Report

Current Biology

Variation in innovation is maintained by disassortative mating and female choice

Highlights

- Female house mice prefer males with opposite innovative skills to their own
- Innovative females prefer large males; non-innovative females prefer innovators
- Males face a trade-off between innovation and competitive ability
- Disassortative mating can allow selection to maintain variation in innovation

Authors

Alexandros Vezyrakis, Fragkiskos Darmis, Valeria Mazza, Anja Guenther

Correspondence

vezyrakis@proton.me

In brief

Vezyrakis et al. show that mate choice in house mice depends on the choosing female's own skills. By using experiments and semi-natural observations, their results demonstrate that a combination of male trade-offs and differential female preference can create the necessary conditions for balancing selection to maintain individual variation in innovation.

Vezyrakis et al., 2026, Current Biology *36*, 555–560
January 19, 2026
https://doi.org/10.1016/j.cub.2025.11.077

CellPress

Current Biology

CellPress
OPEN ACCESS

Report

Variation in innovation is maintained by disassortative mating and female choice

Alexandros Vezyrakis,[1,3,4,*] Fragkiskos Darmis,[1] Valeria Mazza,[2] and Anja Guenther[1,3]
[1]RG Behavioural Ecology of Individual Differences, Max Planck Institute for Evolutionary Biology, 24306 Plön, Germany
[2]Department of Ecological and Biological Sciences, University of Tuscia, 01100 Viterbo, Italy
[3]Zoology and Animal Ecology, University of Hildesheim, 31141 Hildesheim, Germany
[4]Lead contact
*Correspondence: vezyrakis@proton.me
https://doi.org/10.1016/j.cub.2025.11.077

SUMMARY

Innovative birds are seen as more attractive and often achieve higher mating success.[1–4] Assuming this to be a general phenomenon, selection should promote high levels of innovation that allow birds and other animals to solve novel problems or apply new solutions to old ones.[5] However, animal populations show substantial variation in this trait, as not all individuals, even in the same population, innovate at the same rate or even innovate at all. It remains unclear which forces of selection maintain these differences. Here, we show that female mate choice and male trade-offs between innovation and competitive ability can maintain this variation in innovation in wild house mice. By combining observational data from semi-natural enclosures with experimental mate choice tests, we found that female wild house mice with different innovative abilities consistently preferred males with opposing skills, with innovative females choosing based on physical size, regardless of innovative ability, and non-innovative females choosing innovative males regardless of size. This disassortative preference in laboratory conditions resulted in disassortative mating under more natural conditions. Males faced a trade-off between innovation and size, a predictor of competitive potential. By taking females' innovation propensity into account, we demonstrate how female preference and male innovation-competition trade-offs create the conditions necessary for sexual selection to maintain variation in innovation.

RESULTS AND DISCUSSION

Innovative females might prefer to mate with innovative males (assortative mating), or they might prefer to mate with less innovative males (disassortative mating) if there is a trade-off with alternative advantageous traits, such as size or physical dominance.[6] The ability to innovate comes with inherent risk-reward trade-offs, as innovators must invest time and energy into solving problems, which can lead to missed opportunities for essential activities, increased exposure to predation, and the risk of engaging with harmful or inedible resources.[7,8] Less competitive individuals (often smaller, shyer, or less dominant individuals) might seek alternative resources and exploit them through innovative behaviors, while dominant, often larger individuals can easily gain control of readily available resources without the need to innovate (the "bad competitor" hypothesis[5,9,10]). We combined controlled mate choice experiments, considering both male and female innovative abilities, with observations from semi-natural populations of house mice to explore the reproductive outcomes of these mating decisions.

To determine whether innovation propensity influenced mating decisions, leading to assortative or disassortative mating, we released cage-raised wild house mice (focal individuals: $N = 59$ males and $N = 80$ females) into four replicated semi-natural enclosures for 6 months and presented them with a battery of four problem-solving setups they could access voluntarily (in total 100 possibilities to solve per population across several months, an example video of a mouse solving such a setup is available in Video S1). House mice (*Mus musculus domesticus*) are well suited for such an experiment, as they have spread globally and adapted to novel environments quickly through behavioural flexibility. They are capable of innovative problem solving in a foraging context, both in the laboratory as well as in semi-natural conditions.[11–13] In the semi-natural enclosures, on average one-fifth of the population readily innovates, and males and females innovate at similar rates.[13] House mice typically live in small groups, often consisting of one dominant male and several females, together with their offspring. For males, size and physical dominance are important, as they heavily defend their territory from potential intruders.[14,15] Females participate in territorial defense but also devote a considerable amount of their time to communal care of offspring.[15] Overall, 92% (128/139) of the focal individuals participated in the problem-solving tests. Of those, we found approximately one-fourth (22.7%) to be innovators (females: 26%, males: 18.2%), and each innovator solved 3.79 ± 1.19 (mean ± SE) foraging extraction tasks. Using DNA fingerprinting, we found that these focal individuals produced 195 offspring (on average 49 per population) that could be traced back to 70 distinct mating events (as evidenced by surviving offspring) during the 6 months in the enclosures. A null hypothesis assuming random matings predicts that 33% of these matings would occur between mixed pairs (innovators with non-innovators). A lower observed proportion of mixed matings would

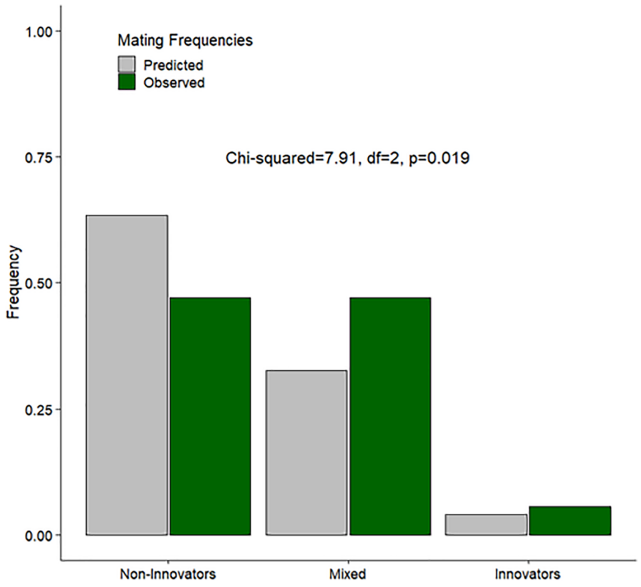


Figure 1. Mating patterns in semi-natural enclosures

Predicted (gray) and observed (green) frequencies of mating. Shown on top is the result of the chi-squared test, which reveals a deviation from the predicted frequencies of random mating (because the frequencies of mating between innovators and non-innovators are higher than expected) and thus suggests disassortative mating. n = 70 matings observed.

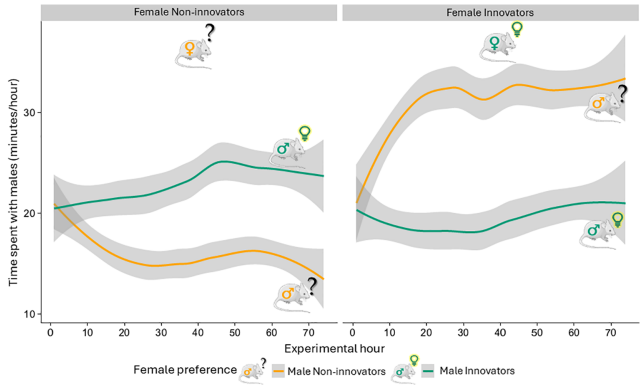


Figure 2. Time spent with males differs for females of different innovative skills

Number of minutes per hour that non-innovative (left) and innovative (right) females spent with innovative (green) and non-innovative (orange) males. Although in both cases females spent a similar amount of time with both males at the beginning, there was a clear differentiation as time passed, with non-innovative females spending more time with innovative males and vice versa. Lines represent loess-smoothed observations and not LMM-predicted values for visualization purposes. Observations from 50 females (23 innovative and 27 non-innovative).

See Figure S4 for a version of this figure including raw data points.

indicate assortative mating, whereas a higher observed proportion of mixed matings would indicate disassortative mating. Using a chi-squared goodness-of-fit test between the predicted and the observed matings, we found evidence for disassortative mating ($\chi^2(2) = 7.91$, $p = 0.019$, see Figure 1). Specifically, there were 45% more mixed pairs than expected (47% against the predicted 33%), and the matings between non-innovators were less than expected (47% against 63%; details at Table S1). This pattern occurred although male innovators (mean ± SE number of matings: 2.14 ± 0.4) mated on average as often as non-innovators (mean ± SE number of matings: 2.2 ± 0.3; Wilcoxon rank-sum test, W = 83, p value = 0.85; Figure 1). Thus, ignoring female skills would have led to the erroneous conclusion that male innovative skills do not influence mating patterns.

Because in this first, observational step, we found evidence of disassortative mating under semi-natural conditions, in a second step, we wanted to test in a controlled experiment whether this pattern arises from female choice. Several studies have examined whether innovation affects mate choice decisions by challenging individuals of one sex (usually males) to innovate by solving experimental problems and then recording how individuals of the other sex (usually females) choose between solvers and non-solver males. These experiments showed that being innovative is attractive, as, for example, female budgerigars (*Melopsittacus undulatus*) choose innovative males that display good problem-solving performance[2]; male bowerbirds (*Ptilonorhynchus violaceus*) with better problem-solving abilities have higher mating success[3]; and female zebra finches (*Taeniopygia guttata*) prefer the songs of males that can solve a foraging task.[4]

To examine how innovation affects female choice in house mice, we employed a standardized mate choice test that is used across taxa,[2,6,16] where a female can select between two males by spending time close to them (see Figure S1A for a graphical representation). Therefore, after letting animals from the semi-natural enclosures habituate to being housed in cages, we let fifty females (23 innovative and 27 non-innovative) choose between an innovative (N = 23) and a non-innovative (N = 20) male each. From each semi-natural population, we selected all innovators and a similar number of age-matched non-innovators. To ensure the mice had no previous contact with each other, we paired unrelated males and females from different enclosures. Females were tested once, and males participated in the tests a median of 2 times (range 1–4 times), to ensure an age and weight balance between the two opponents. We calculated female selectivity based on the procedure of[16] (a selectivity index, SI, of 1 would indicate a female spending 100% of her time with only one male, whereas SI=0 would indicate a female that spends 50% of her time with each male) and found that it was similarly high between innovators (mean ± SE: 0.63 ± 0.02) and non-innovators (mean ± SE: 0.58 ± 0.01, see Figure S1B). This similarity was consistent both when we examined the entire experiment (model 1, LMM: $\beta = 0.07$, SE: ± 0.07, $p = 0.31$) and after excluding the initial 24 h, after which selectivity stabilizes (model 2, LMM: $\beta = 0.07$, SE: ± 0.04, $p = 0.07$). This shows that both innovator and non-innovator females developed clear preferences for one of the two males they could choose from.

When only considering the male innovative skills, there was no difference in female preference for innovators and non-innovators in the mate choice test (model 3, LMM: time spent with males ~ male skill: $\beta = -2.38$, SE: ± 2.42, $p = 0.33$; Table S2.1). However, when we considered female and male abilities simultaneously, we found a striking pattern of disassortative female preference, which emerged from females prioritizing interactions with males of the opposite skill (Figure 2). There was a strong negative interaction between female and male innovative abilities, with female

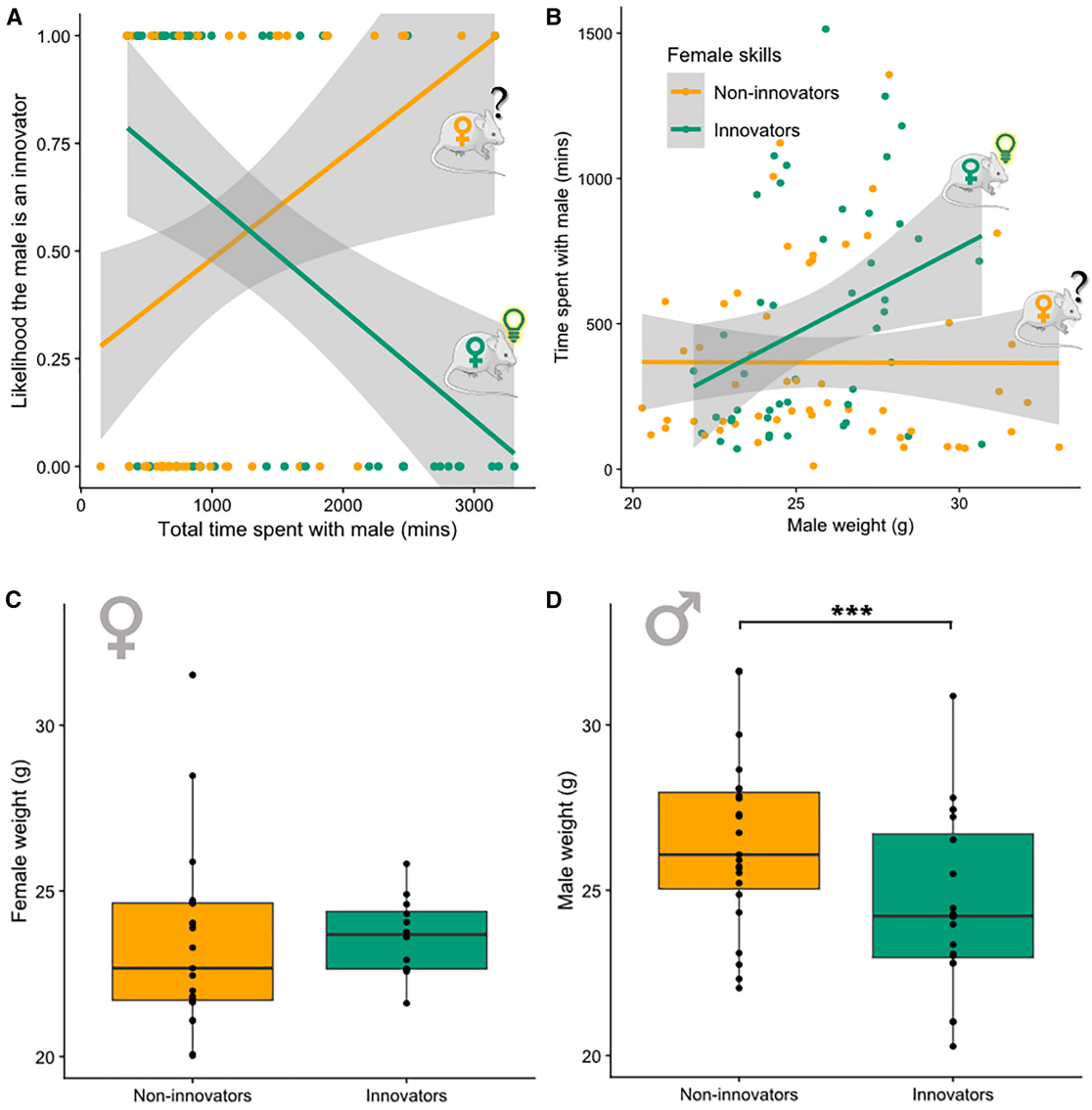


Figure 3. Female preference leads to disassortative mating as a result of a trade-off between male innovation and physical attributes that is not faced by females

Results of the linear models show that: (A) the interaction between female and male problem-solving skills ultimately influences female choice in the controlled experiment, with innovative females (green) choosing non-innovative males and vice versa.

(B) only innovative females (green) base their choice on male weight, in contrast to non-innovative females (orange), for whom male weight played no role in how much time they allocated to potential mates.

(C and D) there are no differences in weight between female non-innovators (left, orange) and female innovators (right, green); and D) male innovators (right, green) were significantly lighter than male non-innovators (left, orange). Together, these results suggest disassortative mating and a trade-off between male innovation and physical attributes. In (A), (B), and (C), observations from 50 females (23 innovative and 27 non-innovative); in (D), observations from 43 males (23 innovative and 20 non-innovative).

innovators spending more time with male non-innovators and vice versa (model 4, LMM: time spent with males ~ female skill × male skill: $\beta = -12.9$, SE: ± 2.51, $p < 0.001$; Figure 3A; Table S2.2). Thus, our results from experimental and semi-natural conditions agree in showing that disassortative mating can be one of the mechanisms that maintains the variation in innovative abilities in a population.

Further, we examined whether a potential trade-off exists between innovation and physical attractiveness of innovators and non-innovators. Male weight is a well-established indicator of male quality and reproductive success in rodents[17,18] and several other taxa.[19,20] Whereas there was no difference in females (model 6, LM: female weight ~ female skill: $\beta = -0.05$, SE: ± 0.04, $p = 0.17$; Figure 3C), male non-innovators were significantly heavier than the innovators (model 7, LMM: male weight ~ male skill: $\beta = -1.88$, SE: ± 0.81, $p = 0.023$; Figure 3D), and male innovative skill predicted almost 95% of the variation in weight (accounting for male identity, conditional $R^2 = 0.94$).

This indicates that males, but not females, face a strong trade-off between innovation and physical size, in line with the bad competitor hypothesis (similarly to other species where innovators show reduced competitive ability[6,10]).

However, does this trade-off affect differential female choice? Once more, our findings confirm that female skill influences how females choose: female innovators spent more time with heavier males (model 5, LMM: time spent with males ~ female skill x male weight: β = 2.3, SE= ± 0.84, p = 0.007; Figure 3B; Table S2.3), in contrast to female non-innovators, for whom male weight played no role (model 5, LMM: β = 0.04, SE = ± 0.44, p=0.94; Figure 3B; Table S2.3). In other words, innovative females preferred heavier males, even if they were non-innovators, whereas female non-innovators preferred innovative males without being affected by their physical attributes (weight and thus dominance). This finding suggests that female innovative skill directly influences which male traits they consider attractive and further reinforces that not all females choose their partner based on the same set of traits.

Innovation propensity differs between individuals of a species,[21] and we currently lack an understanding of whether this behavior is affected by natural or sexual selection, as well as how it is maintained across generations. Darwin already proposed that cognition is under sexual selection,[1] and recent experimental evidence suggests that innovators are attractive to potential mates.[2–4] Here, we present a possible solution to the conundrum of the maintenance of variation in innovative ability in animal populations. We show that males face a trade-off between innovation and physical characteristics, such as weight or dominance, and that females of different skills make choices based on different male attributes. As this female choice leads to disassortative matings, variation in innovative behaviors is maintained in the population via balancing selection.

The key to our findings was to also assess females' innovative skills. If presenting females with a two-choice test in which only the males' skills would be considered, we would have erroneously concluded that there is no female preference for innovation, something that may account for the contradictory evidence on the attractiveness of innovators.[2–4,6,22,23] Only by considering the skills of both the choosing as well as the chosen individuals, do we revealed that female choice can be the trigger to maintain variation in innovation despite all males reproducing successfully, i.e., that variation in reproductive success can be seen only through an interaction between both sexes' traits. Thus, innovation may be part of a larger suite of traits that females can use to choose their partners, correlated with secondary sexual signals (i.e., USV communication, scent, and nest building), as similar relationships have been found in other species.[3,4,24]

Recent studies that quantified innovation propensity or explored the link between innovation and fitness[2,3,6,21,25,26] have reported considerable between-individual variation in performance. Here, we provide evidence that such variation might be explained by a trade-off between innovation and investment in traits predicting competitive ability, in line with the "bad competitor hypothesis."[9] In this study, by combining both experimental and semi-natural observations, we uncovered how female preference and male trade-offs create the conditions necessary to maintain individual differences in innovation.

Why individuals consistently vary in their behavior, even within the same population, remains a fundamental issue in behavioural and evolutionary ecology. Our findings suggest that forces of balancing selection, mediated through mate choice, can create the conditions necessary for these consistent individual differences to arise and to be maintained. Because innovation can help animals cope with fast-changing conditions, it is important to understand the impact of both sexual and natural selection on its evolution. We hope that these findings can advance future research on the selective pressures shaping innovation propensity by highlighting the crucial importance of concurrently considering the skills of both sexes. Further studies are needed to understand the evolvability of such a complex, crucial trait, by investigating the extent to which innovative behavior is heritable, its fitness consequences, and its potential link to consistent differences among individuals.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Alexandros Vezyrakis (vezyrakis@proton.me).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All data have been deposited at Mendeley and are publicly available as of the date of publication at doi.org/10.17632/my9wfhy9tb.1.
- All original code has been deposited at Dryad and is publicly available at https://doi.org/10.17632/my9wfhy9tb.1 as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

ACKNOWLEDGMENTS

We are thankful to Milan Jovicic for taking care of the mice throughout their lives in the enclosures and to Alica Merkens and Ekaterina Gorshkova for assisting with some of the mate-choice experiments. We would also like to thank Diethard Tautz and Fritz Trillmich for insightful comments on an earlier version of this manuscript. Funding was provided by the German Science Foundation (DFG – Deutschen Forschungsgemeinschaft – project number 493860801), with a joint grant to V.M. (MA 9757/2-1) and A.G. (GU 1665/5-1).

AUTHOR CONTRIBUTIONS

Conceptualization, A.V., V.M., and A.G.; data curation, A.V. and F.D.; formal analysis, A.V. and F.D.; funding acquisition, V.M. and A.G.; investigation, A.V. and F.D.; methodology, A.V., F.D., V.M., and A.G; project administration, A.V., V.M., and A.G.; resources, V.M. and A.G.; software, A.V., F.D., and A.G.; supervision, V.M. and A.G.; validation, A.V., F.D., V.M., and AG; visualization, A.V. and F.D.; writing – original draft, A.V. and F.D.; writing – review & editing, A.V., F.D., V.M., and A.G.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2025.11.077.

Received: July 7, 2025
Revised: October 6, 2025
Accepted: November 27, 2025
Published: December 30, 2025

REFERENCES

1. Darwin, C. (1871). The Descent of Man and Selection in Relation to Sex (John Murray).
2. Chen, J., Zou, Y., Sun, Y.-H., and ten Cate, C. (2019). Problem-solving males become more attractive to female budgerigars. Science *363*, 166–167. https://doi.org/10.1126/science.aau8181.
3. Keagy, J., Savard, J.-F., and Borgia, G. (2009). Male satin bowerbird problem-solving ability predicts mating success. Anim. Behav. *78*, 809–817. https://doi.org/10.1016/j.anbehav.2009.07.011.
4. Howell, C., Anderson, R., and Derryberry, E.P. (2020). Female zebra finches prefer the songs of males who quickly solve a novel foraging task to the songs of males unable to solve the task. Ecol. Evol. *10*, 10281–10291. https://doi.org/10.1002/ece3.6690.
5. Reader, S.M., and Laland, K.N. (2003). Animal Innovation: An Introduction. In Animal Innovation, S.M. Reader, and K.N. Laland, eds. (Oxford University Press), pp. 3–36. https://doi.org/10.1093/acprof:oso/9780198526223.003.0001.
6. Álvarez-Quintero, N., Velando, A., and Kim, S.-Y. (2021). Smart mating: the cognitive ability of females influences their preference for male cognitive ability. Behav. Ecol. *32*, 803–813. https://doi.org/10.1093/beheco/arab052.
7. Brosnan, S.F., and Hopper, L.M. (2014). Psychological limits on animal innovation. Anim. Behav. *92*, 325–332. https://doi.org/10.1016/j.anbehav.2014.02.026.
8. Reader, S.M., and Laland, K.N. (2002). Social intelligence, innovation, and enhanced brain size in primates. Proc. Natl. Acad. Sci. USA. *99*, 4436–4441. https://doi.org/10.1073/pnas.062041299.
9. Amici, F., Widdig, A., Lehmann, J., and Majolo, B. (2019). A meta-analysis of interindividual differences in innovation. Anim. Behav. *155*, 257–268. https://doi.org/10.1016/j.anbehav.2019.07.008.
10. Laland, K.N., and Reader, S.M. (1999). Foraging innovation is inversely related to competitive ability in male but not in female guppies. Behav. Ecol. *10*, 270–274. https://doi.org/10.1093/beheco/10.3.270.
11. Mazza, V., and Guenther, A. (2021). City mice and country mice: innovative problem solving in rural and urban noncommensal rodents. Anim. Behav. *172*, 197–210. https://doi.org/10.1016/j.anbehav.2020.12.007.
12. Vrbanec, L., Matijević, V., and Guenther, A. (2021). Enhanced problem-solving ability as an adaptation to urban environments in house mice. Proc. Biol. Sci. *288*, 20202504. https://doi.org/10.1098/rspb.2020.2504.
13. Vezyrakis, A., Guenther, A., and Mazza, V. (2025). Effects of behavioural types on the problem-solving performance of wild house mice under controlled and semi-natural conditions. Oikos *2025*, e10787. https://doi.org/10.1111/oik.10787.
14. Palanza, P., Re, L., Mainardi, D., Brain, P.F., and Parmigiani, S. (1996). Male and Female Competitive Strategies of Wild House Mice Pairs (Mus Musculus Domesticus) Confronted With Intruders of Different Sex and Age in Artificial Territories. Behaviour *133*, 863–882. https://doi.org/10.1163/156853996X00288.
15. Darmis, F., Vezyrakis, A., and Guenther, A. (2025). Male reproductive tactics in house mice: Consistent individual differences, intrinsic factors and density effects. J. Anim. Ecol. *94*, 1244–1258. https://doi.org/10.1111/1365-2656.70039.
16. Linnenbrink, M., and von Merten, S. (2017). No speed dating please! Patterns of social preference in male and female house mice. Front. Zool. *14*, 38. https://doi.org/10.1186/s12983-017-0224-y.
17. Solomon, N.G., and Keane, B. (2008). Reproductive Strategies in Female Rodents. Chapter 4. In Reproductive Strategies in Female Rodents (University of Chicago Press), pp. 42–56. https://doi.org/10.7208/9780226905389-006.
18. Kruczek, M., and Zatorska, M. (2008). Male rank affects reproductive success and offspring performance in bank voles. Physiol. Behav. *94*, 611–615. https://doi.org/10.1016/j.physbeh.2008.04.016.
19. Andersson, M. (1994). 11. Sexual Size Dimorphism. In Sexual Selection (Princeton University Press), pp. 247–294. https://doi.org/10.1515/9780691207278-013.
20. Clutton-Brock, T., and McAuliffe, K. (2009). Female Mate Choice in Mammals. Q. Rev. Biol. *84*, 3–27. https://doi.org/10.1086/596461.
21. Morand-Ferron, J., Cole, E.F., Rawles, J.E.C., and Quinn, J.L. (2011). Who are the innovators? A field experiment with 2 passerine species. Behav. Ecol. *22*, 1241–1248. https://doi.org/10.1093/beheco/arr120.
22. Cauchard, L., Boogert, N.J., Lefebvre, L., Dubois, F., and Doligez, B. (2013). Problem-solving performance is correlated with reproductive success in a wild bird population. Anim. Behav. *85*, 19–26. https://doi.org/10.1016/j.anbehav.2012.10.005.
23. Isden, J., Panayi, C., Dingle, C., and Madden, J. (2013). Performance in cognitive and problem-solving tasks in male spotted bowerbirds does not correlate with mating success. Anim. Behav. *86*, 829–838. https://doi.org/10.1016/j.anbehav.2013.07.024.
24. Templeton, C.N., Laland, K.N., and Boogert, N.J. (2014). Does song complexity correlate with problem-solving performance in flocks of zebra finches? Anim. Behav. *92*, 63–71. https://doi.org/10.1016/j.anbehav.2014.03.019.
25. Huebner, F., Fichtel, C., and Kappeler, P.M. (2018). Linking cognition with fitness in a wild primate: fitness correlates of problem-solving performance and spatial learning ability. Philos. Trans. R. Soc. Lond. B Biol. Sci. *373*, 20170295. https://doi.org/10.1098/rstb.2017.0295.
26. Morand-Ferron, J., Cole, E.F., and Quinn, J.L. (2016). Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. Biol. Rev. Camb. Philos. Soc. *91*, 367–389. https://doi.org/10.1111/brv.12174.
27. ASAB Ethical Committee/ABS Animal Care Committee (2025). Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching. Anim. Behav. *219*, 123065. https://doi.org/10.1016/S0003-3472(24)00376-2.
28. König, B., Lindholm, A.K., and Pialek, J. (2012). The complex social environment of female house mice (Mus domesticus). In Evolution of the House Mouse, M. Macholán, S.J.E. Baird, and P. Munclinger, eds. (Cambridge University Press), pp. 114–134. https://doi.org/10.1017/CBO9781139044547.007.
29. Prabh, N., Linnenbrink, M., Jovicic, M., and Guenther, A. (2023). Fast adjustment of pace-of-life and risk-taking to changes in food quality by altered gene expression in house mice. Ecol. Lett. *26*, 99–110. https://doi.org/10.1111/ele.14137.
30. Bulk, J., Schmehr, J.N., Ackels, T., de Oliveira Beleza, R., Carvalho, A., Gouveia, A., Rigoux, L., Hellier, V., Cremer, A.L., Backes, H., et al. (2025). A food-sensitive olfactory circuit drives anticipatory satiety. Nat. Metab. *7*, 1246–1265. https://doi.org/10.1038/s42255-025-01301-1.

31. Price, C.J., and Banks, P.B. (2017). Food quality and conspicuousness shape improvements in olfactory discrimination by mice. Proc. Biol. Sci. *284*, 20162629. https://doi.org/10.1098/rspb.2016.2629.

32. O'Connor, D.H., Clack, N.G., Huber, D., Komiyama, T., Myers, E.W., and Svoboda, K. (2010). Vibrissa-Based Object Localization in Head-Fixed Mice. J. Neurosci. *30*, 1947–1967. https://doi.org/10.1523/JNEUROSCI.3762-09.2010.

33. Severson, K.S., Xu, D., Yang, H., and O'Connor, D.H. (2019). Coding of whisker motion across the mouse face. eLife *8*, e41535. https://doi.org/10.7554/eLife.41535.

34. Linnenbrink, M., Wang, J., Hardouin, E.A., Künzel, S., Metzler, D., and Baines, J.F. (2013). The role of biogeography in shaping diversity of the intestinal microbiota in house mice. Mol. Ecol. *22*, 1904–1916. https://doi.org/10.1111/mec.12206.

35. Montero, I., Teschke, M., and Tautz, D. (2013). Paternal imprinting of mating preferences between natural populations of house mice (Mus musculus domesticus). Mol. Ecol. *22*, 2549–2562. https://doi.org/10.1111/mec.12271.

36. Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. *67*, 1–48. https://doi.org/10.18637/jss.v067.i01.

37. Lüdecke, D. (2013) sjPlot: Data Visualization for Statistics in Social Science. https://doi.org/10.32614/CRAN.package.sjPlot.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Mate choice data	This paper	https://doi.org/10.17632/my9wfhy9tb.1
Software and algorithms		
R (version 4.4.1)	R Core Team 2024	https://www.r-project.org/
GeneMarker (Version 2.6.4)	SoftGenetics	https://www.softgenetics.com/products/genemarker/
Colony	Zoological Society of London	https://www.zsl.org/about-zsl/resources/software/colony

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Animals and ethics

All experiments conformed to ASAB/ABS guidelines for animal experiments[27] and were carried out under the licence V244 - 57612/2022(43-4/19) of the Ministerium für Energiewende, Landwirtschaftliche Räume und Umwelt, Kiel. Keeping and breeding of mice was approved and is regularly controlled by the Veterinäramt Plön under permit: 1401–144/PLÖ-004697.

We set up four replicated semi-natural enclosures (19.6 m^2 each) and released individually marked (with RFID chips, ISO Transponders, PlanetID, 1.4 × 9 mm) 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, aged 50-100 days) as a founding generation. These focal individuals were descendants of wild-caught mice from the Cologne/Bonn region in Germany. Each enclosure contained woodchip bedding, nesting materials (toilet paper and cotton rolls) as well as thirteen nest boxes for mice to build nests/breed, and *ad libitum* food (Altromin 1324, Germany) and water (from nine feeding stations that were equally distributed in each enclosure). Temperature and light-dark cycle varied naturally, but light was supplemented between 8am and 5pm, and underfloor heating prevented temperatures below 10°C. Enclosures were covered by a roof, inaccessible to predators and, overall, closely matched the natural conditions under which house mice populations live.[28] For a detailed schematic and view of the enclosures see Figure S2. These semi-natural enclosures are an established system for wild house mouse colonies, leading to close-to-natural population development and social and genetic structure,[28] allowing mice to exhibit their natural behaviours (estimated carrying capacity of 140 individuals per enclosure, for more details on the enclosures see[29]). Finally, we conducted monthly monitorings during which all mice within an enclosure were caught, weighed, new individuals (W>10g) were fitted with RFID transponders.

METHOD DETAILS

Problem-solving

One month after introducing the founding generation, we presented four consecutive problem-solving setups[11] that mice could voluntarily access and solve (see Figure S3). Each setup was presented for two hours per night, in five different locations per enclosure simultaneously, for five consecutive nights. Locations were chosen to be in the empty space between nest boxes to minimize the chances that a box would be inside a defended territory, and therefore mice not belonging to the family could be denied access (see Figure S2). After a minimum two-week gap, the following setup was tested in the same manner. The setups were presented inside a closed test box which allowed access only through a single entrance fitted with an RFID antenna (EuroID, Netherlands) to record the mice that entered/exited. Mice could visit voluntarily and repeatedly throughout the experimental time. The bottom of the test boxes was covered with bedding from the respective enclosure to keep the olfactory cues of the environment consistent. All activity was filmed from the top (Panasonic HC-V 180, for the camera view see Video S1). Mice predominantly visit and attempt to solve alone.[13] Additionally, all seminatural enclosure experiments were performed at night under red light (which mice cannot meaningfully perceive), making it impossible for mice to visually observe the movements of each other from outside the boxes and thus reducing the possibility for any instance of observational learning to negligible levels. Mice rely on olfactory cues to locate food sources[30,31] and tactile perception to identify and manipulate objects,[32,33] making problem-solving possible without the use of vision.

The four setups required a simple movement and minimal force to be solved, ensuring that all mice, regardless of age, size, or physical strength could potentially solve. The setups were presented in the following order, and all mice could voluntarily access them: (i) omnidirectional slider, (ii) inverted cup, (iii) one-directional slider, and (iv) petri-dish (see Figure S3). To solve setup (i), individuals could push, pull, or slide the metal lid in any direction. To solve (ii), the mice could push, pull, or lift the semi-transparent cup while the base remained stable. To solve (iii) mice could do the same as in (i), but using only one direction. Last, for setup (iv), individuals should lift the lid of the petri dish. A dried mealworm (one *Tenebrio molitor* larva) was provided as reward in all setups, because mealworms

were a novel food expected to enhance the interest of mice which are neophilic towards food sources (all individuals would engage with novel problems when tested alone, i.e., in the absence of distractions,[13] 93% of the population in semi-natural enclosures visited the problem-solving boxes, and 87% interacted with the problems throughout their lives[13]). The mealworm was placed at the beginning of the trial and not replaced throughout, as rarely all five setups were solved in the same night (43% of problems were solved on average[13]). Therefore, there was ample opportunity for all mice to solve problems, regardless of their latency or frequency of attempts as the majority of problems remained unsolved at the end of the experimental night. We categorised as ''innovators'' all individuals which solved at least one setup, while ''non-innovators'' were the ones that visited the boxes, attempted to open but ultimately failed to solve any setup.

Matings and parentages

Once every month, we caught all individuals of each population and took genetic samples of the offspring as soon as they reached a minimum body mass of 10g. Following the procedure of,[34] we used seventeen microsatellite loci to assign parentage. DNA was extracted and amplified using a Multiplex PCR kit (QIAGEN) and subsequently analysed on an ABI 3730 Sequencer (Applied Biosystems). We then used GeneMarker (V2.6.4) to call alleles, and Colony (Zoological Society of London) to assign the parentages based on the maximum likelihood of each potential parental pair. We assumed sexual reproduction, a polygynandrous mating system, possible inbreeding, and all animals present the month before sampling (i.e., when juveniles were born) being possible parents.

Every pair that produced at least one offspring in a distinct litter was considered a successful mating event.[35] In the same litter, multiple offspring sired by the same father were considered to come from the same mating event, while offspring sired by different fathers in the same litter were considered multiple mating events. For all analyses concerning the reproductive decisions in the semi-natural enclosures, we examined the fitness output and the matings of the founding generation.

The results from the enclosures represent the outcomes influenced not only by female preferences but also by male-male competition, spatial constraints, and post-copulatory factors (e.g. sperm competition, cryptic female choice, and embryo loss). Furthermore, we cannot distinguish between successful matings that resulted in viable offspring and those that failed due to factors such as pup mortality (e.g., cannibalism, infanticide), which may obscure any underlying mate preferences. Additionally, females in the same social group mated with the same male at the same time in only one case, suggesting that while some form of female mate-choice copying may be present in our population, it is not a phenomenon that influences mating decisions.

Mate choice

After six months in the semi-natural enclosures, we moved all individuals to Macrolon Type III cages (LxWxH: 382 x 220 x 150 mm) containing woodchip bedding, a shelter, nesting material and a running wheel for enrichment. Adult males were housed individually to avoid aggressive interactions between them, and females were housed in pairs with former nest-mates, i.e., likely related animals originating from the same founding animals or founding females that created a bond over time. The mice were kept in the same light-dark and temperature conditions as in the enclosures, food and water were provided *ad libitum*. The animals were given several weeks to habituate to the new housing situation, and allow pregnant females to raise and wean their litters before the next phase of experiments. The mate-choice setup consisted of three standard Macrolon Type III cages with woodchip bedding, nesting material, and a carton shelter (for a graphical representation see Figure S1A). Food and water were provided *ad libitum* in the central cage and the outer parts of the satellite cages, and light and temperature were similar to conditions in the semi-natural enclosures. The central cage was connected to a satellite cage on each long side via Plexiglass tubes. Each tube was fitted with two RFID antennas (EuroID) to record the movements of the female. The satellite cages were divided by a metal grid, with roughly one-third of the cage towards the central cage and two-thirds on the outer side. Females were placed in the central cage with access to both satellite cages and males were placed in the separated parts of the satellite cages, allowing sensory interaction via smell and vocalisation but no full physical contact or mating.

The experiment lasted five days (Monday to Friday, approx. 96 hours). On the first day, we placed one innovative and one non-innovative male (from the same enclosure) in the outer parts of the two satellite cages to allow them to accept and mark them as their territory. On the morning of the second day, we placed a female of known skill (innovator or not; from a different enclosure than the males) in the central cage, and monitored her movements (time spent by the female in each location, home cage and the two satellite cages) throughout the next three days (approx. 75 hours) using the RFID antennas until noon of the fifth day when all individuals were removed. Female house mice preference has been found to stabilise after approximately 37 hours,[16] yet we allowed the experiment to run for twice that time to estimate preference with certainty.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical tests were carried out using R (version 4.4.1, R Core Team, 2024).

Mating in the enclosures

Using the known number of innovators and non-innovators of each sex in each enclosure, we calculated the expected proportion of matings between pairs of innovators, pairs of non-innovators and mixed pairs (innovators and non-innovators) assuming mating was random (see Table S1). For example, if in an enclosure 30% of males and 30% of females were innovators, we would expect 9% of matings to occur between innovator pairs (♀0.3*♂0.3), 49% of matings between non-innovators (♀0.7*♂0.7) and the remaining 42% of

matings between mixed pairs (♀0.7*♂0.3+♀0.3*♂0.7). We then used a chi-square goodness of fit test to explore if there was any significant deviation between the observed frequencies and the predicted ones.

Mate-choice experiments

We used linear models (LM, models 1 and 6) or linear mixed models (LMM, models 2–5 and 7) to detect relationships between the variables measured in the mate-choice test using the *lme4* package[36] (all models are shown in Table S2). We checked model assumptions using histograms of the residuals, and all results are presented using the *tab_model* function of the *sjPlot* package.[37] In all models, female and male skill were binary variables (i.e. 0/1; non-innovator & innovator respectively), weight was measured in grams, and time was measured in seconds.

To understand female selectivity (i.e. the strength of female choosiness), we calculated the selectivity index (SI = SD/SD(max)[16]), where SD is the standard deviation of the proportion of time spent with each male and SD(max) is the maximum possible SD (i.e. if a female spent 100% of her time with one male and 0% with the other). As a result, SI values ranged from 0 (no selectivity, equal time spent with both males) to 1 (absolute selectivity, time spent with only one male). We calculated the SI for all females for each one-hour interval as well as for the whole experiment. Then, we ran an LM (Model 1) using the mean selectivity value for every female as the response, and the female skill as a predictor variable. To understand whether the selectivity changes after the initial acclimatisation in the setup, we ran another LMM (Model 2) using the hourly selectivity value for each female, the female skill as a predictor and the female identity as a random effect, using the data collected after the first 24 hours of the experiment.

Then, we ran an LMM to assess if females spent more time with male innovators or non-innovators in the controlled mate choice test (Model 3). We used the square root (so that the data follow a Gaussian distribution) of the total time each female spent with each male across the whole duration of the experiment as a response, the male skill as a predictor and the identity of the male mouse as a random effect to control for the repeated use of males (see "Mate choice" in STAR Methods).

Then, we examined if the interaction of male and female skills affected female choice (Model 4). Similar to Model 3, this LMM had the total time each female spent with each male (square-rooted) as the response variable and the male ID as the random effect, but the predictor variable was the interaction of female skill with male skill.

Furthermore, we tested if female choice depended on the interaction of female skill and male weight, the latter being a well-established indicator of male quality and reproductive success in several rodents[17] and across animals in general.[19] Here, we ran another LMM (Model 5), which, similar to the previous two models, had the total time each female spent with each male (square-rooted) as the response variable and the male ID as the random effect, but the interaction of female skill with male weight as a predictor. Additionally, we examined, for both sexes, whether innovators and non-innovators differed in weight during the mate choice experiment to explore if there is a potential trade-off between being innovative and physical size. For the females, as each was tested only once, we ran a linear (non-mixed) model with the female weight as the response (log-transformed) and the female skill as the predictor (Model 6). Lastly, as some of the males were used multiple times, we ran an LMM with the weight as the response, the male skill as the predictor and the male identity as the random effect (Model 7). All models and the results are summarised in Table S2.

Current Biology, Volume *36*

Supplemental Information

Variation in innovation is maintained by disassortative mating and female choice

Alexandros Vezyrakis, Fragkiskos Darmis, Valeria Mazza, and Anja Guenther

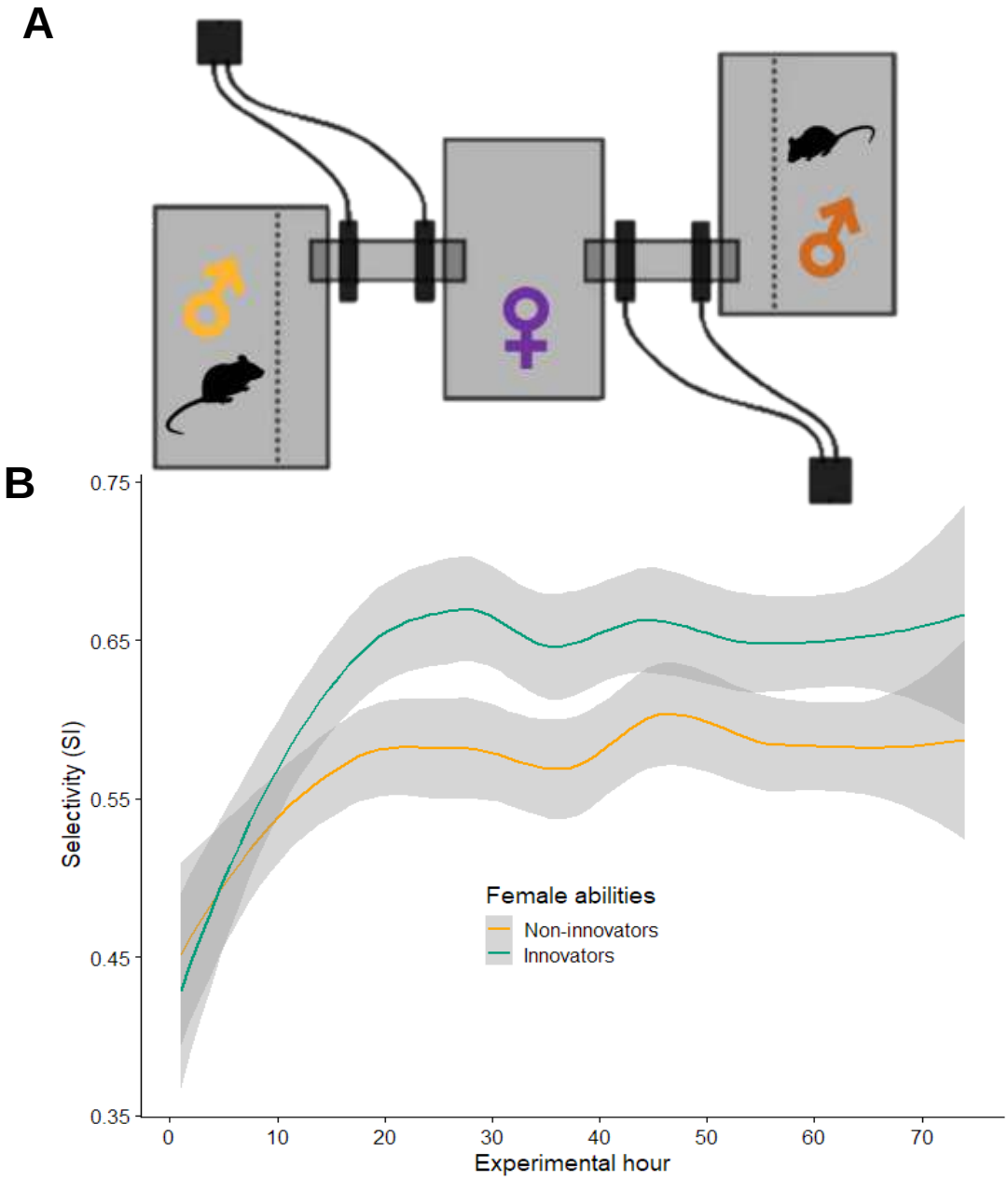
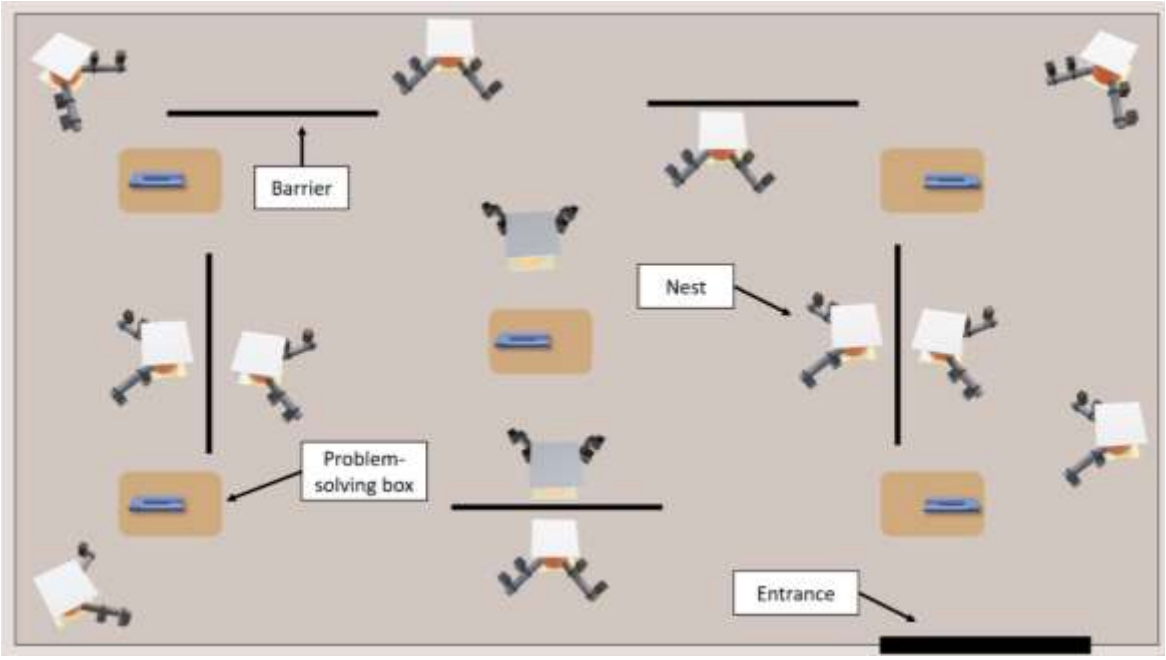


Figure S1. The two-choice setup used in the mate choice test (A) and the Selectivity Index (B). Related to STAR methods. A) A female mouse is placed in the central cage, from where she can access two satellite cages, each containing one male. The female can enter the cage of the male but they are separated by a metal mesh, here depicted as a dotted line. We placed RFID antennas that tracked the movements of the female mouse within the apparatus in the tubes connecting the satellite cages to the central cage. The cages were standard Macrolon Type III cages (L × W ×H: 382 × 220 × 150 mm), connected by clear tubes (L: 20cm, ø 5cm). B) The Selectivity Index (SI) quantifies the choosiness of a female in the mate choice test, and takes values between 0 (no selectivity, the female spends her time equally with both males) and 1 (absolute selectivity, the female spends all of her time with one male). We found no significant differences (model 1: LMM, β=0.07, SE =±0.07, p=0.31) in the SI of innovators throughout the experiment (mean±SE: 0.63±0.02) and of non-innovators (mean±SE: 0.58±0.01). This was also the case when we excluded the initial 24h, after which selectivity stabilises (model 2: LMM, β=0.07, SE =±0.04, p=0.07).

A



B

Figure S2. The seminatural enclosures. Related to STAR Methods. A diagram (A) and a picture (B) of the seminatural enclosures (3.6m × 5.5m, 19.8 m^2) when the first part of the problem-solving experiment took place. Thirteen nesting boxes were provided distributed across the enclosure. In the empty spaces between them, the five problem-solving boxes were introduced for two hours each testing night.

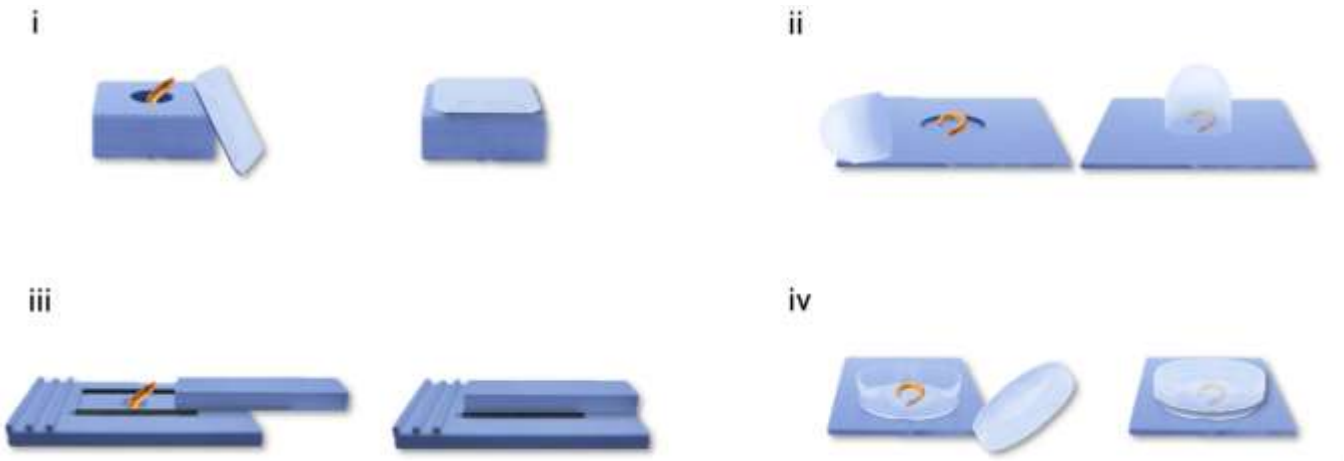


Figure S3. The four problem-solving test setups. Related to STAR methods. The setups were presented in the following order: (i) Omnidirectional slider, (ii) Inverted cup, (iii) One-directional slider and (iv) Petri-dish. Setups were baited with a dried mealworm (one *Tenebrio molitor* larva). Each setup is shown in the open (solved) configuration on the left and the closed (unsolved) configuration on the right. Overall, each setup was presented 100 times (in five locations, on five separate nights, across four enclosures) and success rates were (i) 40%, (ii) 59%, (iii) 36% and (iv) 28%. To solve each setup, 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. Setups (i) and (ii) could be solved by pushing, sliding or pulling the metal lid or plastic cup, respectively, in any direction. Setup (iii) required mice to push or pull the white block towards only one direction, and setup (iv) required them to lift the lid of the petri dish.

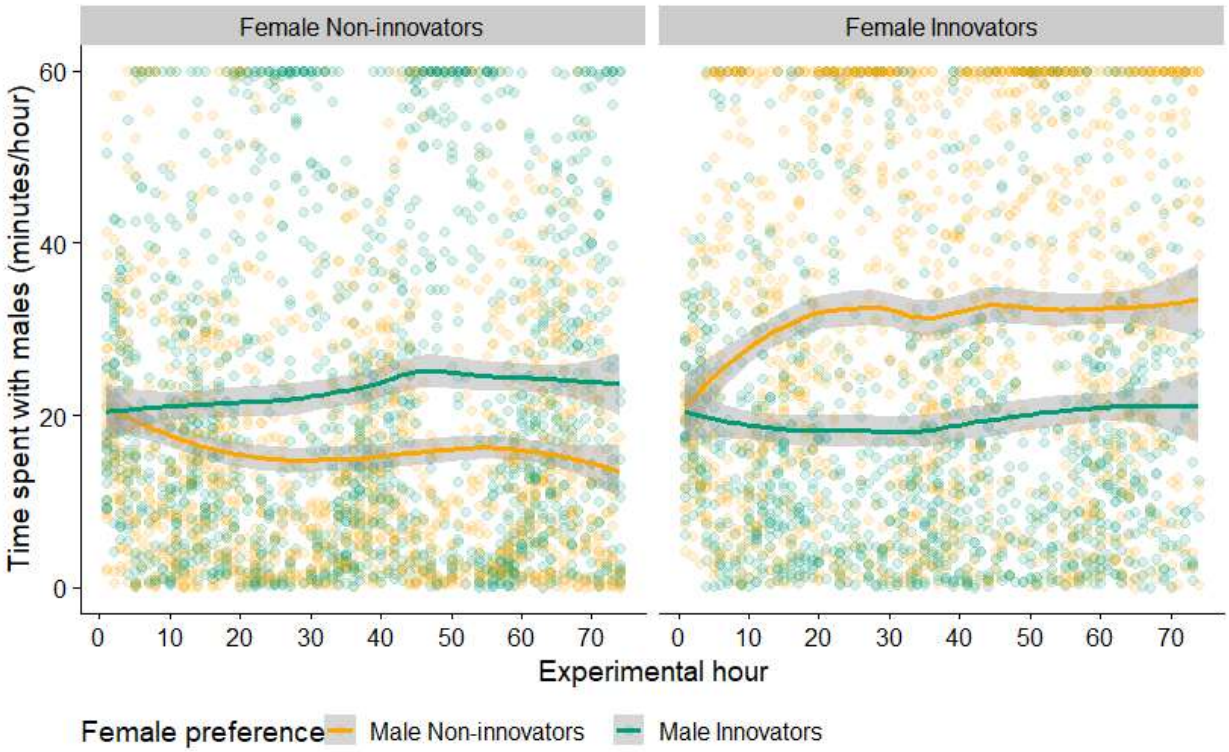


Figure S4. Time spent with males differs for females of different innovative skill, including raw data points. Related to Figure 2. Number of minutes per hour non-innovative (left) and innovative (right) females spent with innovative (green) and non-innovative (orange) males. Although in both cases females spent similar time with both males at the beginning, there was a clear differentiation as time passed, with non-innovative females spending more time with innovative males and vice versa. Lines represent *loess* smoothed observations and not LMM predicted values for visualisation purposes. Observations from 50 females (23 innovative and 27 non-innovative).

Group	No observed matings	Observed frequency	Predicted frequency	Proportional change
Non-innovators	33	0.471	0.633	-0.256
Mixed	33	0.471	0.326	0.448
Innovators	4	0.057	0.041	0.391

Table S1. **Predicted vs observed frequencies of matings in the enclosures. Related to STAR methods.**

2.1) Model 1 **Mean Selectivity index**

Predictors	*Estimates*	*SE*	*CI*	*p*
(Intercept)	0.33	0.05	0.24 – 0.43	**<0.001**
Female skill	0.07	0.07	-0.07 – 0.20	0.312
Observations	50			
R^2 / R^2 adjusted	0.021 / 0.001			

2.2) Model 2 **Selectivity index (hourly)**

Predictors	*Estimates*	*SE*	*CI*	*p*
(Intercept)	0.57	0.03	0.52 – 0.63	**<0.001**
Female skill	0.07	0.04	-0.01 – 0.15	0.071
Random Effects				
σ^2	0.10			
$\tau_{00\ female}$	0.02			
ICC	0.15			
N $_{female}$	50			
Observations	2107			
Marginal R^2 / Conditional R^2	0.011 / 0.164			

2.3) Model 3 **Total time spent with male (sqrt)**

Predictors	*Estimates*	*SE*	*CI*	*p*
(Intercept)	34.84	1.71	31.45 – 38.23	**<0.001**
Male skill	-2.38	2.42	-7.19 – 2.43	0.328
Random Effects				
σ^2	119.54			
$\tau_{00\ male}$	10.37			
ICC	0.08			
N $_{male}$	43			
Observations	100			
Marginal R^2 / Conditional R^2	0.011 / 0.090			

2.4) Model 4 **Total time spent with male (sqrt)**

Predictors	*Estimates*	*SE*	*CI*	*p*
(Intercept)	28.17	2.03	24.15 – 32.19	**<0.001**
Female skill	14.22	2.92	8.43 – 20.01	**<0.001**
Male skill	6.18	2.86	0.51 – 11.86	**0.033**
Female skill x Male skill	-18.26	4.10	-26.40 – -10.13	**<0.001**
Random Effects				
σ^2	98.41			
$\tau_{00\ male}$	5.86			
ICC	0.06			
N $_{male}$	43			
Observations	100			
Marginal R^2 / Conditional R^2	0.216 / 0.260			

2.5) Model 5 **Total time spent with male (sqrt)**

Predictors	*Estimates*	*SE*	*CI*	*p*
(Intercept)	30.35	11.50	7.52 – 53.18	**0.010**
Female skill	-53.75	21.57	-96.57 – -10.93	**0.014**
Male weight	0.04	0.44	-0.85 – 0.92	0.935
Female skill x Male weight	2.30	0.84	0.64 – 3.96	**0.007**
Random Effects				
σ^2	113.59			
$\tau_{00\ male}$	0.36			
ICC	0.00			
N $_{male}$	43			
Observations	100			
Marginal R^2 / Conditional R^2	0.142 / 0.144			

2.6) Model 6 **Female weight (log)**

Predictors	*Estimates*	*SE*	*CI*	*p*
(Intercept)	3.13	0.02	3.08 – 3.18	**<0.001**
Female skill	-0.05	0.04	-0.13 – 0.02	0.171
Observations	44			
R^2 / R^2 adjusted	0.044 / 0.021			

2.7) Model 7			**Male weight**	
Predictors	*Estimates*	*SE*	*CI*	*p*
(Intercept)	26.45	0.55	25.35 – 27.56	**<0.001**
Male skill	-1.88	0.81	-3.49 – -0.27	**0.023**
Random Effects				
σ^2	0.79			
$\tau_{00\ male}$	6.63			
ICC	0.89			
N_{male}	43			
Observations	100			
Marginal R^2 / Conditional R^2	0.107 / 0.905			

Table S2. Outcome of statistical models used in the analyses. Related to STAR methods. The response is the outcome variable of the model; the estimate shows the effect size of the indicated predictor; the *SE* is the standard error; *CI* is the confidence interval and *p* is the p value. All model estimates are given in the linear scale.