29.5%). This was not statistically significant ($\chi^2_1 = 1.1$, $P = 0.29$; see Fig. S1).

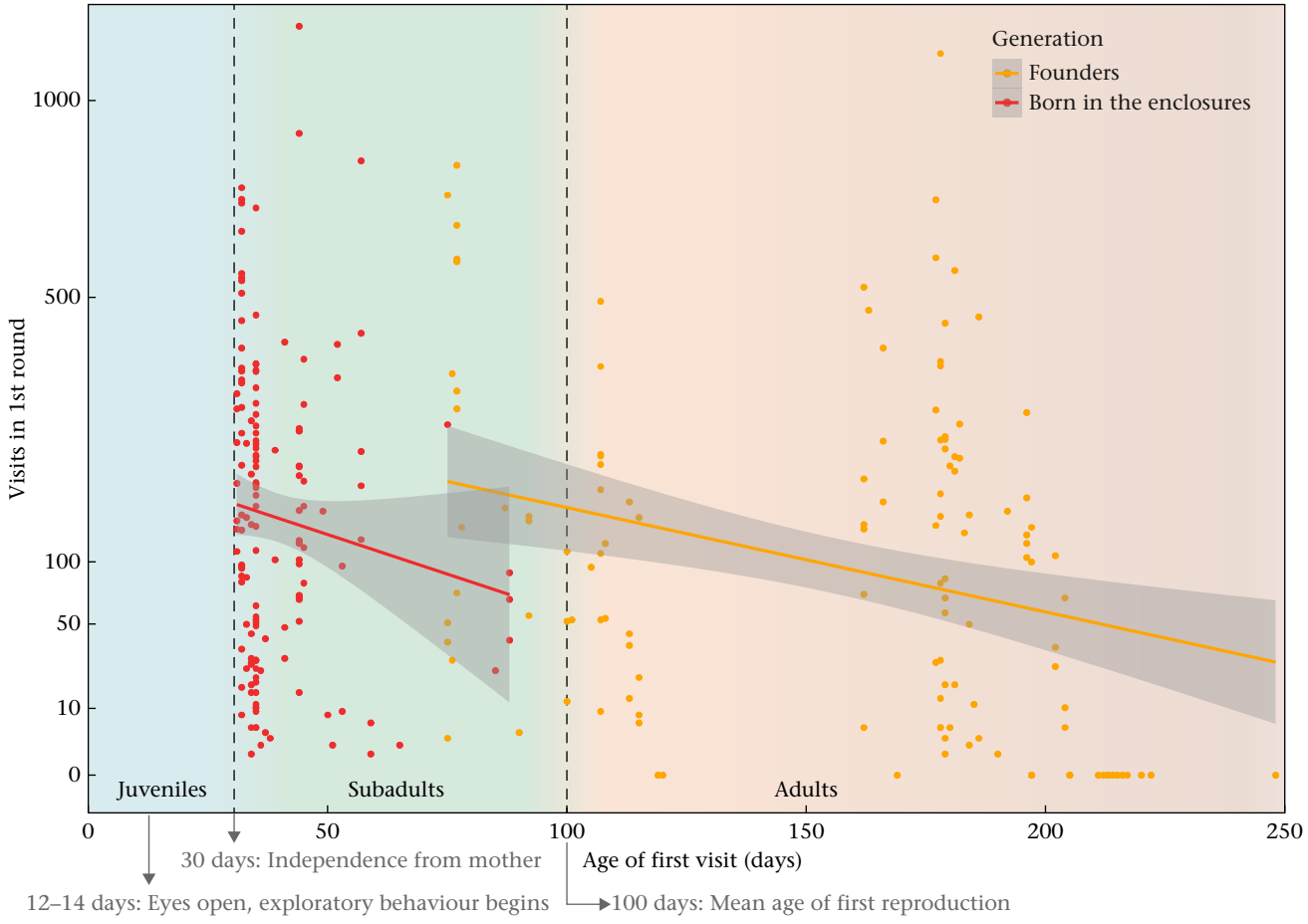

Figure 4. Number of visits (square-root) during the first problem each individual visited throughout their life. Different life stages are shown in different background colours (light blue: birth - weaning, light green: weaning-first reproduction, light red: first reproduction onwards) and age groups are shown in different point colours (orange: founding generation, red: mice born in the enclosures). Linear regressions represent the mean visits for each age group and shading represents the 95% CI for each regression. Axes are in square-root scale.

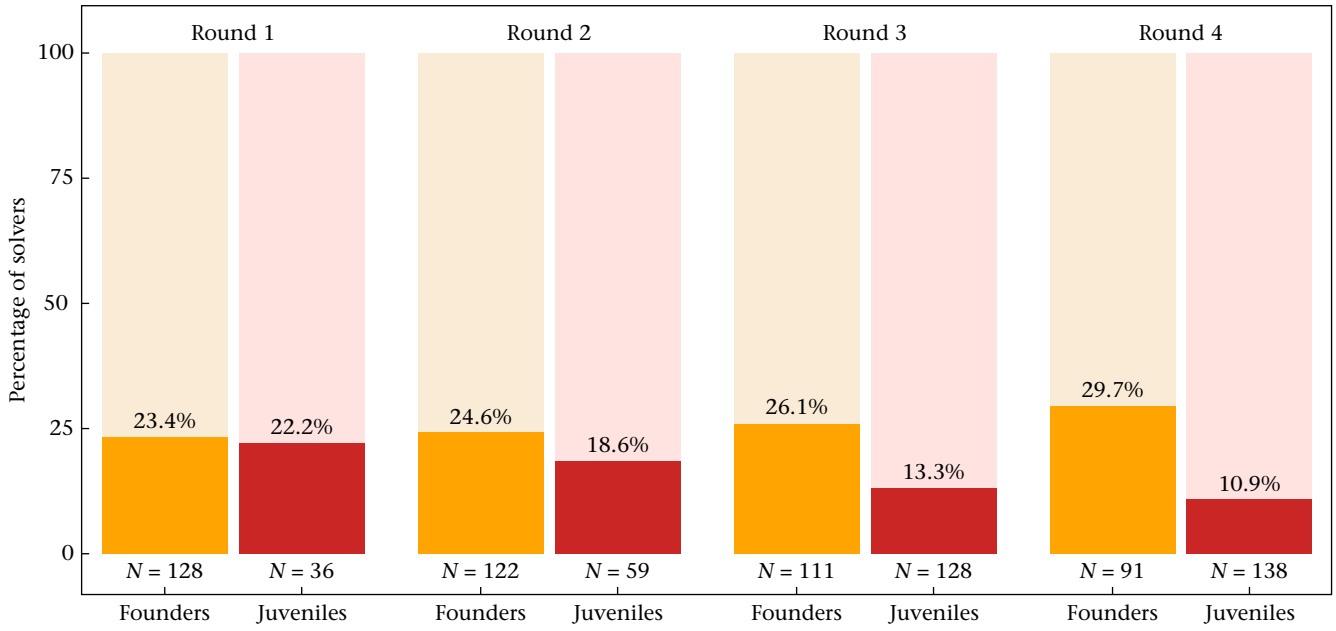

Figure 5. Percentage of solvers in each age group (orange: founding generation, red: mice born in the enclosures/juveniles) for each round of problem solving.

Three adults and four juveniles did not participate in the second trial because of lack of motivation, and all remaining individuals were highly consistent in their performance across the two trials (logit-scale repeatability: R = 0.54, SE ±0.16, $P_{[LRT]} < 0.001$, $P_{[Permutation]} = 0.001$).

The individuals of the 'exposure' group did not improve in the second trial (model 7, GLM: $\beta = 18.93$, SE ±20.69, $P = 0.993$, Table S7), and they showed no improvement in their performance in the second trial when compared with nonexposed individuals (model 8, GLM: $\beta = -1.36$, SE ±0.76, $P = 0.073$; see Fig. S1 and Table S8). Both generations performed similarly in the second trial (GLM: $\beta = -1.15$, SE ±0.76, $P = 0.131$; see Fig. S1 and Table S8).

DISCUSSION

Our study provides insight into the ontogeny of innovative behaviours in wild house mice by examining their performance in voluntary problem solving under seminatural conditions paired with controlled experiments. Our key findings were that (1) certain aspects involved in innovative problem solving such as exploration and active engagement with the test set-ups emerge very early in the development of house mice, essentially as soon as they open their eyes and start exploring their surroundings; (2) in seminatural enclosures, more adults were successfully solving problems, whereas, in a controlled experiment, there was no difference in solving success among age classes; and (3) experience did not help nonsolvers solve problems in controlled conditions but all solvers, regardless of age, solved more problems as they became more experienced in seminatural conditions. Overall, we found a contrasting pattern. In complex seminatural environments, adults were more likely to solve problems. In contrast, under controlled conditions, juveniles and adults perform similarly. We also found that, in the seminatural enclosures, repeated visits improved the future problem-solving performance of mice that were already solvers, regardless of age. These results suggest that the propensity to innovate may vary among individuals and is strongly influenced by the testing condition, whereas experience can improve the performance of those individuals already capable of solving problems.

In many species, innovation propensity increases with age (Amici et al., 2019; Rowell et al., 2021; Rowell & Rymer, 2023; Thornton & Samson, 2012); however, in other cases juvenile and subadult individuals outperform adults (Benson-Amram & Holekamp, 2012; Loepelt et al., 2016; Morand-Ferron et al., 2011). It seems that these conclusions are heavily species- and context-specific (Amici et al., 2019; Rowell et al., 2021; Vezyrakis et al., 2025). While aiming to understand how innovative problem-solving develops, it is often suggested that opposing forces of cognitive and noncognitive factors change throughout an individual's life, leading to differences in performance over different life stages. On the one hand, juveniles are often considered more neophilic, explorative and generally more likely to engage in novel situations (Bishnoi et al., 2021; Lafaille & Féron, 2014; Petelle et al., 2013; Romeo, 2010). On the other hand, cognitive traits such as learning and memory often improve with past experiences. In addition, as individuals accumulate experiences throughout their lives, older individuals perform better in cognitive tasks (Tello-Ramos et al., 2018; Thornton & Lukas, 2012). Our results suggest that changes in innovative problem-solving may not be shaped by age-related changes. Instead, there seem to be inherent individual differences in innovative ability. However, an individual's performance in problem-solving tasks is context-dependent, and the performance of innovators (that is, individuals that already showed spontaneous problem-solving before) improves as they become more experienced.

As innovative behaviour comes with multiple risk–reward trade-offs, particularly exposure to predators and the time invested in innovating, not all individuals assess the reward as worthy of the investment. Being innovative requires individuals to invest time and effort into often uncertain rewards of possibly unknown value while decreasing the time they can spend on reproduction or more conventional resource acquisition. We saw that young mice, very shortly after the age when they open their eyes and explore their immediate surroundings (Brust et al., 2015), were very keen to engage with a novel problem-solving set-up. Then, around the age of weaning, more than 40% were already very capable problem solvers, already performing similar to adults in problem-solving tasks. In this safe and familiar environment, where these missed

opportunity costs are minimized, all individuals seem to be willing to engage with novel problems. These results suggest that some components of innovative problem solving emerge very early in life, rather than suddenly develop during adulthood.

Given that not all individuals continue engaging in problem solving as they age, what drives these differences? The 'bad competitor' hypothesis suggests that these individuals that are willing to take these risks are individuals that, because of their lower competitive abilities, are driven to develop innovative behaviours as an alternative means of acquiring resources (Amici et al., 2019; Laland & Reader, 1999; Reader & Laland, 2003). These innovative behaviours can be entirely novel or the redeployment of a typical behaviour in a novel context, as in both cases they allow animals to access these alternative resources (Ramsey et al., 2007; Reader & Laland, 2003; Tebbich et al., 2016). Our results show that some individuals are good problem solvers consistently throughout their lives and others do not innovate as they, presumably, prioritize other functions rather than innovation (e.g. they invest their time into raising offspring, territorial defence or seeking mates (Bandyopadhyay et al., in press), rather than engaging with the available problems). As such, through repeated exposure, it is only these innovators that improve their performance. This is confirmed by the results of the controlled experiment where targeted, short-term exposure to already solved tests was not enough to help the noninnovators innovate in their second attempt.

More individuals were problem solvers when tested alone, agreeing with our previous findings where even the same individuals dramatically improved their performance when tested alone versus when tested in a dense social setting (Vezyrakis et al., 2025). Because individuals tested in cages did not have to devote their time into other functions outside of problem solving (e.g. raising offspring, territorial defence, seeking mates), the differences between participation and solving-rates in cages versus seminatural enclosures seem to support the 'free time hypothesis' hypothesis (Kummer & Goodall, 1985); when individuals had more time available, they were more likely to problem solve. When tested alone, individuals have ample free time and energy to engage in problem solving. However, in social settings, competition and social hierarchy can hinder innovative problem solving in some individuals more than others.

Here, we find a contrasting age effect. Specifically, adults were better at solving problems in the seminatural enclosures, whereas they performed similarly to juveniles in the controlled experiment. Younger mice visited the problems more than their adult conspecifics in the enclosures; however, their performance was significantly worse. This result supports previous evidence that mice do not monopolize resources, such as the problem-solving boxes (Vezyrakis et al., 2025). A partial explanation may be that the adults, as founders of the populations in the enclosures, experienced a wider range of conditions, although not to the extent that, for example, wild-caught individuals would have possibly experienced. A more compelling explanation is that the adults timed their visits better than the juveniles, who were more likely to visit a problem after it was solved, thus not being able to solve it. This seems to contradict both existing hypotheses (bad competitor and free time hypotheses), which would both agree in predicting that younger individuals are less competitive and have more free time (potentially shown here by them visiting the problems more); therefore, they should be the more competent problem solvers. Our findings suggest that the timely discovery and exploitation of a problem may also be important for problem-solving success.

We also saw that, under both conditions, individuals were consistent in their performance through time: the probability that each individual was a problem solver did not change, either with repeated visits to the problem-solving boxes in the seminatural enclosures or when they were exposed to open problems in the controlled experiment. Instead, even though the overall visit patterns remained stable over time in the seminatural enclosures, we saw that the innovators solved more problems as the experiment progressed. This further supports that an individual's propensity to innovate may be an inherent trait rather than something acquired through repeated exposure or experience. For these inherent innovators, experience may contribute to increasing problem-solving success over the few months of the experiment. Although the social context within the enclosures certainly plays a role in shaping access to problem-solving opportunities, our set-up is not facilitating direct observational learning. All seminatural experiments were conducted under red light conditions, which limit visual cues and make it unlikely that mice could observe the specific actions of their conspecifics. In a previous study (Vezyrakis et al., 2025), mice were predominantly alone while attempting (88%) or successfully solving (93%) these tasks, suggesting that problem-solving behaviour in this context is primarily shaped by individual tendencies rather than observational learning.

Our results do not suffice to claim a full understanding of how, or why, only some individuals seem to often engage in innovative behaviours in the first place. Consistent individual differences may partially explain the heterogeneity we see in innovative performance across individuals, in multiple species (Carere & Locurto, 2011; Griffin & Guez, 2014; Reader & Laland, 2003; Sih et al., 2011), but the mechanisms that drive these differences remain unknown. If innovation is an inherent trait, its development may be shaped by early-life experiences. A few recent studies have examined the ontogeny of problem solving and suggest that early-life experiences direct future behaviours linked with innovation (Garcia et al., 2022; Johnson-Ulrich & Forss, 2025; Rowell & Rymer, 2023). For example, siblings compete for parental resources and space (Hudson & Trillmich, 2008), and this may create the dynamics that require some individuals (perhaps the least competitive, according to the 'bad competitor' hypothesis) to engage in alternative behaviours rather than trying to directly compete with their siblings. Human studies suggest that early social dynamics, such as birth order, may influence future innovation and decision-making (Berisha et al., 2022; Wan et al., 2021), although these aspects are currently underexplored in nonhuman animals.

Conclusions

Our study investigated the effects of age and experience on the innovative problem solving of wild house mice across seminatural and controlled conditions. We found that individual differences in innovative problem solving emerge early in life and remain mostly stable throughout life, with experience not influencing whether noninnovators innovate later in life. Instead, experience improves the performance of individuals that inherently innovate. While juveniles and adults performed similarly in controlled conditions, adults were more successful in seminatural environments, suggesting that testing conditions directly influence how different age groups innovate. It is still unclear how innovative behaviour emerges in each individual, but understanding how early-life experiences impact future behaviours may provide useful insight into the ontogeny of innovation.

Author Contributions

Alexandros Vezyrakis: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources,

Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Valeria Mazza:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **Anja Guenther:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization.

Data Availability

Data are available at OSF: https://doi.org/10.17605/osf.io/8t32u.

Declaration of Interest

The authors declare no competing interests.

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Supplementary Material

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Appendix

How Long Do Mice Remember a Learned Association?

Housing conditions for mice were identical to those described for the controlled experiments in the main text. Animals were kept in same-sex sibling pairs that were briefly separated for the duration of tests.

To evaluate how well wild house mice remember an association between a task and a reward, we tested 30 adults using a simple associative learning task. We then assessed their memory of the learned association after 1 week, 1 month and 3 months.

Each mouse was tested individually, with trials lasting 20 min. In the learning task, we presented three distinct plastic shapes (a star, a triangle and a rectangle, see Fig. S2), each containing a well with a reward inside. The rewards were covered by a mesh, and only the mesh at the correct shape, randomly assigned for each mouse, was removable. Mice were given up to 20 trials to reach the learning criterion of three consecutive correct choices. Trials where a mouse remained inactive were excluded from this count.

Mice that reached the learning criterion proceeded to the memory test. In this test, each mouse was given a single trial to revisit the correct shape from the learning task at three time points. First, they were tested 1 week after completing the learning task. Individuals who succeeded at this step were retested 1 month later, and those who succeeded again were tested a final time 3 months after that. At each stage, we recorded the percentage of mice that made the correct choice and compared it to the proportion expected if the mice would visit one of the shapes by chance using an exact binomial test with the null hypothesis that the choice is made at random.

Out of $N = 30$ adults that participated, 70% (21/30) reached the learning criterion. Of those, 57.1% (12/21) made the correct choice after 1 week. This proportion was significantly higher than expected by chance ($P = 0.02$). However, only 41.7% (5/12) of those individuals made the correct choice 1 month later, a proportion not significantly different to the one expected by chance ($P = 0.37$). Finally, none of these $N = 5$ individuals made the correct choice when tested 3 months later.

Therefore, we conclude that wild house mice can remember learned associations (between a food reward and an artificial object) in the short term, approximately 1 week, but these associations are not maintained for longer time periods.