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Alternative reproductive tactics affect spatial cognition and innovative problem solving in male house mice

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Male alternative reproductive tactics (ARTs) are distinct behavioural mating strategies that members of this sex follow. While these strategies lead to observable differences in behaviour, it remains unclear whether such differences arise from how individuals allocate their time or reflect true intrinsic differences in ability. To address this, we examined the relationship between two ARTs (territoriality or roaming) and problem solving, space use, spatial cognition and social interaction in male house mice, *Mus musculus domesticus*. Combining observations from seminatural enclosures and controlled laboratory experiments, we tested 72 adult males following one of the two tactics, identified as either 'territorial' or 'roamer'. We found that ARTs influenced space use and problem solving only under ecologically relevant conditions. Specifically, in the seminatural enclosures, roamers visited more and spent more time near novel problems, leading them to be more likely to solve them, as well as exhibiting greater tolerance towards conspecifics compared to territorials. Territorials, on the other hand, engaged in more competitive interactions but limited their exposure to problem-solving opportunities. Under controlled conditions, ARTs showed no differences in spatial learning, problem solving or persistence in engaging with problems, showing that these differences probably exist due to the ecological constraints imposed by the social environment on individuals following different ARTs. Overall, while roamers solved more problems, this probably reflected their higher encounter rate with problems, rather than inherent differences in problem-solving ability. These findings highlight the importance of the ecological and social context when studying the link between behavioural polymorphisms, such as ARTs, and complex traits such as innovative problem solving or cognition.

Male alternative reproductive tactics (ARTs) are distinct male mating strategies that coexist within the same population. Typically, some males defend territories and monopolize access to females ('territorials'), while others forego territorial defence and instead attempt to exploit these investments through 'sneaky' or opportunistic matings ('roamers' or 'sneakers'). While territoriality often confers fitness benefits, such as increased reproductive success (Da Silva et al., 2025), it also entails significant costs (Ord, 2021), such as substantial time and energetic investment.

Although recent research has highlighted the complexity of multiple interacting factors in maintaining ARTs (Darmis et al., 2025), their adoption is still primarily mediated by differences in competitive ability in many taxa (Taborsky, 2008). Larger, dominant males typically defend territories, while smaller, less competitive males adopt roaming or 'sneaking' tactics to avoid costly aggressive interactions (Schradin, 2022; Schütz et al., 2010). For example, in rodents such as house mice, *Mus musculus domesticus*, African striped mice, *Rhabdomys pumilio*, and prairie voles, *Microtus ochrogaster*, competitive ability, often quantified by body mass or age, is positively correlated with territorial defence and the monopolization of females (Darmis et al., 2025; Rice et al., 2022; Schradin, 2008).

A direct consequence of adopting a specific tactic is the emergence of differences in responsibilities, space use and time

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budgets. Territorial males must devote substantial time to a restricted area, defending resources and chasing off competitors to maintain paternity (Ophir, 2017; Shuster & Wade, 2003). In contrast, roamers range widely across territories in search of receptive females (Ophir, 2017). These differences in responsibility, spatial behaviour and free time availability generate distinct time-use patterns between tactics. In turn, such differences can shape other traits that depend on time investment or that are constrained by limited time (Dunbar et al., 2009), such as 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).

Two hypotheses may explain how initial differences in competitive ability, which mediate the adoption of ARTs, in turn cascade into differences in time availability, and can affect behaviours such as innovation: the 'free time' (FT) and the 'bad competitor' (BC) hypotheses. According to the former (Amici et al., 2019; Kummer & Goodall, 1985), individuals are more likely to engage in behaviours that are not directly linked to survival and reproduction (such as exploration and innovation) when they have extra time and energy beyond what is required for their basic needs. In contrast, according to the latter, individuals with lower competitive ability are more likely to seek alternative resources out of necessity (Amici et al., 2019; Laland & Reader, 1999; Reader & Laland, 2003). Because ARTs are closely tied to both competitive ability and time allocation, these frameworks predict that roamer males (who are considered worse competitors, and spend less time on territory defence and more time navigating) should be more likely than territorials to engage in innovative problem solving and perform better in innovative tasks. Importantly, while both hypotheses predict that roamers should be the better innovators, this is hypothesized to be through different mechanisms: the 'bad competitor' hypothesis predicts that they would perform better out of necessity, as they seek out alternative ways to access resources, while the 'free time' hypothesis predicts that they would perform better because they have more surplus time that can be invested in innovative problem solving.

Indeed, a few studies have examined the cognitive differences associated with ARTs (Rochais et al., 2021, 2023) but, to our knowledge, they have mostly been limited to field observations with almost no controlled laboratory experiments. For example, in Cape ground squirrels, *Xerus inauris*, roamers are less competitive than territorials but occupy broader home ranges, which increases their likelihood of encountering and solving novel problems (Scantlebury et al., 2008). However, it remains unclear whether these differences in problem solving reflect intrinsic abilities, such as navigation, problem solving or cognitive skill, or simply arise as a consequence of ecological and social constraints. Roamers and territorials may have similar cognitive abilities, but differences in their responsibilities could affect how they allocate time to behaviours such as problem solving. To address this question, combining observations under natural conditions with controlled experimental approaches, such as direct measurements of problem solving and cognition, can help disentangle the relationship between ARTs and traits such as innovative problem solving and spatial cognition.

In the present study, we investigate how ARTs affect innovation (by measuring innovative problem-solving performance), spatial learning (i.e. cognition) and space use in wild house mice, *M. m. domesticus*, across two conditions: in seminatural enclosures and in a controlled experimental setting. House mice are an ideal species to study ARTs as their social structure is characterized by a polygynous deme formation (Drickamer, 2001) with males flexibly switching between territoriality and roaming mostly based on their competitive ability (Darmis et al., 2025). Additionally, they are well suited to study innovation and cognition, as they have spread globally and have quickly adapted to novel environments through their behavioural flexibility. They can be accurately studied for both innovative problem solving in a foraging context as well as spatial learning using established tests (Delacoux & Guenther, 2023; Gorshkova et al., 2024; Vrbanec et al., 2021). They can also be studied both in controlled laboratory and in seminatural conditions that mimic their natural environment, allowing for high ecological validity (König & Lindholm, 2012; König & Lindholm, 2012; Lopez-Hervas et al., 2024).

First, we assigned the mice to one of two groups according to tactics adopted (either 'roamer' or 'territorial'), and then assessed the problem-solving performance of males following different ARTs in a battery of voluntary food-rewarded tasks presented directly in the seminatural enclosures. To complement these tests, we then examined a subset of the same males under controlled conditions, where they were individually tested for problem solving and spatial learning. This dual approach allowed us to evaluate whether the patterns observed in the socially and ecologically complex enclosures persist when social and ecological dynamics are removed. We hypothesized the following: in the enclosures (1) roamers would range more widely than territorials in search of receptive females; (2) roamers would be more likely to problem solve than territorials, consistent with both the 'bad competitor' hypothesis (they must compensate for lower competitive ability) and the 'free time' hypothesis (they are freed from mate guarding and territory defence and thus have more time to engage with problems); (3) tactics would differ in interactions with conspecifics, with territorials expected to show higher aggression, whereas roamers would be more likely to tolerate other individuals in problem-solving boxes and avoid unnecessary conflicts; and in the controlled conditions (4) if problem solving and cognitive differences between tactics are intrinsic, rather than emerging from the ecology of ARTs, roamers would outperform territorials in spatial learning.

METHODS

Animals and Housing

We set up four replicated seminatural enclosures (19.6 m^2 each) into which were released $N = 139$ adult wild house mice, all aged 50–100 days: in three enclosures, $N = 35$ (20 females, 15 males), while in one enclosure, $N = 34$ (20 females, 14 males). These founders were descendants of wild-caught individuals from the Cologne/Bonn region, Germany. Each enclosure contained woodchip bedding, nesting material (cotton rolls, toilet paper) and 13 nestboxes where mice were free to build nests and breed. All nests were equipped with radio frequency identification (RFID) readers (FBI systems, Viersen, Germany, https://fbiscience.com/wp/) at their entrances. Equally distributed in each enclosure, we placed nine feeding stations where mice could access food (Altromin 1324, Germany, https://altromin.com) and water ad libitum. Temperature and light–dark cycle varied naturally, but light was supplemented between 0800 hours and 1700 hours, and underfloor heating prevented temperatures dropping below 10 °C. Enclosures were covered by a roof, inaccessible to predators and generally designed to mimic the natural conditions under which house mice would establish a colony, such as in a barn (König & Lindholm, 2012; Lopez-Hervas et al., 2024). These seminatural enclosures are an established system for wild house mouse colonies, leading to close-to-natural population development and social and genetic structure, and thereby allowing mice to exhibit their natural behaviours (Lopez-Hervas et al., 2024; Prabh et al., 2023; see Figs. A1 and A2 for a photo and a schematic layout of

the enclosures). During monthly monitoring, experienced animal caretakers conducted population checks, combined with cleaning of enclosures, starting early in the morning to record body mass and reproduction and to replace bedding for animal wellbeing. Each monitoring lasted a few hours, depending on the population size, during which all mice were caught and weighed, and new individuals (weight > 10 g) were fitted (by restraining the mice briefly) with RFID transponders (ISO Transponders, PlanetID, https://www.planet-id.com) for individual identification. No behavioural data were collected throughout this monitoring. For all following analyses concerning the seminatural enclosures, we used a subset of individuals with stable tactics for 3 months (N = 38: territorial = 19, roamers =19; for more details see Tactic Assignment, below). Six months after the start of the enclosures, when the founding generation was 7–10 months old, we moved individuals from two enclosures (N = 34: territorial = 12, roamers = 22) based on their latest tactics (see Tactic Assignment) to standard Makrolon Type III cages (382 × 220 mm and 150 mm high) for controlled experiments. The cages had woodchip bedding and contained a shelter (e.g. egg cartons), nesting material (e.g. toilet paper) and physical enrichment. Since adult males are aggressive towards other males, all animals were housed singly. Cages were maintained in the same light–dark and temperature conditions as the enclosures, with food (Altromin 1324, Germany) and water ad libitum. A schematic representation of the experimental timeline is shown in Fig. A3.

Tactic Assignment

We assigned adult males to one of two tactic groups ('territorial' or 'roamer') according to behaviours observed, using two techniques (RFID or location during monitoring) that yield identical results, following the processes described in Darmis et al. (2025). We used the appropriate technique for each part of the study (longitudinal measurements using the RFID data for the time the individuals were in the enclosures and their last known tactic from the monitoring data right before they were transferred to cages).

For all metrics in the seminatural enclosures, we used the continuous data collected by the RFID readers at the entrances of the nests. In short, all 13 nestboxes in each enclosure were equipped with RFID antennae that recorded data from the transponders of the mice as they entered and exited. In this way, we recorded the amount of time each mouse spent inside each nest and the number of nests they visited. For each nest, we assigned the adult male that spent the most time in that specific nest as territorial. All males that spent less than half of the time of the territorial male in that nest were assigned as roamers whereas males that spent more than half of the territorial male's time in the nest were not assigned a tactic and were not included in the study. This technique allowed us to quantify which individual was a territorial or a roamer over a long period of time (i.e. at least 3 months).

For the controlled experiments, we used the last known tactic each individual followed at the last monitoring (i.e. when they were removed from the enclosures and transferred to cages). To obtain the last known tactic, we used a second assignment procedure as described in Darmis et al. (2025). In short, during monitoring, when we enter each enclosure to collect data about the population, the territorial males typically retreat to their nests and deny entrance to mice not belonging to the family, whereas roamers usually remain outside. Those territorial males are heavier than roamers, and consequently the heaviest male caught in each nest was identified as territorial.

Problem-Solving and Spatial Cognition Tests

Seminatural enclosures

One month after introducing the mice into the seminatural enclosures, we started testing their problem-solving abilities using a battery of four different problem-solving set-ups previously used for small rodents (see Mazza & Guenther, 2021; Vrbanec et al., 2021). These involved (1) an omnidirectional slider (54 × 54 mm and 40 mm high), (2) an inverted cup (36 mm diameter, 32 mm height), (3) a one-directional slider (63 × 121 mm and 10 mm high) and (4) a Petri dish (80 × 123 mm; for all set-ups, see Fig. 1a). Each set-up required a single movement to access a food reward, and all mice could participate regardless of their age or physical size. 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. All these tasks could be solved either through trial and error or using more insightful approaches (Hohlbaum et al., 2024; Mazza et al., 2025). Each set-up was baited with a dried mealworm (*Tenebrio molitor* larva), which was a novel food source at the start of the experiment, and generally highly attractive for mice. The mice could voluntarily enter the testing boxes and engage with the set-ups. In each testing round, one of the set-ups was presented in five problem-solving boxes (same set-up in each box) for 2 h per night over 5 nights (following a regime of 2 consecutive testing nights, then a break of 5 nights to boost motivation, then 3 more nights of testing; Fig. A3), and there was a minimum gap of 2 weeks between testing rounds. There were four testing rounds in total, one for each set-up. For each testing night, the five problem-solving boxes were placed at specific locations in each enclosure, in the open spaces between nestboxes (Fig. A2). The surfaces of the problem-solving boxes were covered with bedding taken from the exact location where the box was placed to ensure consistent olfactory cues. Each box had a single entrance with an RFID antenna (EuroID, Netherlands, https://www.euroid.com) to track when mice entered or exited. On each testing night, the boxes were introduced into the enclosures at least 1 h after sunset and left for 2 h. During this time, activity in and around the boxes was recorded (using a Panasonic HC-V 180 camera, https://www.panasonic.com; see Data Availability, Video 1, for an example of a mouse solving a problem, recorded by a camera set up beside each problem-solving box on an extended tripod to provide a top-down view. In total we used five cameras to record all five problem-solving boxes). After the 2 h window, the boxes and set-ups were removed (for detailed protocol, see Vezyrakis et al., 2025). To assist with video analysis, the RFID readings from the antennas were synchronized with the video footage and embedded as subtitles, allowing us to identify the mice in real time. We followed each focal individual for up to a total of 1 h, within the 5 nights of each testing round. For each individual, we analysed their behaviour during the first three set-ups (testing rounds) they encountered in their lives, to account for some individuals being born later into the experiment. During this time, we recorded the following: (1) the time spent by each mouse inside each problem-solving box, per testing round (the time difference in seconds between the RFID reads of the mouse entering and leaving the box; for analyses, these values were converted to minutes); (2) the number of different problem-solving boxes visited by each mouse, per testing round (number of unique problem-solving boxes visited per round, confirmed by RFID detections); (3) whether or not the mouse successfully solved each set-up (defined as opening the set-up and accessing the food reward); and (4) the number of interactions when another mouse was present in the problem-solving box, for each tactic.

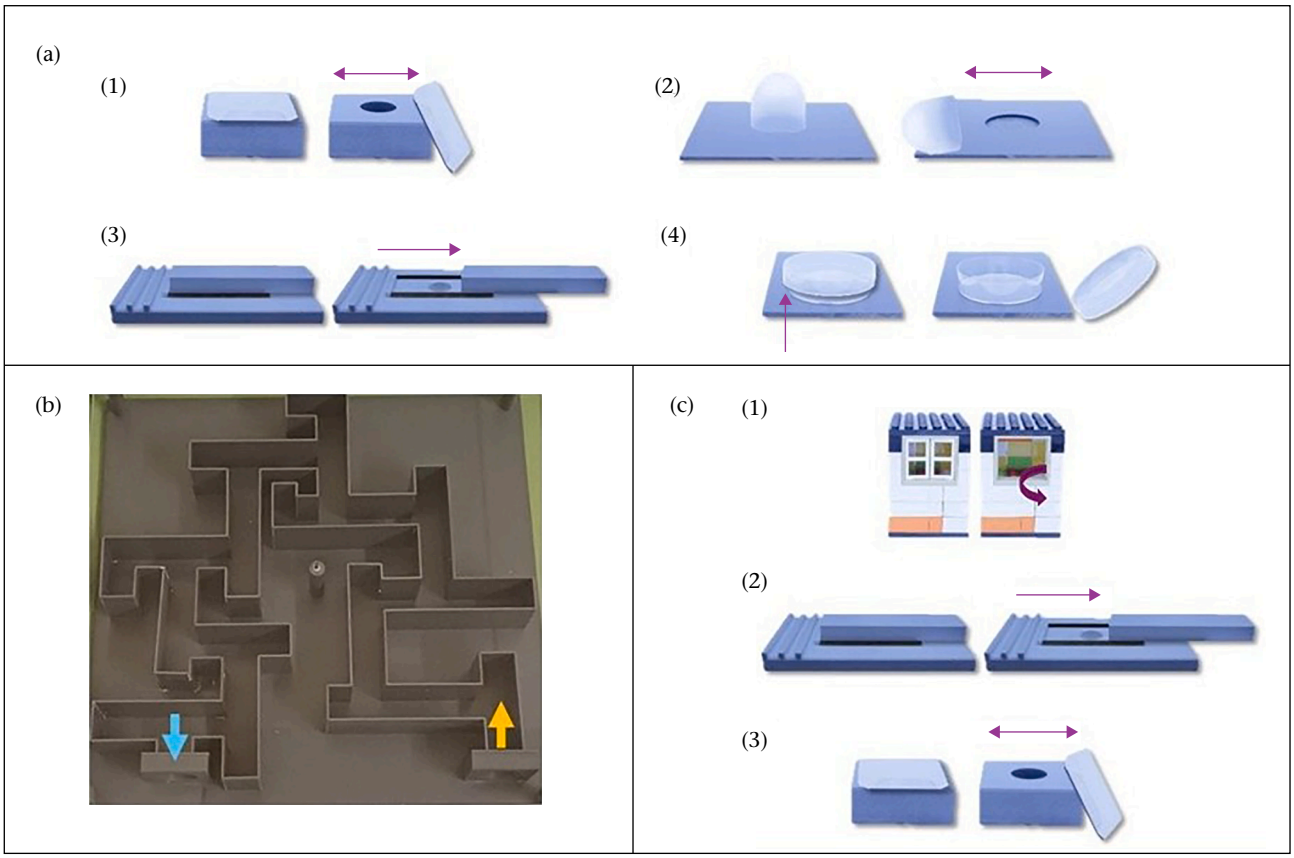

Figure 1. (a) Problem-solving set-ups used in the seminatural enclosures: (1) omnidirectional slider, (2) inverted cup, (3) one-directional slider and (4) Petri dish. (b) Maze used for spatial learning. Arrows indicate the entrance (black box position, shown in yellow) and exit (home cage position, shown in blue) of the maze. (c) Problem-solving set-ups used in the controlled experiment: (1) Lego house, (2) one-directional slider, (3) omnidirectional slider. In (a) and (c) each set-up is shown in the closed/unsolved state on the left and the open/solved state on the right. Purple arrows show the direction of force required to open each of them.

Interactions were classified as aggressive (behaviours such as chasing or fighting) or neutral (at least two individuals coexisting in the box while showing social tolerance).

Controlled conditions: spatial learning

One month after habituation to the cages, we tested spatial learning performance using a complex maze, following the protocol established by Delacoux and Guenther (2023). The maze was dark grey, poorly illuminated, relatively small (154 cm long) with narrow corridors (5 cm wide), and covered by a Plexiglas lid (Fig. 1b). To begin each trial, a small black box (15 × 10 cm), which mice readily enter as it provides a dark and safe environment, was placed at the end of each individual's home cage. Once the focal individual entered, the box was placed at the starting point of the maze, while the focal individual's home cage was positioned at the maze exit. Each individual had 10 trials on consecutive days (one trial per day). All individuals voluntarily participated in the trials, with no physical contact from the experimenter. If an individual did not enter the maze within 5 min of trial onset, the trial was discarded, not included in the analysis, and the mouse was returned to its home cage. We video recorded each trial from above (using a Panasonic HC-V 180) until the mouse successfully reached its home cage, and there was no time limit imposed on the experiment (see Data Availability, Video 2, for a camera view). The videos were later analysed using BORIS (Friard & Gamba, 2016), recording the following behaviours for each trial: (1) latency (time taken to leave the starting box and enter the maze, measured in s; entry was defined by all four paws touching the maze), (2) time to complete the maze (time until all four paws of the mouse entered the home cage, measured in s) and (3) number of mistakes (number of times the mouse's snout entered a dead-end within the maze).

Controlled conditions: problem solving

The day after completing all spatial learning trials, we habituated each mouse to three problem-solving set-ups and food rewards (mealworm, oats and dried mango). When each individual successfully ate three times from an open plate, it was presented with an open problem (solved) with the same rewards. After eating three times, individuals were presented with a closed set-up that they needed to solve to access the rewards. Each individual followed the above process for each of these three problems consecutively: (1) Lego house (47 × 48 mm and 65 mm high, with a window opening 30 × 30 mm in the front; the mice needed to open the window outwards to access the reward); (2) one-directional slider (63 × 121 mm and 10 mm high; mice had to push or pull the white block in one direction); and (3) omnidirectional slider (54 × 54 mm and 40 mm high; could be solved by pushing, sliding or pulling the metal lid in any direction). All set-ups had been previously used with house mice (Vrbanec et al., 2021) and are shown in Fig. 1c. As for the seminatural experiment, all these tasks could be solved either through trial and error or because the mice understood how the mechanism worked (i.e. showed insight), regardless of their age or physical size (Hohlbaum

et al., 2024; Mazza et al., 2025). We video recorded from above the performance of each mouse with the closed set-up for 1 h (using a Panasonic HC-V 180; see Data Availability, Video 3) and analysed the following behaviours using BORIS: (1) latency to first touch the set-up (in s), (2) number of targeted touches (any physical contact, using any body part, with the movable parts of the set-up that could lead to a solution) and (3) outcome of the trial (whether the problem was solved or not).

Statistical Analyses

All statistical analyses were conducted using R version 4.2.2 (R Core Team, 2022). We ran (generalized) linear mixed-effects models (GLMMs) using the package lme4 (Bates et al., 2015). Overdispersion in models was checked using the check_overdispersion function of the performance package (Lüdecke et al., 2021). For all models involving seminatural experiments (that is, models 1, 2 and 3), year and enclosure were initially included as fixed effects but were sequentially removed as they explained no variation in the respective response ($P > 0.05$). All model outputs are presented in Table 1.

Seminatural enclosures

To understand if territorials and roamers differed in solving success, we performed a chi-square test comparing the proportion of solvers (individuals that solved at least one problem) between

Table 1
Full model outputs for (generalized) linear mixed models 1–5

Predictor	Estimate (Log-Mean/Odds)	SE	CI	*P*
Model 1: Number of problem-solving boxes visited				
(Intercept)	0.38	0.14	(0.11, 0.65)	**0.005**
Tactic [territorials]	−0.41	0.2	(−0.80, −0.02)	**0.042**
σ2	0.58			
τ00	0.10_{ID}			
ICC	0.15			
N	38_{ID}			
Observations	114			
Marginal R2 / Conditional R2	0.058 / 0.199			
Model 2: Time spent in problem-solving box (min)				
(Intercept)	1.25	0.15	(0.96, 1.55)	**<0.001**
Tactic [territorials]	−0.49	0.23	(−0.93, −0.04)	**0.031**
(Zero inflated model intercept)	−0.37	0.23	(−0.82, 0.07)	0.102
Random effects				
σ2	0.02			
τ00	0.16_{ID}			
ICC	0.87			
N	38_{ID}			
Observations	114			
Marginal R2 / Conditional R2	0.247 / 0.905			
Model 3: Aggression/Tolerance				
(Intercept)	−10.38	4.34	(−18.87, −1.88)	**0.017**
Tactic [territorials]	20.65	6.49	(7.94, 33.36)	**0.001**
Random effects				
σ2	3.29			
τ00	0.00 (ID1) / 488.75 (ID2)			
ICC				
N	16 (ID1) / 23 (ID2)			
Observations	44			
Marginal R2 / Conditional R2	0.966 / NA			
Model 4: Number of targeted touches				
(Intercept)	3.03	0.18	(2.67, 3.39)	<0.001
Tactic [territorials]	−0.37	0.22	(−0.79, 0.06)	0.09
Problem type [lid]	−0.56	0.22	(−1.00, −0.12)	**0.012**
Problem type [sliding]	−0.13	0.23	(−0.57, 0.31)	0.571
Random effects				
σ2	0.57			
τ00	0.07_{ID}			
ICC	0.1			
N	34_{ID}			
Observations	98			
Marginal R2 / Conditional R2	0.123 / 0.213			
Model 5: Latency to approach				
(Intercept)	0.27	0.40	(−0.51, 1.05)	0.494
Tactic [territorials]	−0.73	0.46	(−1.63, 0.17)	0.113
Problem type [lid]	−0.86	0.53	(−1.90, 0.17)	0.100
Problem type [sliding]	0.72	0.52	(−1.74, 0.30)	0.165
Random effects				
σ2	3.29			
τ00	0.00_{ID}			
ICC	0.16			
N	34_{ID}			
Observations	98			
Marginal R2 / Conditional R2	0.075 / NA			

Statistically significant results ($P<0.05$) are shown in bold.

the ARTs. We performed this analysis using only those individuals that visited at least one set-up and using only one measurement per set-up for every individual. Thus, repeated solutions of the same set-up did not contribute to this measurement.

To understand if there is a difference in space use in the seminatural enclosures between roamers and territorials, we first used a GLMM with a Poisson distribution (model 1, Table 1) with the number of RFID recorded visits as the response variable, the individual tactic as the fixed effect and male ID as the random effect. Next, we built a linear mixed model (LMM; model 2, Table 1) using the time individuals spent in the boxes (in min) as the response variable, the tactic as the fixed effect and male ID as a random effect to analyse space use and especially persistence (i.e. time spent inside the problem-solving boxes).

Further, to understand if there is a relationship between tactic and social interactions, we ran a GLMM with a binomial distribution (model 3, Table 1), with the behaviour type as the response variable (aggression or tolerance), the focal individual's tactic as the fixed effect and the individual IDs of the focal and the target individuals as random effects.

Controlled conditions: spatial learning

We then analysed if spatial learning performance in the controlled experiment differed between roamers and territorials. In the first trial in which every individual actively participated, we compared the two tactics using Wilcoxon rank sum tests, as the data were not normally distributed: (1) the latency to enter the maze; (2) the time needed to solve the maze; (3) the number of mistakes. Additionally, we quantified the best trial for every individual in terms of latency to enter the maze, time needed to solve the maze and mistakes made (i.e. the trial with the lowest latency to enter, shortest time to navigate the maze and fewest mistakes). From this, we compared the two tactics in terms of the trials needed for mice to reach their best trial in the above three metrics. As our goal was to characterize differences in exploratory behaviour, rather than to quantify learning per se, we summarized performance using the first and best trial for each individual to capture biologically meaningful variation.

Controlled conditions: problem solving

As for the seminatural enclosures, we performed another chi-square test to compare the proportion of solvers and nonsolvers between the two tactics, using their overall performance in the controlled conditions. All individuals who solved a problem at least once were characterized as solvers, while those that never solved a problem in the controlled conditions were characterized as nonsolvers.

To investigate potential differences in persistence between the territorials and roamers in the controlled environment, we used the number of targeted touches as a response variable in a GLMM assuming a negative binomial log link distribution (model 4, Table 1) and individual tactic as a predictor. The type of problem was further included as a fixed effect to account for variation in contact initiation due to differences in the problem type and ID was included as a random effect. For this model we chose to proceed with a negative binomial distribution because the Poisson model showed overdispersion.

Lastly, we wanted to assess whether individuals following different tactics differed in their latency to approach each problem. For this, as the distribution of the values was highly skewed, we divided individuals into two groups, those that initiated the first contact before the population median and those that did so after, for each one of the three problems. Thus, for every individual and for each problem, we had a binary value of 0 if their latency was smaller or equal to the median and a value of 1 if their latency was higher than the median. Consequently, we built a binomial GLMM (model 5, Table 1) with this binary latency value as the response variable, the tactic and the problem type as fixed effects and the individual ID as the random effect. We also repeated the analysis using the mean instead of the median, but the model output remained the same showing no effect of tactics or problem type on latency to approach a problem.

Ethical Note

All experiments conformed to the ASAB Ethical Committee/ABS Animal Care Committee (2025) guidelines for animal experiments and were carried out under licence V244-57612/2022(43-4/19) issued by the Ministerium für Energiewende, Landwirtschaftliche Räume und Umwelt, Kiel. The keeping and breeding of mice were approved and are regularly monitored by the Veterinäramt Plön under permit 1401-144/PLÖ-004697. All animals used in this study were descendants of wild-caught individuals and were born and raised under the conditions described above. The experiments were entirely voluntary, with no handling or trapping involved. The seminatural enclosures provided an established system allowing mice to exhibit natural behaviours (Prabh et al., 2023), and population size was maintained well below the carrying capacity. To maintain an environment as natural as possible, we did not interfere with any aggressive interactions or other natural behaviours between territorials and roamers. The animals were completely free to behave as they would in the wild. During monthly monitoring, the mice were removed from the seminatural enclosures together with their nestboxes (whenever we entered the enclosure, they would typically run into their respective nests on their own), taken out of their nestbox by tube handling and weighed, and newly identified individuals (weighing more than 10 g) were fitted with RFID transponders (ISO Transponders, PlanetID, https://www.planet-id.com) for individual identification. The transponders were inserted subcutaneously into the loose skin flap at the back of the neck by experienced animal caretakers. The procedure took less than 10 s, caused minimal disturbance and the wound typically did not bleed and closed within minutes, with no recorded injuries or deaths. The entire monitoring process took approximately 30 seconds per mouse, after which they were briefly placed into a mouse cage with a shelter, food and water until the process was completed for the whole family. Thereafter, the house and the whole family were placed back into the place from where they were collected.

For the controlled experiments, male mice were singly housed in enriched cages containing nesting material, shelters, an elevated perch and a running wheel. During the controlled condition experiments, all procedures were carried out directly in the room where the mice were housed. Problem-solving tasks were conducted in the home cage following habituation to ensure the animals were not stressed. The spatial learning experiment was conducted in a narrow, covered grey maze with dimensions that allowed the mice to feel the walls with their whiskers. To transfer mice from their home cage to the maze, we placed their home cage (opened) inside a larger changing box together with a small black box with a single entrance. Since the black box was darker and more enclosed, the mice voluntarily entered it without any handling or force. This design simulated a confined and safe space, helping reduce stress during testing (Delacoux & Guenther, 2023; Vrbanec et al., 2021). All animals from the seminatural experiments remained alive for further studies. In contrast, animals from the controlled experiments were killed for organ collection for further experiments outside the present work, under permit number 1400, as approved by the animal welfare officers of Kiel University. At the end of the controlled experiments, 34 mice were

euthanized one at a time in a CO_2 chamber. Each individual was euthanized directly in its home cage, with no other animals present in the room to avoid distress. Reflexes (e.g. eye and paw twitch) were checked after euthanasia to confirm brain death before organ collection.

RESULTS

We used 38 male mice (19 territorials and 19 roamers) for the seminatural experiments and 34 male mice (12 territorials and 22 roamers) for controlled experiments.

Seminatural Enclosures

In the seminatural enclosures, approximately 16 % (6/38) of the individuals solved at least one problem. A higher proportion of roamers were solvers when compared to territorials (mean ± SD: territorials: 0.05 ± 0.05, roamers: 0.32 ± 0.11; $\chi^2_1 = 4.37$, $N = 38$, $P = 0.036$; Fig. 2).

There was a significant difference in space use between the tactics as roamers visited more problem-solving boxes per testing round (model 1, mean ± SD: territorials: 1.02 ± 0.668, roamers: 1.54 ± 1.38; GLMM: $\beta = -0.41$, SE = 0.20, $P = 0.042$; Fig. 3a).

Additionally, $N = 45$ social interactions took place and there was a strong statistical association between tactic and the type of social interaction (mean ± SD: territorials: 15.5 ± 13.44, roamers: 7 ± 7.07; $\chi^2_1 = 15.039$, $N = 45$, $P < 0.001$; Fig. 3b). Inspection of residuals revealed that territorials engaged in significantly more aggressive events than roamers, which were significantly more 'tolerant' (i.e. engaged in significantly fewer fights).

In the enclosures, roamers spent significantly more time in the problem-solving boxes (model 2, mean ± SD: territorials: 1.23 ± 1.79 min, roamers: 2.44 ± 2.85 min; LMM: $\beta = -1.21$, SE = 0.46, $P = 0.009$; Fig. 4a).

The complete results of all models are summarized in Table 1.

Controlled conditions: spatial learning

Two roamers and one territorial did not participate in more than half of the trials and were thus excluded from further analysis. Roamers navigated the maze faster than territorials in their first trial (mean ± SD, roamers: 37.4 ± 32.4 s, territorials: 106.1 ± 114.8 s, $W = 61.5$, $P = 0.048$) but the two tactics did not differ in their latency to enter the maze or in the number of mistakes made during that first trial (latency to enter the maze: $W = 66$, $P = 0.072$, number of mistakes: $W = 92.5$, $P = 0.48$). There was also no significant difference in the number of trials needed to reach their best performance (trials to lowest latency to enter: $W = 109$, $P = 0.98$; trials to fastest trip: $W = 117$, $P = 0.79$; trials to fewest mistakes: $W = 114.5$, $P = 0.87$; Fig. A4).

Controlled conditions: problem solving

Approximately 70 % (24/34) of the mice in the controlled experiment solved at least one problem. When examining the proportion of solvers (individuals that solved at least one problem), there was no significant difference between tactics in the controlled experiment (mean ± SD: territorials: 0.75 ± 0.13, roamers: 0.68 ± 0.10; $\chi^2_1 = 0.17$, $N = 34$, $P = 0.68$; Fig. 2b).

There was also no difference between the tactics in the number of targeted touches (mean ± SD: territorials: 12.2 ± 9.44, roamers: 17.9 ± 14.3; model 3, $\beta = -0.37$, SE = 0.22, $P = 0.09$; Fig. 4b). Finally, there was no effect of tactic on the latency to touch each problem for the first time (model 4, mean ± SD: territorials: 46.6 ± 126 s, roamers: 62.3 ± 112 s; GLMM: $\beta = -0.73$, SE = 0.46, $P = 0.113$; Fig. 4c).

DISCUSSION

In this study, we explored the link between alternative reproductive tactics (ARTs), problem solving and spatial cognition in male wild house mice using seminatural and controlled experiments. We found differences between reproductive tactics in spatial cognition and problem solving, but, crucially, effects depended on the experimental conditions: while there were no differences in problem-solving performance under controlled conditions, in the seminatural enclosures, roamers were more likely to solve problems. In the enclosures, roamers visited more problem-solving boxes and spent more time inside them, while they were also more tolerant to conspecifics compared to

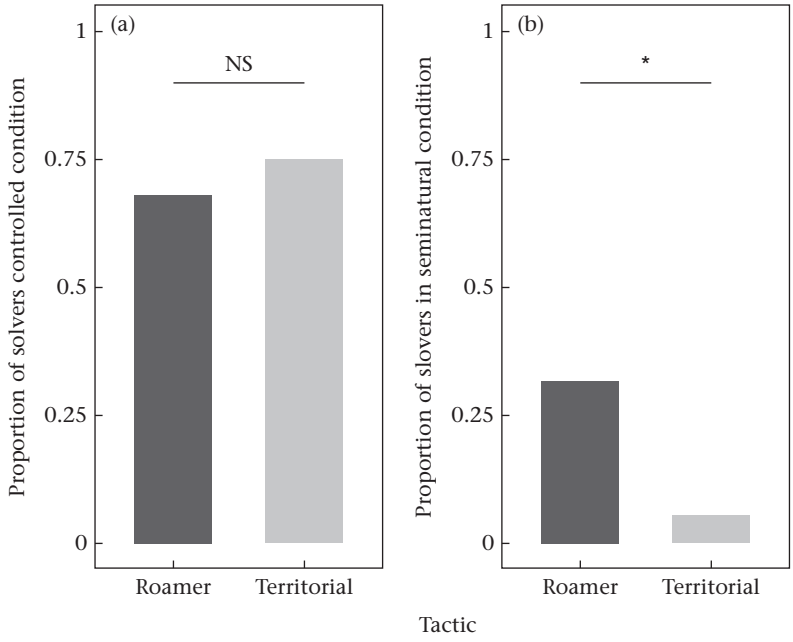

Figure 2. Proportion of solvers in (a) controlled and (b) seminatural conditions. *$P < 0.05$.

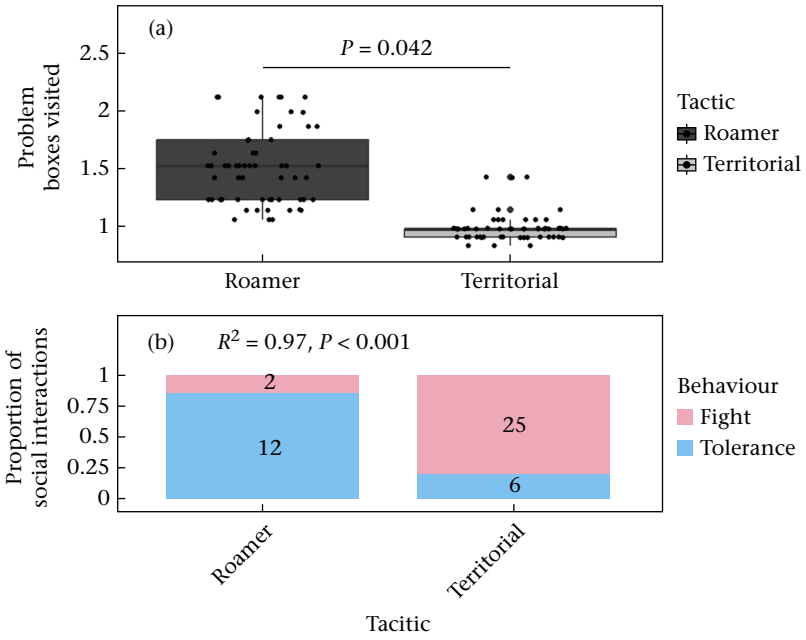

Figure 3. (a) Number of problem-solving boxes visited by each tactic (internal line represents the median predicted visits for each tactic, the lower and upper edges of the box represent the 25th and 75th percentiles, the whiskers represent the range of predicted values and the circles represent individual predicted values for each mouse). (b) Count of social interactions and results of the GLMM.

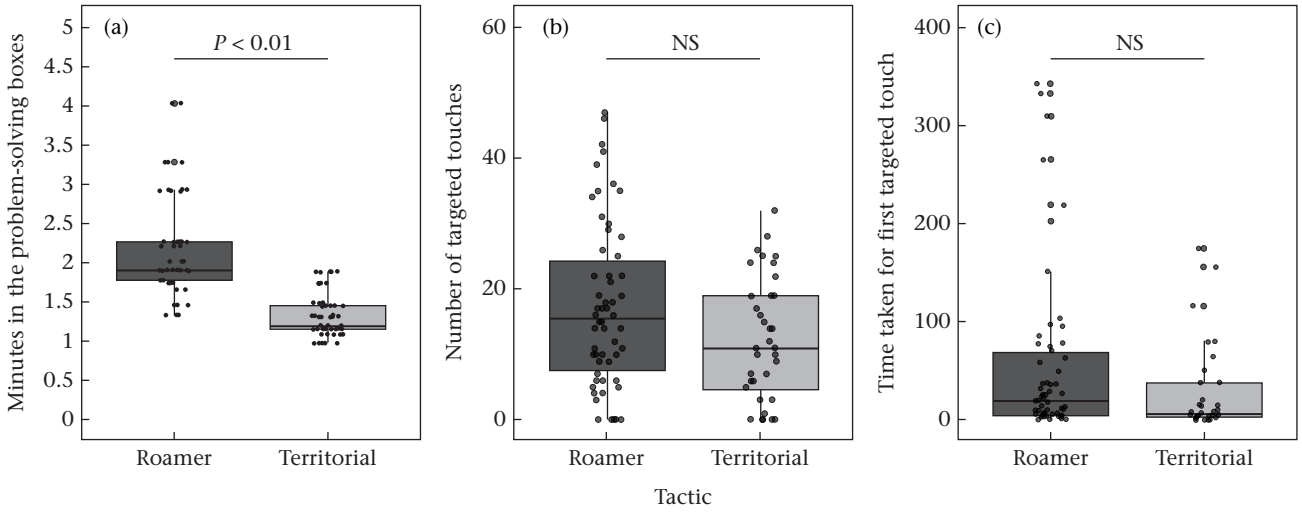

Figure 4. (a) Persistence in seminatural enclosure (time spent inside the problem-solving box, in min per 1 h). (b) Persistence in controlled experiment (number of targeted touches). (c) Curiosity in the controlled experiment (time taken to initiate the first contact with the problem, in s); in all cases, internal line represents the median predicted time taken for the first targeted touch for each tactic, the lower and upper edges of the box represent the 25th and 75th percentiles, the whiskers represent largest and smallest values within 1.5 × the interquartile range and the circles represent individual predicted values for each mouse.

territorials. In contrast, under controlled conditions, mice adopting each of the two tactics did not differ in their curiosity and persistence to engage with the problems or in their problem-solving success. When tested for spatial learning, roamers were faster to navigate a novel maze in their first trial, but the two tactics did not differ in the latency to enter the maze or the number of mistakes mice made in this initial trial. Similarly, both tactics needed a similar number of trials to reach their best performance in latency to enter, navigation time and number of mistakes, showing similar spatial learning performance overall. Our findings highlight that the effects of behavioural polymorphisms, here in the form of alternative reproductive tactics, on cognition and problem solving are strongly context dependent, influenced by the social conditions as well as by the ecological constraints faced by each individual.

Tactic Affects Space Use and Social Interactions, but not Spatial Learning

Our findings validate that space use and movement patterns differ between ARTs, as roamers covered more space than territorials in an ecologically relevant context. Specifically, roamers visited multiple problem-solving boxes while territorials visited mostly one, presumably the box closest to their territory. This is unsurprising, as territorials need to efficiently guard their territories and exclude roamers, who rely predominantly on random

matings with receptive females they cannot monopolize (Taborsky, 2008). These findings align with previous research on other rodents (Schradin et al., 2009) where roamers tend to have larger home ranges than territorials. This pattern is further supported by behaviours observed inside the problem-solving boxes: roamers tolerated other individuals, reflecting a reluctance to engage in aggressive interactions, whereas territorials were regularly aggressive towards other mice they encountered. These differences in social interactions highlight the distinct ecological responsibilities of each tactic: territorial males prioritize defending their territory and adjacent areas, which requires them to remain close to their nest and exclude all individuals not belonging to their family. In contrast, roamers spend more time moving in a larger portion of their environment in search of receptive females, while avoiding trespassing into territorial areas. This expanded movement could result from roamers actively avoiding territorial males or from territorial exclusion, forcing roamers to increase their range to secure mating opportunities.

Interestingly, none of the differences observed in the seminatural enclosures persisted under controlled conditions. In these tests, we found no differences between ARTs in spatial navigation, although there was some evidence that roamers navigated slightly faster during their first encounter with a novel area. In other words, despite differences in space use in the enclosures, roamers and territorials do not differ in intrinsic navigation abilities or their spatial learning performance. This suggests that the space-use patterns seen in ecologically relevant settings arise from fine-grained ecological demands, such as locating mates, and from the roles associated with each tactic, rather than from inherent differences in ability. The slightly faster initial navigation by roamers may reflect their greater experience exploring broader areas in the enclosures, or a heightened motivation or caution when encountering a novel environment.

Tactic Affects Problem Solving Only in an Ecological Context

Our findings showcase how problem-solving performance was dependent on the testing condition: in an ecological context, roamers were more likely to be problem solvers, while in controlled conditions the two tactics performed similarly. This is not due to inherent differences in problem-solving ability between ARTs, but rather an outcome of the roamers encountering more problems in the ecologically relevant conditions of the enclosures. This idea is supported by the results of the controlled experiment, where all mice had a similar amount of time to invest in solving these tasks: there, both tactics performed significantly better than in the seminatural enclosures while, importantly, there was no difference between them. Similarly to our findings, Rochais et al. (2021) observed that older males, presumably less competitive, were more motivated to escape from a box to return to their nest, where unguarded females and pups were present. Thus, the worse problem-solving performance of territorials could stem from their responsibilities being centred around resource maintenance rather than a lack of ability. Indeed, when both roamers and territorials had the same time available to problem solve, their performance was similar.

Apart from problem-solving, we also tested whether differences in ARTs affect curiosity and persistence, both of which are known to influence problem solving. Studies have shown that motivation is a key determinant of problem-solving success, with curiosity (Wat et al., 2020) and persistence (measured as the time spent engaging with a problem; Griffin & Guez, 2014), acting as strong proxies for it. For instance, more persistent grey squirrels, *Sciurus carolinensis*, and Eurasian red squirrels, *Sciurus vulgaris*, are more likely to solve a puzzle box than less persistent individuals (Chow et al., 2016; 2018). Our results show, again, how these differences are heavily dependent on the ecological context, which defines the available time each individual has to engage and attempt to solve each problem. In a socially complex setting, such as our seminatural enclosures, most individuals had little time to invest in visiting and attempting to solve the problem-solving set-ups, because they had more responsibilities like mate guarding. In controlled conditions, however, where each individual has fewer responsibilities and thus significantly more time to invest in novelty seeking and problem solving, we see that all individuals perform similarly irrespective of their tactics. This improved performance in controlled settings is consistent with previous results from house mice (Vezyrakis et al., 2025) and other species (Benson-Amram et al., 2013; Griffin & Guez, 2014).

Our results align with the predictions of both the 'bad competitor' and 'free time' hypotheses. We found that roamers use more space and spend more time close to novel problems compared to territorials. This increased space use naturally leads to more encounters with novel problems and, consequently, higher problem-solving rates, a pattern consistent with previous work showing that greater exposure to problems promotes problem solving (Chow et al., 2018; Vezyrakis et al., 2025). Our results can only partially disentangle the mechanisms underlying these patterns. One possibility is that roamers' greater space use reflects necessity, as predicted by the 'bad competitor' hypothesis: individuals unable to monopolize territories must roam more extensively to avoid dominant males and to locate mating opportunities. Importantly there is also a difference in time allocation: because roamers do not invest heavily in territory defence, they devote more of their activity to searching. This roaming inherently exposes them to more novel problems, increasing opportunities for interacting and solving more. In this sense, higher problem-solving rates emerge as a by-product of different reproductive tactics and the associated time–space trade-offs. In other words, the space-use patterns, dictated by the reproductive tactics of each individual, simply create different opportunities to encounter and solve problems. In contrast to roamers, who regularly visit multiple problem-solving boxes around the enclosure, territorials invest most of their time in mating efforts and mate guarding as part of their reproductive strategy, staying close to their nest. In our controlled experiments, we found no differences in curiosity, persistence or problem-solving performance between ARTs, thus indicating that the differences measured in the enclosures do not represent inherent differences in ability. As roamers cover a broader area and interact with more problems, they are more likely to solve them. Thus, the measured differences in problem-solving performance probably emerge as a by-product of life-history variation.

The seminatural enclosures presented a socially and ecologically complex setting where mice navigated dynamic social interactions (König & Lindholm, 2012; Vezyrakis et al., 2025), territorial defence (Darmis et al., 2025) and competition for space and mates. While resources such as food and nesting sites were readily available, as is often the case in wild house mouse populations (Bronson, 1979; König & Lindholm, 2012), individuals still needed to invest time and energy for reproduction stemming from their choice of ART, which then created different time allocation patterns. In turn, these differences probably limited the extent to which they could engage with problems in the enclosures (Kummer & Goodall, 1985), and thus ARTs indirectly affect innovative problem solving by imposing different ecological constraints on each individual. We suggest that future studies could test for differences in time and energy allocation using a mediation analysis.

In contrast, the controlled environment eliminated social and territorial pressures, as each individual was tested alone with no external distractions and reproductive opportunities, and provided all mice with equal opportunity to engage with a problem and solve it. As both tactics problem solved similarly there, we hypothesize that the social and reproductive context of the enclosures may be necessary to express these tactic-driven differences.

Conclusions

Overall, our study provides evidence that cognition and problem-solving performance are linked to ARTs in males but only when studying ARTs in an ecologically relevant context. There, we found differences in space use (roamers covering more space and engaging more with novel problems) and problem solving (roamers were more likely to solve novel problems), which revealed that ARTs trade off with investment in other traits via differences in their time allocation (Dunbar et al., 2009). Since ARTs influence space use by limiting roamers' access to receptive females that aggregate in nestboxes, they (roamers) visit larger areas to increase their fertilization chances and by doing so are more likely to encounter novel opportunities, increasing their chances of solving novel problems. Importantly, we found that these differences were not present when the individuals were tested outside of a reproductive context, showing that individual differences in spatial navigation and innovative abilities might only exist when ecological constraints create the conditions necessary for time (and not just energy) to be limited at the between-individual level.

Author Contributions

Anustup Bandyopadhyay: Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation. **Fragkiskos Darmis:** Writing – review & editing, Visualization, Formal analysis, Data curation, Conceptualization. **Anja Guenther:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Alexandros Vezyrakis:** Writing – review & editing, Visualization, Formal analysis, Data curation, Conceptualization.

Data Availability

Data and R code used in this study are available from the Figshare Digital Repository, at https://doi.org/10.6084/m9.figshare.30199990. Videos 1–3, showing mice solving problems in semi-natural and controlled experiments and in the maze learning experiment, are available at https://figshare.com/s/8075a65cdaf794032565.

Declaration of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2026.123544.

References

Amici, F., Widdig, A., Lehmann, J., & Majolo, B. (2019). A meta-analysis of interindividual differences in innovation. *Animal Behaviour, 155*, 257–268. https://doi.org/10.1016/j.anbehav.2019.07.008

ASAB Ethical Committee/ABS Animal Care Committee. (2025). Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching. *Animal Behaviour, 219*, Article 123065. https://doi.org/10.1016/S0003-3472(24)00376-2

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Grothendieck, G., Green, P., & Bolker, M. B. (2015). Package 'lme4'. *Convergence, 12*(1), 2. https://github.com/lme4/lme4-convergence.

Benson-Amram, S., Weldele, M. L., & Holekamp, K. E. (2013). A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, *Crocuta crocuta*. *Animal Behaviour, 85*(2), 349–356. https://doi.org/10.1016/j.anbehav.2012.11.003

Bronson, F. H. (1979). The reproductive ecology of the house mouse. *Quarterly Review of Biology, 54*(3), 265–299. https://doi.org/10.1086/411295

Chow, P. K. Y. (2016). The 'how': The role of learning and flexibility in problem solving in grey and red squirrels *[Doctoral thesis*. University of Exeter, U.K.. https://hdl.handle.net/10871/21369

Chow, P. K. Y., Lurz, P. W., & Lea, S. E. (2018). A battle of wits? Problem-solving abilities in invasive eastern grey squirrels and native Eurasian red squirrels. *Animal Behaviour, 137*, 11–20. https://doi.org/10.1016/j.anbehav.2017.12.022

Da Silva, A. V., De Almeida, J. G. L., Ventura, S. P., Oliveira, R., & Peixoto, P. E. C. (2025). A meta-analysis on alternative mating tactics: When the main and the alternative yield similar reproductive success. *Biological Reviews, 100*(1), 85–98. https://doi.org/10.1111/brv.13129

Darmis, F., Vezyrakis, A., & Guenther, A. (2025). Male reproductive tactics in house mice: Consistent individual differences, intrinsic factors and density effects. *Journal of Animal Ecology, 94*(6), 1244–1258. https://doi.org/10.1111/1365-2656.70039

Delacoux, M., & Guenther, A. (2023). Stressfulness of the design influences consistency of cognitive measures and their correlation with animal personality traits in wild mice (*Mus musculus*). *Animal Cognition, 26*(3), 997–1009. https://doi.org/10.1007/s10071-023-01748-3

Drickamer, L. C. (2001). Urine marking and social dominance in male house mice (*Mus musculus domesticus*). *Behavioural Processes, 53*(1–2), 113–120. https://doi.org/10.1016/S0376-6357(00)00152-2

Dunbar, R. I., Korstjens, A. H., Lehmann, J., & British Academy Centenary Research Project. (2009). Time as an ecological constraint. *Biological Reviews, 84*(3), 413–429. https://doi.org/10.1111/j.1469-185X.2009.00080.x

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution, 7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Gorshkova, E., Kyomen, S., Kaucká, M., & Guenther, A. (2024). Food quality influences behavioural flexibility and cognition in wild house mice. *Scientific Reports, 14*(1), Article 16088. https://doi.org/10.1038/s41598-024-66792-6

Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: A review of common mechanisms. *Behavioural Processes, 109*, 121–134. https://doi.org/10.1016/j.beproc.2014.08.027

Hohlbaum, K., Andresen, N., Mieske, P., Kahnau, P., Lang, B., Diederich, K., Palme, R., Mundhenk, L., Sprekeler, H., Hellwich, O., Thöne-Reineke, C., & Lewejohann, L. (2024). Lockbox enrichment facilitates manipulative and cognitive activities for mice. *Open Research Europe, 4*, 108. https://doi.org/10.12688/openreseurope.17624.2

König, B., & Lindholm, A. K. (2012). 5 – The complex social environment of female house mice (*Mus domesticus*). In M. Macholan, S. J. Baird, P. Munclinger, & J. Pialek (Eds.), *Evolution of the House Mouse* (pp. 114–134). Cambridge University Press. https://doi.org/10.1017/CBO9781139044547.007.

Kummer, H., & Goodall, J. (1985). Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences, 308*(1135), 203–214. https://doi.org/10.1098/rstb.1985.0020

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). Performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software, 6*(60), 3139. https://doi.org/10.21105/joss.03139

Laland, K. N., & Reader, S. M. (1999). Foraging innovation in the guppy. *Animal Behaviour, 57*(2), 331–340. https://doi.org/10.1006/anbe.1998.0967

Lopez-Hervas, K., Porwal, N., Delacoux, M., Vezyrakis, A., & Guenther, A. (2024). Is the speed of adjusting to environmental change condition dependent? An experiment with house mice (*Mus musculus*). *Current Zoology, 70*(3), 350–360. https://doi.org/10.1093/cz/zoae005

Mazza, V., & Guenther, A. (2021). City mice and country mice: Innovative problem solving in rural and urban noncommensal rodents. *Animal Behaviour, 172*, 197–210. https://doi.org/10.1016/j.anbehav.2020.12.007

Mazza, V., Schianini, V., Canestrelli, D., & Carere, C. (2025). Quick on their paws: Mice living in human-disturbed areas are faster problem-solvers than mice in strictly protected areas. *Animal Cognition, 28*(1), 1–17. https://doi.org/10.1007/s10071-025-02013-5

Ophir, A. G. (2017). Navigating monogamy: Nonapeptide sensitivity in a memory neural circuit may shape social behavior and mating decisions. *Frontiers in Neuroscience, 11*, 397. https://doi.org/10.3389/fnins.2017.00397

Ord, T. J. (2021). Costs of territoriality: A review of hypotheses, meta-analysis, and field study. *Oecologia, 197*(3), 615–631. https://doi.org/10.1007/s00442-021-05068-6

Prabh, N., Linnenbrink, M., Jovicic, M., & Guenther, A. (2023). Fast adjustment of pace-of-life and risk-taking to changes in food quality by altered gene expression in house mice. *Ecology Letters, 26*(1), 99–110. https://doi.org/10.1111/ele.14137

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.r-project.org.

Reader, S. M., & Laland, K. N. (Eds.). (2003). *Animal innovation* (Vol. 10). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198526223.001.0001.

Rice, M. A., Wong, G. H., & Ophir, A. G. (2022). Impacts of spatial learning on male prairie vole mating tactics in seminatural field enclosures are context dependent. *Animal Behaviour, 191*, 57–73. https://doi.org/10.1016/j.anbehav.2022.06.011

Rochais, C., Pillay, N., & Schradin, C. (2021). Do alternative reproductive tactics predict problem-solving performance in African striped mice? *Animal Cognition, 24*(4), 703–716. https://doi.org/10.1007/s10071-020-01459-z

Rochais, C., Schradin, C., & Pillay, N. (2023). Cognitive performance is linked to survival in free-living African striped mice. *Proceedings of the Royal Society B: Biological Sciences, 290*(1994), Article 20230205. https://doi.org/10.1098/rspb.2023.0205

Scantlebury, M., Waterman, J. M., & Bennett, N. C. (2008). Alternative reproductive tactics in male Cape ground squirrels *Xerus inauris*. *Physiology & Behavior, 94*(3), 359–367. https://doi.org/10.1016/j.physbeh.2008.02.003

Schütz, D., Pachler, G., Ripmeester, E., Goffinet, O., & Taborsky, M. (2010). Reproductive investment of giants and dwarfs: Specialized tactics in a cichlid fish with alternative male morphs. *Functional Ecology, 24*(1), 131–140. https://doi.org/10.1111/j.1365-2435.2009.01605.x

Schradin, C. (2008). Differences in prolactin levels between three alternative male reproductive tactics in striped mice (*Rhabdomys pumilio*). *Proceedings of the Royal Society B: Biological Sciences, 275*(1638), 1047–1052. https://doi.org/10.1098/rspb.2008.0004

Schradin, C. (2022). Alternative reproductive tactics. In J. Vonk, & T. K. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior* (pp. 201–211). Springer International Publishing.

Schradin, C., Scantlebury, M., Pillay, N., & König, B. (2009). Testosterone levels in dominant sociable males are lower than in solitary roamers: Physiological differences between three male reproductive tactics in a sociably flexible mammal. *American Naturalist, 173*(3), 376–388. https://doi.org/10.1086/596534

Shuster, S. M., & Wade, M. J. (2003). *Mating systems and strategies*. Princeton University Press.

Taborsky, M. (2008). 10 – Alternative reproductive tactics in fish. In R. F. Oliveira, M. Taborsky, & H. J. Brockmann (Eds.), *Alternative reproductive tactics: An integrative approach* (pp. 251–299). Cambridge University Press. https://doi.org/10.1017/CBO9780511542602.011.

Vezyrakis, A., Guenther, A., & Mazza, V. (2025). Effects of behavioural types on the problem-solving performance of wild house mice under controlled and semi-natural conditions. *Oikos, 2025*(4), Article e10787. https://doi.org/10.1111/oik.10787

Vrbanec, L., Matijević, V., & Guenther, A. (2021). Enhanced problem-solving ability as an adaptation to urban environments in house mice. *Proceedings of the Royal Society B: Biological Sciences, 288*(1945), Article 20202504. https://doi.org/10.1098/rspb.2020.2504

Wat, K. K., Banks, P. B., & McArthur, C. (2020). Linking animal personality to problem-solving performance in urban common brushtail possums. *Animal Behaviour, 162*, 35–45. https://doi.org/10.1016/j.anbehav.2020.01.013

Appendix

Figure A1. Photo of a seminatural enclosure, as used in this study.

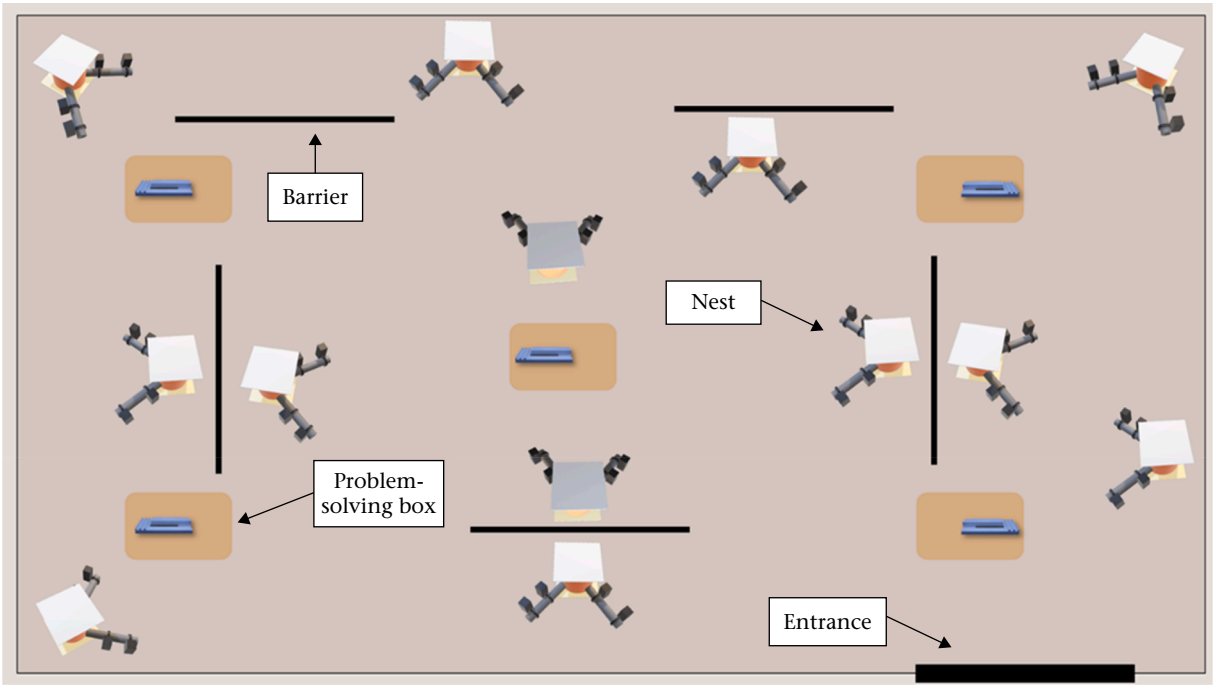

Figure A2. Layout of the seminatural enclosures during the problem-solving experiment. Thirteen nestboxes were distributed across the enclosure, and in the empty spaces between them, five problem-solving boxes were introduced for 2 h on each testing night.

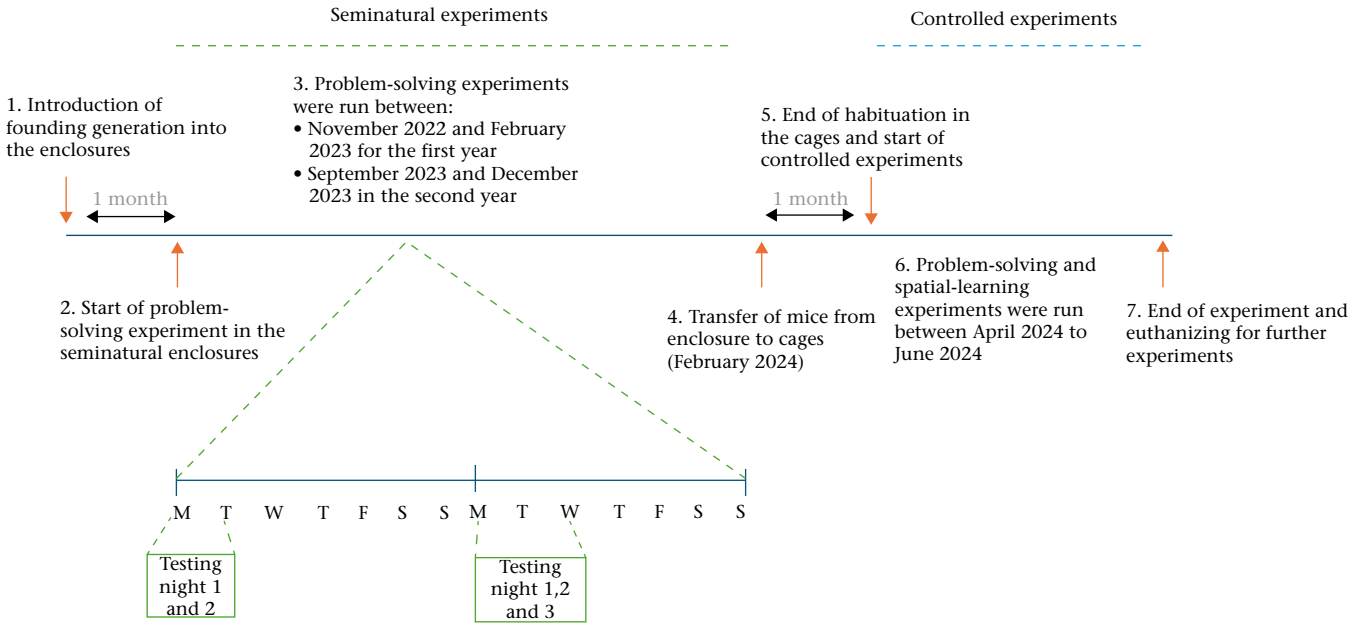

Figure A3. Testing timeline of the experiment.

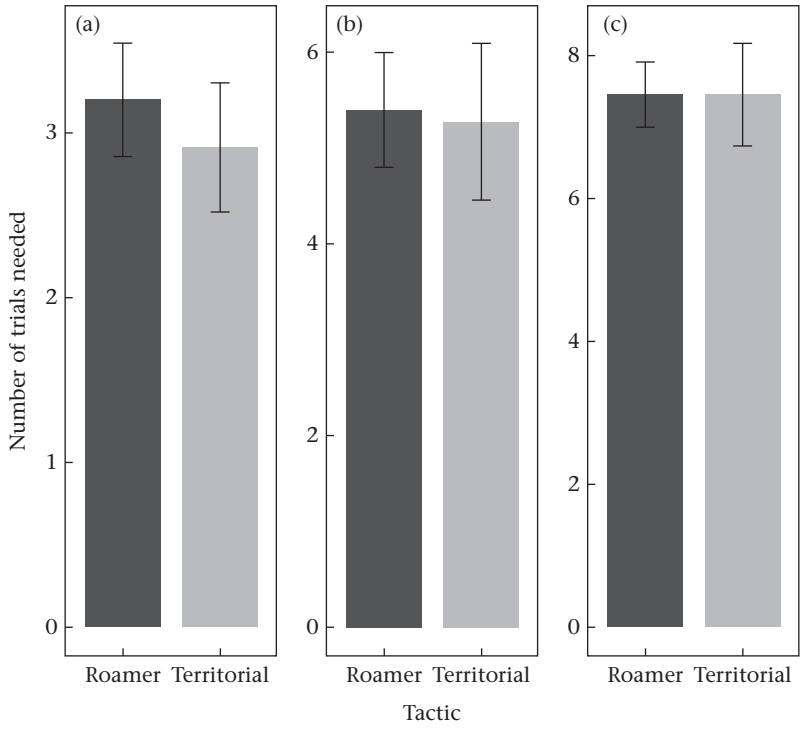

Figure A4. Bar plots showing the number of trials the ARTs needed to reach the best performance: (a) to complete the maze with the fewest mistakes; (b) to complete the maze with the fewest trips; (c) to show the shortest latency (time taken to leave the starting box and enter the maze). The vertical lines represent ± SE around the mean.