



City mice and country mice: innovative problem solving in rural and urban noncommensal rodents

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The ability to produce innovative behaviour is a key determinant in the successful coping with environmental challenges and changes. The expansion of human-altered environments presents wildlife with multiple novel situations in which innovativeness could be beneficial. A better understanding of the drivers of within-species variation in innovation propensity and its consequences will provide insights into the traits enabling animals to thrive in the face of human-induced rapid environmental change. We compared problem-solving performance of 31 striped field mice, *Apodemus agrarius*, originating from rural or urban environments in a battery of eight foraging extraction tasks. We tested whether differences in problem-solving performance were mediated by the extent and duration of the animal's exploration of the experimental set-ups, the time required to solve the tasks, and their persistence. In addition, we tested the influence of the diversity of motor responses, as well as of behavioural traits boldness and activity on problem-solving performance. Urban individuals were better problem solvers despite rural individuals approaching faster and interacting longer with the test set-ups. Participation rates and time required to solve a task did not differ between rural and urban individuals. However, in case of failure to solve a task, rural mice were more persistent. The best predictors of solving success, aside from the area of origin, were the time spent exploring the set-ups and boldness, while activity and diversity of motor responses did not explain it. Problem-solving ability could thus be a contributing factor to the successful coping with the rapid and recent expansion of human-altered environments.

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Urbanization represents one of the most severe threats for biodiversity and causes unparalleled environmental destruction and change (e.g. Grimm et al., 2008; Johnson & Munshi-South, 2017), presenting wildlife with novel challenges related to habitat loss and fragmentation, human disturbance, altered competitive interactions, new predators and parasites, novel food sources, in addition to water, soil, air and light pollution (e.g. Alberti et al., 2017; Johnson & Munshi-South, 2017; McKinney, 2002). These challenges are acting as an ecological filter, favouring species and/or populations whose life history, morphological, physiological, behavioural and cognitive traits allow them to be 'urban tolerant' or 'urban dwellers' (e.g. Charmantier et al., 2017; Fischer et al., 2015; Sol et al., 2014). Characterizing traits that enable successful animals to thrive in urban habitats will help to illuminate the determinants of successful adaptation to human-induced rapid environmental

change (HIREC; Sih et al., 2011), as well as allowing more effective mitigation strategies of the impact on anthropogenic destruction.

Innovation – the ability to produce new behaviours or to apply novel solutions to old problems (e.g. Kummer & Goodall, 1985; Reader & Laland, 2003) – has been proposed as a major predictor to the successful establishment and permanency in novel or altered habitats (e.g. Sol et al., 2002, 2013). Therefore, it might be a key trait in adapting to and persisting in urban landscapes (e.g. Ducatez et al., 2020; Lefebvre et al., 2004; Reader & Laland, 2003; Sih, 2013; Sol, 2009a, 2009b). Notable examples of innovative behaviour include milk-bottle-top opening by tits (*Parus* spp.) to access the cream underneath (e.g. Fisher & Hinde, 1949; Lefebvre, 1995), potato washing in macaques (*Macaca fuscata*) (Kawai, 1965) and dropping nuts in front of passing cars to open them by carrion crows, *Corvus corone* (Nihei & Higuchi, 2001).

Responding to challenges by novel, appropriate behaviours requires a degree of behavioural flexibility that can be cognitively demanding (e.g. Benson-Amram et al., 2016; Ducatez et al., 2020;

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Overington et al., 2011; Sol et al., 2005), which might explain the substantial variation both within and between species in the ability to add novel variants to their behavioural repertoire (e.g. Reader & Laland, 2003). While the degree of complexity and sophistication of the cognitive processes underlying innovation remains under debate (e.g. Camacho-Alpizar et al., 2020; Chen et al., 2020), there is wide support for the idea that cognitive performance underlies differences in innovation (Reader et al., 2016). Growing evidence indicates that innovation propensity represents a stable attribute of individuals (e.g. Laland & Reader, 1999; Morand-Ferron et al., 2011). Trait stability over time is often measured by an index called repeatability, representing the ratio of between-individual variance (i.e. the extent to which individuals differ in their mean trait expression when a trait is measured several times) to the total trait variation within a population (i.e. including flexible individual changes and measurement error). Repeatability normally sets the upper limit to heritability (Falconer & Mackay, 1996; Lessells & Boag, 1987), and therefore provides a rough estimate for the degree to which a specific trait can be shaped by selection and evolve (Boake, 1989; Dohm, 2002).

Recent reports show that species that do not display a high innovativeness might be forced out of anthropogenic environments (e.g. Ducatez et al., 2020), and that urban animals are more innovative than their rural conspecifics (e.g. Audet et al., 2016; Griffin & Guez, 2014; Lowry et al., 2013; Preiszner et al., 2017; Sol et al., 2013). Given the inherent difficulties of counting spontaneous emergences of innovation in the wild, innovative tendencies are often assessed by presenting animals with a novel problem or situation and measuring variation in the ability to solve it (innovative problem solving) (e.g. Griffin & Guez, 2014; Webster & Lefebvre, 2001). Since several of the factors and processes that mediate problem solving were found to overlap with those influencing and underpinning the expression of innovation in the wild, problem solving is widely considered an ecologically meaningful assay for measuring variation in innovation propensity (Griffin & Guez, 2014).

Here, we explore innovative problem-solving performance in a battery of food-extraction tasks using individuals of wild populations of rural and urban small mammals. In the past few years, studies investigating problem solving in urban dwellers have flourished, focusing, however, particularly on avian species (e.g. Bokony et al., 2014; Cook et al., 2017; Diquelou et al., 2016; Papp et al., 2015; Prasher et al., 2019; but see e.g. Daniels et al., 2019; Wat et al., 2020). In contrast, we know very little about the potential role of innovative problem solving in coping with urban environments in species more limited in dispersal, which are equally affected by anthropogenic impact but cannot easily elude the disturbances when circumstances become increasingly difficult to cope with (e.g. Ceballos, 2002; Tarabon et al., 2019). Additionally, there is comparatively little information on whether there are particular morphological or behavioural traits that distinguish successful innovators from noninnovators (e.g. Overington et al., 2011; Prasher et al., 2019; reviewed in e.g. Griffin & Guez, 2014).

An animal's performance in a problem-solving task might depend, for instance, on the extent of its interaction with the problem itself, i.e. its persistence, defined as task-directed motivation and quantified as the number of solving attempts made or time spent manipulating the experimental set-ups (e.g. Griffin & Guez, 2014; Prasher et al., 2019). Higher levels of exploration of the environment and investigation of objects are also expected to increase the encounter rate of novel situations as well as the amount of information gathered about the problem, thereby increasing the chance of solving the task (e.g. Griffin & Guez, 2014; Overington et al., 2011; Reader & Laland, 2003). Similarly, an individual's response to novelty (neophobia and neophilia) and its

propensity to take risks (i.e. boldness, e.g. Réale et al., 2007) will determine which situations and tasks are approached, sampled and learnt about (e.g. Amici et al., 2019; Griffin & Guez, 2014; Reader & Laland, 2003). Lastly, motor diversity, the tendency to produce a broader range of motor actions to accomplish a given act, often accounts for a significant fraction of the variation in innovative problem-solving propensity (e.g. Diquelou et al., 2016; Greenberg, 2003; Griffin & Guez, 2014).

Here, we aimed to compare the problem-solving performance of wild-caught, captive-held rural and urban striped field mice, *Apodemus agrarius*, using a battery of eight foraging tasks. Striped field mice are noncommensal rodents that are commonly found both in rural and urban areas of northern and central Europe (Andrzejewski et al., 1978; Łopucki et al., 2019). We also aimed to identify the potential mechanisms underpinning between-individual differences in innovation, focusing on the relative contribution of the personality traits boldness and activity, persistence and motor diversity (e.g. Guenther & Brust, 2017; Moule et al., 2016; Prasher et al., 2019; Sol et al., 2013). We hypothesized that rural and urban striped field mice consistently differ in their innovation propensity, and that noncognitive aspects such as personality and motor diversity underpin differences in problem-solving performance. Specifically, we predicted (1) that urban striped field mice would be more successful and faster problem solvers than rural conspecifics. Additionally, we predicted (2) a wider repertoire of motor actions would underpin between-individual differences in performance and that (3) bolder, more active and persistent individuals would have higher problem-solving performance. Lastly, we expected (4) that striped field mice would show consistent between-individual differences in problem-solving performance.

METHODS

Study Sites

Animals originated from rural and urban wild populations of northern Germany. Rural striped field mice ($N = 17$; 10 females, 7 males) were trapped in three different sites in the region of Uckermark (53°35'N, 13°71'E) in northwest Brandenburg (see Appendix, Fig. A1). The area is characterized by agricultural landscapes and comparatively low human population density (for further details see Dammhahn et al., 2020; Mazza et al., 2020). Urban striped field mice ($N = 14$; 7 females, 7 males) originated from three different sites in the city of Berlin (52°31'N, 13°24'E) (see Appendix, Fig. A1). Sites were part of the CityScapeLabs and AgroScapeLabs experimental platforms (von der Lippe et al., 2020; <https://www.bbib.org>). Rural trapping sites were fallow lands (ca. 0.85–1.66 ha) between arable fields, composed of grassy areas streaked with nettles, bushes and trees. Urban sites (ca. 0.75–1.16 ha) were characterized by heterogeneous vegetation including grassy areas, bushes and small trees. To get an idea of the degree of the human presence and disturbance that the animals experience in their original environment, we estimated the coverage of natural soil with artificial impervious surface (e.g. buildings and paved roads) for a 5 km buffer around each study site, as a proxy of the degree of urbanization (Buchholz et al., 2018; Dammhahn et al., 2020; Mazza et al., 2020). Sealed surface closely corresponds to other urbanization indices, such as human population density, disturbance by humans and pets, noise and light pollution (e.g. Buchholz et al., 2018; Seress et al., 2014). Sealing indexes ranged from 2.4 to 3.7 for rural sites and from 32.0 to 54.9 for urban sites, indicating a marked contrast between the level of anthropogenic disturbances that the animals were exposed to in their habitats.

Animals and Housing

We captured animals using multiple-capture live-traps (Ugglan Special Traps n. 1–2, Grahnb AB, Hillerstorp, Sweden). After a prebaiting period of two nights, traps were activated every night between 1800 and 1900 hours and checked and de-activated every morning between 0600 and 0700 hours. Captured animals were sexed, weighed and checked for reproductive status. Lactating females were immediately released at the site of capture. All other animals were given additional food and transported to our animal holding facility, where they were housed individually in standard polycarbonate cages (Typ IV, Ehret GmbH, Germany; dimensions: 59 × 38 × 20 cm) equipped with hay, bedding and carton shelters. Food (Ssniff NM/V1244-0) and water were provided *ad libitum*. Light, temperature and humidity mirrored the natural conditions occurring outside the laboratory. The mice were habituated to captivity for approximately 3 months before starting the behavioural tests and had been in captivity for approximately 12 months when the habituation for the problem-solving test battery began.

Problem-solving Test Battery

Experimental procedure

To minimize effects of between-individual variation in neophobia, all animals were habituated to the temporary addition of an unfamiliar, extraneous object (a plastic plate) in a specific corner of the home cage. Testing began once the subject successfully reached the habituation criterion of approaching the object in less than 5 min for three consecutive days (see below for more details on the habituation protocol).

Animals were tested in one task per day, during consecutive days, between 0800 and 2000 hours. We started a test session/trial only when a mouse was perceived moving in the cage (e.g. Mazza et al., 2018); this allowed us to test all animals during comparable activity levels, thereby minimizing state differences that may account for large variation in behavioural measures. Each problem-solving set-up was first presented with unrestricted access to a food reward (open), so the animal could associate the set-up with a reward and learn its location. Animals that consumed the food reward from the open set-up within 20 min were presented with a closed set-up immediately afterwards and given 10 min to solve the task and access the food reward. If an animal did not consume the food from the open set-up within 20 min, the food reward was removed and the empty open set-up was left overnight in the cage. On the following day, a second attempt with the open set-up was carried out. If the animal again did not approach or consume the food reward, it was scored as not participating in the test and was not presented with the closed set-up (3 rural and 4 urban individuals in nine open set-ups). On the following day the animal was tested in the next problem-solving set-up.

The experimenter left the room once the set-ups were placed in the cages. Each test was videorecorded and analysed for approach latency to (1) the open and (2) the closed set-up (s), (3) solving outcome (defined as 0 if the animal did not solve the task, or 1 if the animal solved the task), (4) time spent interacting with the closed set-up (later recategorized as 'latency to solve' in case of successful outcome, or 'persistence' in case of failure to open the set-up) and (5) time spent exploring the open set-up (defined as the total time spent interacting with the set-up, sniffing, touching, walking around it in a radius of 2 cm from it, extracting the food from it).

Habituation phase

The main aim of the habituation was to minimize effects of between-individual variation in neophobic responses of animals to new structures inserted in their cage, without providing information/

familiarization on the actual test set-ups. An opaque plastic plate (8 × 12.3 cm) carrying a food reward was therefore placed every day in the corner of the cage furthest from the mouse's shelter. The experimenter left the room and checked every 5 min whether the food was consumed. In case the food reward was not consumed within 40 min, the plate was left in the cage overnight. Animals advanced into the testing phase when the food was consumed within the first 5 min for three consecutive days. The food reward consisted of four different food items to allow animals to choose their preferred reward: a dry mealworm, a fresh mealworm, a quarter of a peanut and a drop of peanut butter. Food rewards were the same throughout the experiment. This allowed us to provide sufficient motivation for all animals, despite high variability in the preferred treat. All animals reached the habituation criterion within 5 weeks.

Test battery

The test battery consisted of eight tasks (Fig. 1), developed by Vrbanc, Matijević, and Guenther (in press) for house mice, *Mus musculus*, and adjusted here for striped field mice. Set-ups 1–4 tested the mice's differences in problem-solving ability and allowed each set-up to be solved by several different strategies, while set-ups 5–7 required a specific action to be opened. Therefore, while all seven set-ups tested problem solving, set-ups 5–7 specifically tested motor diversity as a potential problem-solving mechanism. Set-up 8 required a sequence of different actions to reach the solution. To prevent unintentional solutions, five of the closed set-ups were designed so that the animals had to repeat the action leading to the opening of the set-ups multiple times to access the food reward (Vrbanc et al., in press). In addition, we used a control set-up (described below) eliciting innate digging for food to investigate potential differences in motivation to interact with the set-ups. To control for the influence of learning, the set-ups were tested in fixed order.

Below is a description of each set-up (see also Fig. 1).

- (1) Slider: required removing a metal lid (4.9 × 5.7 cm) off a plastic cuboid (5.4 × 5.4 × 2 cm) with a circular well in the centre (2 cm diameter) in which the food was placed.
- (2) Petri: required lifting the upper half of a transparent petri dish (diameter 5.5 cm) containing the reward, placed on an opaque plastic plate (8 × 12.3 cm).
- (3) Tube: required extracting a ball of toilet paper from an opaque plastic tube (10 cm in length and 4 cm in diameter), laid in the cage sideways, with the opening rotated towards the animal's shelter. The other side of the tube was blocked with a plastic plug.
- (4) House: required the opening of one or both window panes (1.5 × 1.5 cm) of a LEGO bricks house (4.7 × 6.5 × 4.8 cm) to access the reward placed inside.
- (5) Carrying: the unique solution required lifting a plastic square lid (2 × 2 cm) with two metal rods (1 cm) from a three-dimensional printed plastic cuboid (9 × 9 × 1.5 cm) with a well (1.7 cm diameter) in the centre in which the food reward was placed, with a movement perpendicular to the ground. The metal rods protruded from the lid on the inner side as well (0.4 cm) and served as an anchor to prevent animals from solving the set-up by flipping the lid.
- (6) Sliding: the unique/single solution required pushing a plastic cuboid lid (8.8 × 2.2 × 1 cm) off a three-dimensional printed plastic plate (6.3 × 12.1 × 1 cm) with a circular well in the centre (1.6 cm diameter). The surface of the plate had a series of metal guides and plastic stripes that directed the movement of the lid in only one direction and prevented it from being pulled or flipped.
- (7) Opening: the unique solution required to tilt open a semi-transparent white plastic lid (3.6 cm diameter, 3.2 cm height) shaped as a half-sphere off a plastic plate (11 × 11 cm) to uncover a shallow well (diameter 3.6 cm, depth 0.3 cm) in the centre.

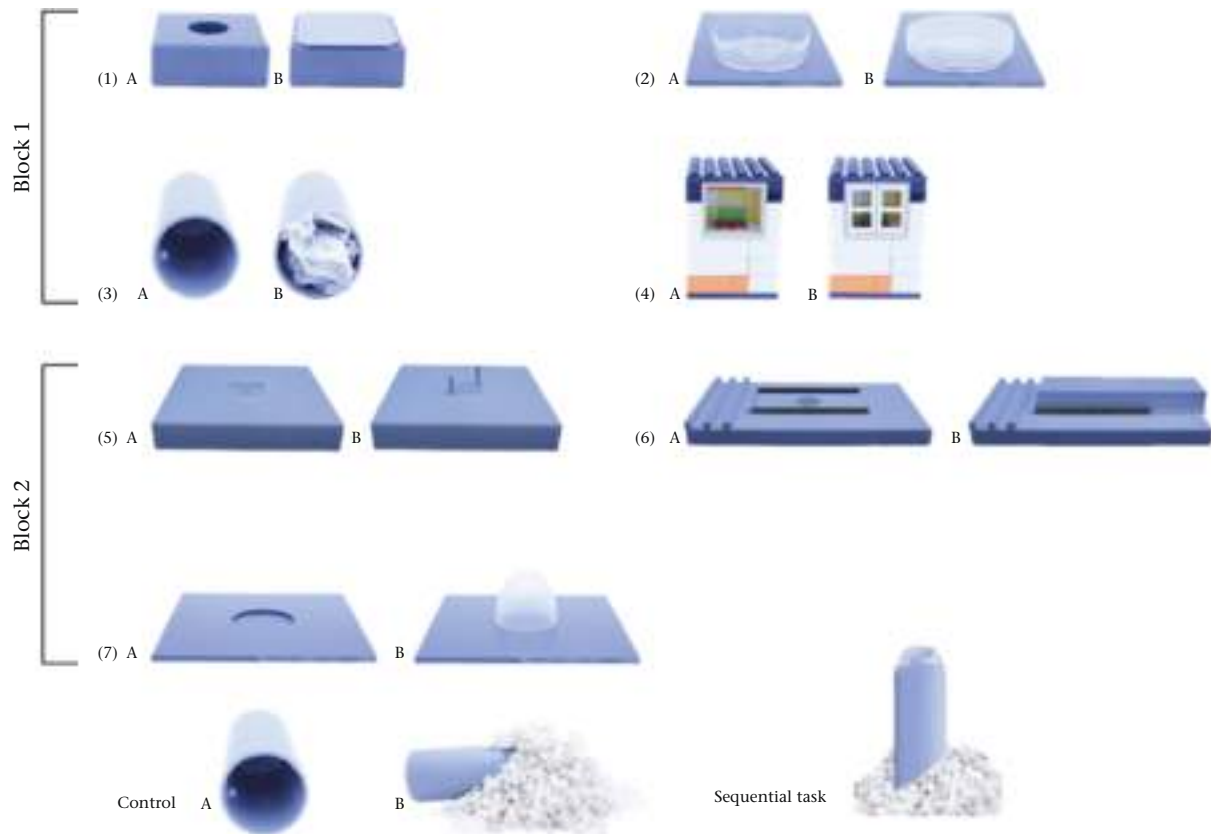


Figure 1. Problem-solving set-ups used in blocks 1 and 2 of the experiment presented open (A) and closed (B) tasks. Block 1: (1) slider; (2) petri; (3) tube; (4) house. Block 2: (5) carrying; (6) pushing; (7) opening. Set-ups 1–4 had multiple solutions; set-ups 5–7 could only be solved in one way. The sequential task was presented closed and required a two-step solution. In the control set-up, the reward could be obtained using innate digging behaviour (adapted from [Vrbanec et al., in press](#)).

Sequential task: a variant of the tube set-up (3) was used as a multiple-steps set-up 3 days after the conclusion of the test battery described above. In this case, animals were not presented with an open set-up to inspect and explore. The tube was laid in the cage vertically, with the opening towards the ceiling of the cage. Animals had to first push over the tube to reach the opening and subsequently extract the toilet paper that blocked the access to the food reward.

Control: another variant of the tube test (3) was used as a control set-up to test for the motivation in problem solving. This set-up required digging through a small pile of the animals' bedding material to free the opening of the tube and access the food reward. Digging is a natural behaviour for mice that can be performed by all animals, so the solving success could be used as a proxy for motivation to problem-solve ([Vrbanec et al., in press](#)). The control set-up was presented between tasks 4 and 5.

Boldness and activity assessment

To quantify interindividual differences in behaviours that might mediate differences in problem solving, we modified and combined standard laboratory tests that are commonly used in personality studies of small mammals – the dark–light test and the open field test (e.g. [Archer, 1973](#); [Mazza et al., 2018](#); [Schirmer et al., 2019](#)). The dark–light test classically measures willingness of individuals to leave a dark and enclosed shelter to enter an unknown, bright and potentially risky area. The open field test quantifies an individual's exploratory activity and risk-taking propensity by assuming different levels of perceived risk in different arena parts (i.e. open, exposed and risky in the centre of the arena and covered and safe along the border; e.g. [Mazza et al., 2018](#); [Schirmer et al., 2019](#)). A detailed

description of the experimental procedure is found in [Schirmer et al. \(2019\)](#). Briefly, in the dark–light test, individuals were transferred from their home cage into an opaque plastic tube (10.5×32 cm) with a swing door at each end, attached to a round arena (diameter 1.30 m, 30 cm height). Within 10 min, we quantified the latency to leave the tube with the whole body, excluding the tail (latency to emerge). If an individual did not leave the tube during the test, the latency was set to 600 s. Once the individual entered the round open field arena, we quantified the proportion of time spent actively exploring the arena (i.e. walking, running or jumping) with instantaneous 1–0 sampling every 10 s for 5 min (e.g. [Martin & Bateson, 1993](#)). All variables were quantified via direct observations. Tests were repeated with an intertrial period of 15 days and the individual mean latency to emerge and time spent active were calculated. The resulting mean values for latency to emerge were transformed inverting the signs, so that a higher score expresses higher boldness and a lower score expresses lower boldness. These average scores, defined as personality traits 'boldness' and 'activity' from here on, were used in all further steps of the analysis. They describe the relative position of each individual on the bold–shy and active–inactive axes (e.g. [Gracceva et al., 2014](#); [Mazza et al., 2018](#)) and are ecologically validated (e.g. [Mazza, Jacob, Dammhahn, Zaccaroni, & Eccard, 2019](#); [Schirmer et al., 2019](#)).

Statistical Analyses

In a first step, we compared the performance (solving outcome coded as 1/0 for success/fail) of rural and urban animals in the control task using general linear models (GLMs) with a binomial error distribution. We included origin of the animals (rural/urban),

approach latency, persistence, boldness, activity and sex of the individual as fixed effects. Nonsignificant predictors were excluded based on stepwise backward model selection using log-likelihood ratio tests comparing nested models ('ltest', 'lmtest' package; Hothorn et al., 2019) (Zuur, 2009). Full outputs of all models can be found in the Appendix (Table A2).

In a second step, we analysed problem-solving performance (solving outcome coded as 1/0 for success/fail) of rural and urban striped field mice across the whole test battery (set-ups 1–7). We used generalized linear mixed models (GLMMs, package 'lme4'; Bates et al., 2015) with a binomial error distribution. We included origin of the animals (rural/urban), set-up type (1–7), approach latency, time spent interacting with the open set-up, persistence, boldness, activity and sex of the individual as fixed effects. To account for repeated measures, we added the mice's individual identity (ID) as random factor. All continuous predictors were rescaled between 0 and 2, and mean-centred prior to running the generalized linear mixed models (e.g. Schielzeth, 2010). Before analyses, we also ensured there was no strong collinearity between model predictor variables (i.e. $r^2 > 0.70$). Differences in set-up types were further analysed by post hoc tests ('lsmeans' package; Lenth, 2016) using the false discovery rate to adjust *P* values for multiple testing, and since there were no significant differences between set-ups, this variable was excluded from further analyses (Appendix, Table A1). We then investigated the role of motor diversity in problem-solving performance by adopting the same statistical procedure as described above with subsets of data including only the tasks that had multiple solutions (set-ups 1–4, block 1) or the tasks that could only be solved by one specific action (set-ups 5–7, block 2).

We compared the problem-solving performance of rural and urban animals in the sequential task using general linear models (GLMs) with a binomial error distribution, and adding origin of the animals (rural/urban), approach latency, persistence, boldness, activity and sex of the individual as fixed effects.

To further investigate the potential role of latency to approach the open set-up, latency to approach the closed set-up and duration of the interaction with the open set-up on problem-solving performance, we used linear mixed models (LMMs, package 'lme4'; Bates et al., 2015) where we fitted the respective variable as response and origin of the animals, boldness, activity and sex of the individual as fixed effects. Animal ID was added as random effect. Based on preliminary data exploration, the time spent interacting with the closed set-up was recategorized as 'latency to solve' in case of successful outcome, or as 'persistence' in case of failure to open the set-up, and analysed with the same statistical procedure.

We compared boldness and activity measures of rural and urban mice with a Mann–Whitney *U* test. To determine whether individuals performed consistently across tasks, we calculated the repeatability of problem-solving success, latencies, time spent exploring the open set-up, latency to solve or persistence in case of failure as well as boldness and activity ('rtpr' package; Nakagawa & Schielzeth, 2010; Stoffel et al., 2017). We estimated 95% confidence intervals (CI) of repeatabilities for each variable by parametric bootstrapping ($N = 1000$ simulation iterations) and *P* values by 1000 permutations. Latencies were log transformed, and the proportion of time intervals animals spent active in the open field was arcsine square-root transformed.

The accepted significance level was ≤ 0.05 . All data analyses were conducted with R version 3.2.3.

Ethical Note

Animal capture and behavioural tests were conducted under the permission of the Landesamt für Umwelt, Gesundheit und

Verbraucherschutz Brandenburg, the Landesamt für Arbeitsschutz, Verbraucherschutz und Gesundheit, Brandenburg, the Landeshauptstadt Potsdam, Fachbereich Soziales und Gesundheit, Veterinär- und Lebensmittelüberwachung, the Senatsverwaltung für Stadtentwicklung und Umwelt and the 'Landesamt für Gesundheit und Soziales. Experiments were performed in accordance with all applicable international, national and/or institutional guidelines for the use of animals, including the ASAB/ABS Guidelines for the use of animals in research. We took great care in ensuring the animals' welfare throughout the experimental procedure and afterwards.

Trapping (reference numbers: IIIB2/OA/AS/G1394, RO7/SOB-0998A-C, 2347-7-2019) was conducted using multiple-capture live-traps (Ugglan Special Traps n. 1-2, Grahnb AB, Hillerstorp, Sweden), equipped with plenty of food and apples as water sources. Traps were activated every night between 1800 and 1900 hours and checked and de-activated every morning between 0600 and 0700 hours. We covered the traps with grass, branches and leaves to provide shade and avoid overheating. In case of rainy nights, trapping was suspended. Lactating females were immediately released at the site of capture. All other animals ($N = 31$ adult striped field mice; 17 females, 14 males) were given additional food and transported to our animal holding facility. If two or more animals were captured in the same trap, they were separated in unoccupied traps to avoid potentially stressful interactions during the transport. For the transport, animals were given additional food, i.e. oat flakes, apples and cucumbers to provide water sources. Traps were firmly secured to avoid shakings and accidental opening. Temperature was kept constant at 20 °C to avoid overheating.

Animals were housed individually in the animal holding facility (reference number: 386-1) in standard polycarbonate cages (Typ IV, Ehret GmbH, Germany; dimensions: 59 × 38 × 20 cm) that incorporated biologically relevant enrichment features such as natural material and refuges. Food (Ssniff NM/V1244-0) and water were provided ad libitum. Light, temperature and humidity mirrored the natural conditions occurring outside the laboratory. We ensured that the mice learnt to recognize the water bottles as water sources by placing fresh apples and cucumbers directly above the bottles for the first week of captivity. Animals were kept captive for 18 months and were released at their capture sites after the conclusion of this experiment, using a soft-release protocol.

Behavioural observations and testing (reference numbers: G 0072/16 and 2347-7-2019) were designed to allow voluntary participation from the animals, and cage set-up allowed animals that did not want to participate to remain undisturbed in their shelters. Animals were offered desirable food rewards and were never food-deprived to increase motivation. Animals were never subjected to any form of potentially harmful manipulation. Disturbance by the experimenter was minimized by video-recording the tests, so that presence in the room was not required.

RESULTS

Participation rates were 93.7% for rural and 89.9% for urban striped field mice. Out of the 145 closed set-ups that were presented, rural striped field mice approached 133 (91.7%) and solved 69 (51.9%), while out of the 126 closed set-ups presented to the urban striped field mice, 108 (86%) were approached and 83 solved successfully (77%). In the control task, animals from both environments performed similarly ($\beta = -0.24 \pm 1.08$, $t = -0.22$, $P = 0.82$; Fig. 2b). Urban striped field mice had higher solving success compared to rural conspecifics in tasks 1–7 ($\beta = 4.33 \pm 1.09$, $t = 3.96$, $P < 0.001$; Fig. 2a, Table 1), although rural striped field mice approached both the open and closed set-ups faster than urban ones (open: $\beta = 0.57 \pm 0.28$, $t = 2.04$, $P = 0.041$; closed: $\beta = 0.91 \pm 0.29$, $t = 3.15$, $P = 0.002$) and spent more time

interacting with the open set-ups ($\beta = -5.38 \pm 0.92$, $t = -5.82$, $P < 0.001$). Urban mice also outperformed rural ones in the sequential task ($\beta = 2.01 \pm 1.01$, $t = 2.00$, $P = 0.046$; Fig. 2a). In addition, solving success was higher for urban animals also when differentiating between set-up types (block 1: $\beta = 1.18 \pm 0.46$, $t = 2.53$, $P = 0.011$; block 2: $\beta = 2.01 \pm 0.81$, $t = 2.47$, $P = 0.014$). Both boldness ($\beta = 0.01 \pm 0.002$, $t = 2.92$, $P < 0.001$) and the amount of time spent exploring the open set-up ($\beta = 2.39 \pm 0.53$, $t = 4.49$, $P < 0.001$) predicted solving success (Fig. 3, Table 1).

Animals approached the set-ups progressively faster with repeated exposure to the set-ups: the mean latency to approach the open set-up decreased from 400.4 ± 342.9 s in the first test of the battery (slider) to 204.8 ± 231.9 s in the last (opening), and the mean latency to approach the closed set-up decreased from 214.9 ± 182.06 s to 145.7 ± 143.7 s (open: $\beta = -0.11 \pm 0.03$, $t = -4.12$, $P < 0.001$; closed: $\beta = -0.08 \pm 0.03$, $t = -2.56$, $P = 0.01$).

When considering only animals that successfully solved the tasks, the latency to solve was similar for rural (mean $\pm$ SD = 89.8 ± 86.2 s) and urban (94.5 ± 122.3 s) striped field mice ($\beta = -0.31 \pm 0.26$, $t = -1.20$, $P = 0.23$). However, rural mice were more persistent than urban conspecifics when they failed to open the set-up ($\beta = -1.10 \pm 0.45$, $t = -2.42$, $P = 0.015$), on average trying for 84.8 ± 66.0 s while urban animals gave up after 64.6 ± 126.1 s. Rural and urban striped field mice exhibited similar levels of boldness (Mann–Whitney U test: $W = 6051.5$, $N_1 = 17$, $N_2 = 14$, $P = 0.63$) and activity ($W = 5390$, $P = 0.34$).

Problem-solving performance, latency to approach the open and closed set-ups, time spent exploring the open set-up, boldness and activity were highly repeatable (all $R \geq 0.30$; Fig. 4, Appendix, Table A3). Latency to solve the set-up was not repeatable, while persistence in case of failure was repeatable (Fig. 4, Appendix, Table A3).

DISCUSSION

The potential to produce and express innovative behaviour is likely to affect an individual's success in novel or challenging environments. In this study we tested whether striped field mice from rural and urban environments differed in their success rate in an innovative problem-solving test battery, and whether possible predictors mediate the difference in problem-solving performance. We found that urban mice performed better than rural conspecifics throughout the battery and that they required less time exploring the experimental set-ups to achieve higher solving probability. In

contrast, rural mice were faster to approach the experimental set-ups and showed higher persistence when they could not solve the task. Furthermore, when analysing the predictors of problem-solving performance, we found that bolder animals had higher rates of success.

Problem Solving of Urban and Rural Mice

In accordance with our first prediction, urban striped field mice outperformed their rural conspecifics in the test battery as well as in the sequential task conducted a few days later. Animals of both environments performed equally well in the control test designed to elicit innate digging behaviour, suggesting that differences between rural and urban animals were not caused by differences in general foraging behaviour, cautiousness in approaching the experimental set-ups or motivation. Both rural and urban individuals had high participation rates, indicating that we could minimize innate differences such as neophobic reactions by the extensive habituation protocol we implemented. Even though striped field mice are noncommensal, and there could be no familiarity or previous knowledge of the structures and set-ups we presented, urban mice might have come across human-made material (e.g. plastic and garbage) in their habitat of origin more often compared to rural mice. The high participation rates and faster approach or rural mice indicate that the results are not driven by lack of familiarity or neophobia. Finding higher problem-solving success in urban-living striped field mice is in line with previous findings on avian species (e.g. Audet et al., 2016; Ducatez et al., 2020; Griffin & Guez, 2014; Lowry et al., 2013; Preiszner et al., 2017; Sol et al., 2013), suggesting a ubiquitous response to human-altered environments even across taxa. The 'cognitive buffer hypothesis' suggests that the variability of the environment would select for increased cognitive abilities due to large brains, based on the assumption that these are associated with flexible use of environmental information and production of novel behavioural responses, that in turn buffer the individual against instability and rapid environmental changes (e.g. Benson-Amram et al., 2016; Sol, 2009a, 2009b). High innovation propensity would prove particularly advantageous in coping with environments that present the individual with challenges never encountered before, fast-paced changes (sensu Sih et al., 2011) or circumstances that would rarely occur in their natural environments (e.g. Cook et al., 2017; Sih, 2013; Sih et al., 2011; Sol et al., 2013). Human alterations of habitats and urbanization are not new processes, but they do

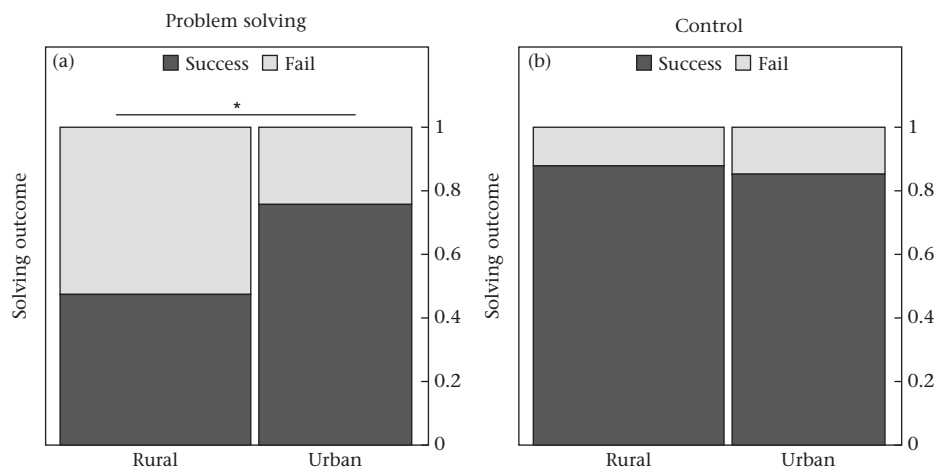


Figure 2. Success rates in (a) the problem-solving battery (set-ups 1–7, $N = 190$ participated tests) for 31 striped field mice, *Apodemus agrarius*, and (b) the control task ($N = 29$ participated tests) targeting innate digging behaviour for 29 striped field mice. Asterisks indicate significant differences from zero with $P < 0.05$.

Table 1
Problem-solving performance for 31 individual striped field mice, *Apodemus agrarius*

Variable	Fixed factors	Estimate	SE	t	P	R _m	R _c
Solving success	Intercept	−1.40	0.61	−2.28	0.023	0.50	0.75
	Area (urban)	4.33	1.09	3.96	<0.001		
	Boldness	1.27	0.436	2.92	0.004		
	Time exploring open set-up	2.39	0.53	4.49	<0.001		
Time exploring open set-up (sqrt)	Intercept	17.11	0.62	27.71	<0.001	0.28	0.42
	Area (urban)	−5.38	0.92	−5.82	<0.001		
	Activity	−4.42	2.32	−1.91	0.057		
Latency to approach open set-up (log)	Intercept	5.25	0.22	24.35	<0.001	0.10	0.51
	Area (urban)	0.57	0.28	2.04	0.041		
	Set-up no.	−0.11	0.03	−4.12	<0.001		
Latency to approach closed set-up (log)	Intercept	4.92	0.23	21.43	<0.001	0.15	0.50
	Area (urban)	0.91	0.29	3.15	0.002		
	Set-up no.	−0.08	0.03	−2.56	0.010		
Latency to solve set-up (log)	Intercept	7.47	0.59	12.57	<0.001	0.07	0.07
	Area (urban)	−0.31	0.26	−1.20	0.230		
	Boldness	−1.81	0.69	−2.63	0.023		
Persistence (log)	Intercept	6.18	0.48	12.89	<0.001	0.23	0.29
	Area (urban)	−1.10	0.45	−2.42	0.015		
	Boldness	0.001	0.001	1.19	0.236		
	Time exploring open set-up	0.001	0.001	0.89	0.376		
Solving success set-ups 1–4 (block 1)	Intercept	−0.002	0.001	−1.27	0.205	0.14	0.15
	Area (urban)	0.02	0.27	0.07	0.946		
	Boldness	1.18	0.46	2.53	0.011		
	Set-up no.	0.46	0.22	2.07	0.039		
Solving success set-ups 5–7 (block 2)	Intercept	−0.62	0.50	−1.25	0.210	0.30	0.50
	Area (urban)	2.01	0.81	2.47	0.014		
	Boldness	1.03	0.44	2.35	0.019		
Solving success control set-up (LM)	Intercept	1.95	0.76	2.57	0.010	0.005	0.005
	Area (urban)	−0.24	1.08	−0.22	0.823		
Solving success sequential task (LM)	Intercept	−0.41	0.65	−0.63	0.530	0.243	0.243
	Area (urban)	2.01	1.01	2.00	0.046		

Shown are the results for the test battery and for the separate experimental blocks, control set-up and sequential task, time spent exploring the open set-ups, latency to approach the open and closed set-ups, latency to solve the set-ups and persistence in relation to area of origin (rural versus urban), boldness, activity, set-up number (1–7) and latency to approach the set-up. Reference levels are given in parentheses. Marginal R^2 values (R_m) are based on fixed factors, conditional R^2 value (R_c) includes random effects, i.e. individual identity (ID). Statistically significant P values are shown in bold.

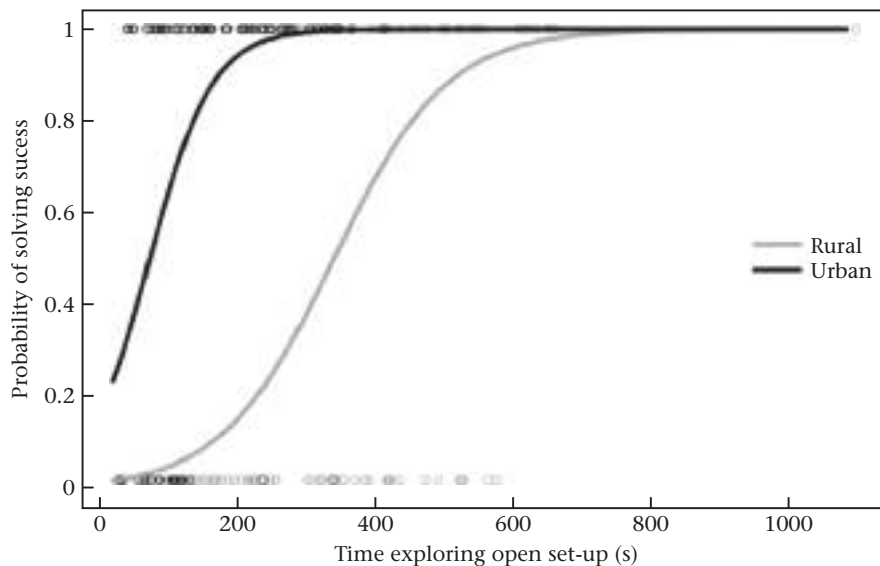


Figure 3. Probability of solving the task projected against the amount of time spent inspecting the set-up for rural and urban striped field mice, *Apodemus agrarius*. Presented are effects obtained from GLMM for visual representation ($R_m = 0.41$; $R_c = 0.72$) and raw data of individuals (dots).

present animals with specific challenges, for which their evolutionary past might not have prepared them (e.g. McDonnell & Hahs, 2015), and they occur at faster rates than ever before, for example, as a consequence of the dramatic increase in human population (e.g. Cohen, 2003; Pimentel & Pimentel, 2006), which in turns leads to unprecedented concentration of human activities, human

presence and direct and indirect disturbances (e.g. Corsini, Marrot, & Szulkin, 2019) that urban dwellers have to cope with.

The city of Berlin, where we captured the urban mice, underwent a process of urbanization and expansion only in the last 250 years (e.g. Arandelovic & Bogunovich, 2014; Reulecke & Reulecke, 1977; <http://atlasofurbanexpansion.org/cities/view/Berlin>). Before

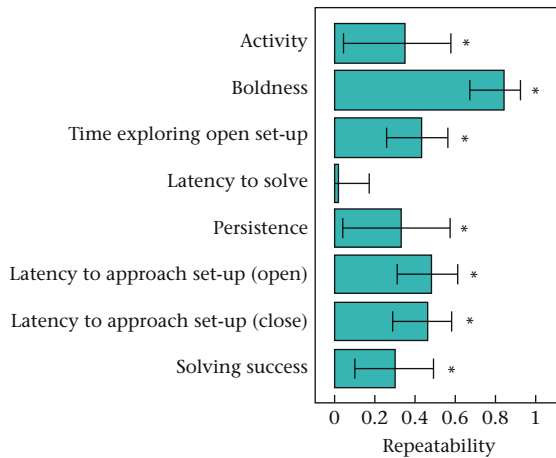


Figure 4. Repeatability estimates and their 95% confidence intervals of problem-solving success, latencies to approach the set-ups, time spent exploring the open set-up, latency to solve the set-up, persistence when failed, boldness and activity for 31 striped field mice, *Apodemus agrarius*. Asterisks indicate significant differences from zero with $P < 0.05$.

that time, it consisted mainly of villages separated by wide rural areas (e.g. Arandelovic & Bogunovich, 2014; Reulecke & Reulecke, 1977). This comparatively recent urbanization process implies that the striped field mice population had to face and solve the challenges associated with anthropogenic expansion and disturbance only relatively recently. These challenges encompass most of an individual's fitness-determining choices, from navigating increasingly fragmented habitats due to structural changes of parks, yards and buildings, compensating the lack of natural food sources, i.e. specific seeds, by identifying and exploiting novel food sources, recognizing and dealing with novel predators and competitors as well as higher numbers of dogs and cats, while coping with the heightened human disturbance and pollution (e.g. Cook et al., 2017; Sih, 2013; Sih et al., 2011; Sol et al., 2013). Expressing innovative behaviours as solutions to the novel forms of these old problems thus would favour certain individuals and could be a key factor in determining their ultimate success in urban environments (e.g. Ducatez et al., 2020; Prasher et al., 2019).

At present, we are unable to determine which mechanisms underlie the observed differences in problem-solving performance between rural and urban striped field mice. Sol et al. (2013) suggested three potential mechanisms that would explain the widespread phenotypic differences observed between rural- and urban-living animals: (1) higher behavioural plasticity in urban individuals compared to rural ones, (2) nonrandom sorting and (3) evolutionary change via divergent selection. The ability to plastically modify behaviours is one of the main adaptive mechanisms through which animals can solve ecological problems and cope with novel environmental pressures (e.g. Ducatez et al., 2020; Lefebvre et al., 1997; Reader & Laland, 2002; Sol et al., 2016). However, in the present study, animals were kept in captivity for ca. 12 months before being tested for problem solving, and if the differences in performance were due to the flexible adjustment to environmental circumstances, mice from all environments should have achieved comparable success. Further studies adopting a common garden approach should investigate whether these differences can arise from developmental processes such as canalization or higher learning abilities (i.e. flexibility) (e.g. Bateson, 1982; Bergmüller, 2010; Braithwaite & Salvanes, 2005;

Waddington, 1942). Similarly, we still lack information on whether and how individuals disperse along and across the urban gradient to gain insights into potential nonrandom sorting of the individuals. Lastly, our study is no proof that microselection is actually happening since long-term studies and/or replacement studies with matching and nonmatching conditions would be needed; however, we find considerable evidence that problem-solving performance is a stable individual trait on which selection is likely to act.

Evolutionary inferences can be drawn from phenotypic observations only to the degree to which observed phenotypic variation corresponds to underlying additive genetic variation (the phenotypic gambit; Grafen, 1984) (e.g. Dochtermann et al., 2015). The stable between-individual component of behavioural responses was shown to have a genetic basis (e.g. Carere et al., 2005; Dingemanse et al., 2002; Dochtermann et al., 2015; van Oers et al., 2004). Repeatability estimates, representing the ratio of between-individual variation to the whole phenotypic variation, often represent an upper boundary of genetic influences and are considered a valid and promising tool for making evolutionary inferences (Dochtermann, 2011; Dochtermann et al., 2015). We found problem-solving performance to be a repeatable trait in striped field mice with a comparable amount of repeatable variation in comparison to other behavioural traits for which a heritable basis has been proven (e.g. Bell et al., 2009; Dochtermann et al., 2015). In addition, we also found the approach and interaction with test set-ups to show repeatable behavioural variation, indicating that the way in which individuals investigate novel aspects of their environment is a stable trait that might influence behavioural and especially cognitively challenging decisions and strategies in general (e.g. Dall et al., 2005; Rojas-Ferrer et al., 2020). These findings are in line with the conclusions of several other studies, which have shown that problem-solving performance is consistent across time and different tasks, and consolidates the idea that innovation propensity represents a stable attribute of individuals (e.g. Cole et al., 2011; Griffin, Lermite, et al., 2013; Guenther & Brust, 2017; Laland & Reader, 1999; Morand-Ferron et al., 2011; Papp et al., 2015), which could be the target of natural selection (e.g. Bell et al., 2009; Morand-Ferron et al., 2011). And since the costs and benefits of innovating in any given environment may fluctuate faster than an individual's behavioural propensities can change (Overington et al., 2011), species with large variation in innovativeness would be able to adjust to a broader range of habitats, which would in turn yield marked population differences (Griffin, Guez et al., 2013; Griffin, Lermite, et al., 2013).

Urban striped field mice also performed better than rural ones in the sequential task. In this task, animals had only one trial with the set-up, and no chance to explore it open beforehand. To obtain the reward, they had to perform a specific sequence of goal-directed actions. Although we can only speculate on the underlying mechanisms (chaining, generalization, insight), our results suggest that urban mice were more successful in performing the sequence of connected actions required to solve the complex problem compared to rural ones, perhaps reflecting the more complex challenges that anthropogenic environments present to animals. Papp et al. (2015) reported that urban house sparrows, *Passer domesticus*, were more successful than rural ones only in the most difficult problem-solving task, provided they had relatively larger body mass. Future studies explicitly addressing the mechanisms required to complete multistep problem-solving tasks and varying both the sequence and the previous experience of the individuals will help illuminate the processes underpinning the solution of cognitively demanding tasks and the potential role of a

variety of cognitive traits in adjusting to complex, novel environments.

Mediators and Predictors of Problem-solving Performance

According to our second prediction, bolder animals were better problem solvers. This finding is in line with previous studies showing that boldness, defined as an individual's reaction to any risky situation (Réale et al., 2007) often correlates positively with innovativeness (e.g. Bouchard et al., 2007; Overington et al., 2011; Webster & Lefebvre, 2001). Innovation potentially offers benefits in terms of discovery of new resources or mating success, but is also likely to carry costs, like the risk of ingesting poisonous food or increased predation risk (e.g. Reader & Laland, 2003); risk-prone individuals might therefore be more likely to express innovative behaviour and accept the risks it implies in the pursuit of bigger rewards. While responses connected to boldness often differ in field studies of rural and urban conspecifics (e.g. Lowry et al., 2013; Sol et al., 2013), our measures of risk taking in the laboratory did not show differences between rural and urban striped field mice. We believe that the lack of differences in boldness might have arisen from an adjustment to prolonged captivity. We base this interpretation on the results of a similar experiment conducted with another small mammal species (common voles, *Microtus arvalis*); while animals tested in their natural environment showed differences in exploration and risk-taking tendencies, these differences were annulled after a few months in a common environment (Mazza et al., 2020). Interestingly, rural striped field mice approached the set-ups faster than urban ones, although this difference in latency did not influence the probability of solving the set-ups. This also suggests that the latency to approach the experimental set-ups did not strictly reflect boldness, i.e. risk taking. Responses to novel, unfamiliar objects in the cages are a standard measure of neophobia/neophilia. Neophobia is defined as the aversion that an animal displays towards approaching a food item, object or place simply because it is novel (Greenberg, 2003). Studies comparing problem-solving abilities and neophobia of populations that experience different degrees of environmental harshness and instability reported mixed findings (e.g. Kozlovsky et al., 2015; Roth et al., 2010; Tebbich & Teschke, 2014). The same inconsistency characterizes studies conducted in urbanized contexts (e.g. Audet et al., 2016; Ducatez et al., 2017). Our results support the conclusions reached by Griffin and Guez (2014) and Audet et al. (2016) that neophobia does not necessarily covary with problem solving and that urbanization affects each of these traits (problem-solving ability, boldness, neophobia) independently.

The second behavioural variable we measured, activity in the open field, did not explain problem-solving performance. Conflicting results have been reported concerning the relation between spatial exploration and innovativeness across taxa (e.g. Lermite et al., 2017; Prasher et al., 2019), suggesting that links between spatial exploration and problem-solving performance might be task and species dependent (e.g. Cole et al., 2011).

We also found no indication that problem-solving performance was mediated by population differences in motor diversity (Vrbanec et al., in press). The animals' performances did not differ for the different set-ups used, both when analysed for an effect of set-up and when investigating set-ups with multiple versus specific solving strategies. This suggests that both populations possessed similar repertoires of motor actions in general. This finding contrasts with results reported both in avian and primate literature that found motor diversity to be an important predictor of problem-solving performance (e.g. Benson-Amram et al., 2016; Griffin & Guez, 2014; Manrique et al., 2013). Further attention is

needed on this aspect regarding small, short-lived mammals such as rodents, in order to understand the potential significance of this difference.

In the present study, the extent of the interaction with the open set-up was one of the best predictors of problem-solving performance for all animals, in line with our third prediction. Interindividual comparisons have pointed consistently to a central role of object/task exploration in problem-solving ability, with those individuals that engage more with the task being more likely to solve and/or solve faster (e.g. Griffin & Guez, 2014; Johnson-Ulrich et al., 2019; Thornton & Samson, 2012), although explorative tendencies alone are not sufficient for innovation to arise (Thornton & Samson, 2012). One possible explanation is that longer interaction provides the individual with more information about the set-up, thus enabling it to later perform an appropriate action (i.e. the opening of the lid) to access the reward. In the present study, rural animals spent more time interacting with the open set-ups than urban conspecifics but still achieved lower problem-solving success. In other words, urban mice needed to invest less time in gathering information to achieve better success.

Rural animals were faster in approaching and, if they successfully solved the task, they did it within a similar latency to solve compared to urban animals, suggesting that the difference in solving success was not due time constraints but to the potential to innovate. When successfully solving a task, the latency to do so was highly variable both within and between individuals, as each set-up might have presented each subject with specific challenges. Interestingly, persistence when unsuccessful was instead repeatable. When not being successful in solving, urban mice desisted after a few attempts, possibly because they either have shorter attention span, or because in their original environment multiple food sources are available throughout the year and investing too much time in attempting to get one item would create a higher missed opportunity cost compared to rural habitats where food sources could be more unevenly distributed in space or time, thus making persistence advantageous (e.g. Chow et al., 2016; Prasher et al., 2019; Shochat et al., 2006).

In conclusion, this study shows environment-related differences in problem solving, with better performance associated with urbanization, one of the most widespread human-induced environmental changes. Overall, our results are consistent with the idea that living in human-altered environments might favour increased problem-solving performance and that urban striped field mice combine a higher potential to express innovative behaviour with need for less time to gather information. Innovation may thus play a key role in the individual's success in the colonization of human-altered environments. Understanding the role of innovation, boldness and other behavioural traits in the repertoire of urban-dwelling animals is thus an important step to understand why some species can persist and thrive in human-altered habitats while others perish.

Declarations of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2020.12.007>.

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Appendix

Table A1

Results of the post hoc test comparing the experimental set-up, with *P* values adjusted for multiple comparisons using Tukey method

	Lsmean	SE	Asymptote confidence limit (CL)	
			Lower CL	Upper CL
<i>Set-up type</i>				
Carrying	0.45	0.72	−0.96	1.86
House	0.59	0.76	−0.90	2.07
Opening	0.98	0.69	−0.38	2.33
Petri	0.55	0.70	−0.82	1.92
Slider	1.40	0.67	0.09	2.72
Sliding	1.68	0.75	0.22	3.15
Tube	1.05	0.70	−0.32	2.43
	Estimate	SE	z	P
<i>Contrast</i>				
Carrying–House	−0.14	0.95	−0.14	1.00
Carrying–Opening	−0.53	0.86	−0.61	1.00
Carrying–Petri	−0.10	0.89	−0.11	1.00
Carrying–Slider	−0.95	0.84	−1.13	0.92
Carrying–Sliding	−1.24	0.90	−1.37	0.82
Carrying–Tube	−0.60	0.87	−0.69	0.99
House–Opening	−0.39	0.91	−0.43	1.00
House–Petri	0.04	0.91	0.04	1.00
House–Slider	−0.82	0.89	−0.92	0.97
House–Sliding	−1.10	0.96	−1.15	0.91
House–Tube	−0.47	0.91	−0.51	1.00
Opening–Petri	0.43	0.85	0.50	1.00
Opening–Slider	−0.43	0.81	−0.53	1.00
Opening–Sliding	−0.71	0.85	−0.83	0.98
Opening–Tube	−0.08	0.83	−0.09	1.00
Petri–Slider	−0.85	0.82	−1.04	0.94
Petri–Sliding	−1.13	0.87	−1.31	0.85
Petri–Tube	−0.50	0.84	−0.60	1.00
Slider–Sliding	−0.28	0.85	−0.33	1.00
Slider–Tube	0.35	0.82	0.43	1.00
Sliding–Tube	0.63	0.87	0.72	0.99

Table A2

Full models output for problem-solving performance for 31 individual striped field mice, *Apodemus agrarius*

Variable	Fixed factors	Estimate	SE	t/z	P	R _m	R _c
Solving success	Intercept	−1.85	0.96	−1.93	0.053	0.51	0.76
	Area (urban)	4.34	1.16	3.75	<0.001		
	Boldness	1.32	0.56	2.35	0.019		
	Time exploring open set-up	2.48	0.57	4.34	<0.001		
	Set-up type (house)	0.14	0.95	0.14	0.886		
	Set-up type (opening)	0.53	0.86	0.61	0.539		
	Set-up type (petri)	0.10	0.89	0.11	0.910		
	Set-up type (slider)	0.95	0.84	1.13	0.257		

Table A2 (continued)

Variable	Fixed factors	Estimate	SE	t/z	P	R _m	R _c
Time exploring open set-up (sqrt)	Set-up type (sliding)	1.24	0.90	1.37	0.172	0.29	0.42
	Set-up type (tube)	0.60	0.87	0.69	0.488		
	Latency approach set-up	0.30	0.39	0.76	0.447		
	Persistence	0.11	0.26	0.41	0.680		
	Sex (M)	-0.02	0.84	-0.03	0.976		
	Activity	0.13	0.49	0.27	0.791		
	Intercept	17.79	0.78	22.90	<0.001		
	Area (urban)	-5.00	0.94	-5.34	<0.001		
	Boldness	0.002	0.003	0.56	0.573		
	Latency approach set-up	-0.002	0.002	-0.95	0.343		
Latency to approach open set-up (log)	Sex (M)	-1.04	0.92	-1.12	0.262	0.14	0.53
	Activity	-5.70	2.80	-2.03	0.042		
	Intercept	5.18	0.25	20.96	<0.001		
	Area (urban)	0.57	0.28	2.02	0.043		
	Boldness	-0.001	0.001	-0.55	0.583		
	Set-up no.	-0.11	0.03	-4.12	<0.001		
	Sex (M)	0.15	0.29	0.53	0.596		
	Activity	-0.75	0.87	-0.86	0.390		
	Intercept	4.71	0.89	5.28	<0.001		
	Area (urban)	0.87	0.29	2.96	0.003		
Latency to approach closed set-up (log)	Boldness	-0.001	0.001	-0.84	0.402	0.18	0.52
	Set-up no.	-0.08	0.03	-2.56	0.011		
	Sex (M)	0.25	0.30	0.83	0.408		
	Activity	-0.27	0.84	-0.32	0.746		
	Intercept	6.47	0.99	6.52	<0.001		
	Area (urban)	-0.11	0.35	-0.32	0.752		
	Boldness	-0.001	0.001	-0.50	0.615		
	Sex (M)	-0.07	0.29	-0.23	0.822		
	Time exploring open set-up	0.001	0.001	1.34	0.179		
	Latency approach set-up	0.0003	0.001	0.30	0.765		
Latency to solve set-up (log)	Activity	-0.88	0.88	-0.99	0.321	0.09	0.09
	Intercept	7.64	1.24	6.15	<0.001		
	Area (urban)	-1.11	0.48	-2.31	0.021		
	Boldness	0.002	0.001	1.66	0.098		
	Sex (M)	0.43	0.40	1.07	0.285		
	Time exploring open set-up	0.001	0.001	0.43	0.666		
	Latency approach set-up	-0.002	0.001	-1.61	0.108		
	Activity	-1.62	1.16	-1.40	0.163		
	Intercept	0.02	0.35	0.07	0.946		
	Area (urban)	1.63	0.59	2.76	0.006		
Solving success set-ups 1–4 (block 1)	Boldness	0.52	0.30	1.77	0.078	0.17	0.18
	Latency approach set-up	-0.33	0.33	-1.00	0.317		
	Persistence	0.04	0.27	0.15	0.883		
	Sex (M)	-0.46	0.45	-1.02	0.308		
	Activity	-0.18	0.28	-0.64	0.520		
	Intercept	-0.68	0.65	-1.05	0.294		
	Area (urban)	2.16	0.85	2.55	0.011		
	Boldness	1.39	0.65	2.13	0.033		
	Latency approach set-up	-0.06	0.48	-0.13	0.894		
	Persistence	0.26	0.32	0.80	0.423		
Solving success set-ups 5–7 (block 2)	Sex (M)	-0.13	0.74	-0.17	0.863	0.34	0.52
	Activity	-0.29	0.48	-0.60	0.548		
	Intercept	4.04	2.03	1.99	0.047		
	Area (urban)	-0.79	1.68	-0.47	0.639		
	Boldness	0.64	0.83	0.76	0.445		
	Time exploring open set-up	-0.01	1.00	-0.01	0.990		
	Latency approach set-up	0.81	1.54	0.52	0.601		
	Persistence	0.54	0.96	0.57	0.569		
	Sex (M)	-2.59	1.83	-1.42	0.156		
	Activity	-1.16	1.10	-1.06	0.290		
Solving success control set-up (LM)	Intercept	-0.94	0.91	-1.04	0.297	0.44	0.44
	Area (urban)	2.42	1.37	1.76	0.078		
	Boldness	-1.06	1.05	-1.00	0.317		
	Latency approach set-up	0.19	0.61	0.31	0.754		
	Persistence	0.25	0.69	0.36	0.720		
	Sex (M)	1.20	1.27	0.95	0.342		
	Activity	0.73	0.75	0.98	0.325		
	Intercept	-0.94	0.91	-1.04	0.297		
	Area (urban)	2.42	1.37	1.76	0.078		
	Boldness	-1.06	1.05	-1.00	0.317		
Solving success sequential task (LM)	Latency approach set-up	0.19	0.61	0.31	0.754	0.53	0.53
	Persistence	0.25	0.69	0.36	0.720		
	Sex (M)	1.20	1.27	0.95	0.342		
	Activity	0.73	0.75	0.98	0.325		
	Intercept	-0.94	0.91	-1.04	0.297		
	Area (urban)	2.42	1.37	1.76	0.078		
	Boldness	-1.06	1.05	-1.00	0.317		
	Latency approach set-up	0.19	0.61	0.31	0.754		
	Persistence	0.25	0.69	0.36	0.720		
	Sex (M)	1.20	1.27	0.95	0.342		

Shown are results for the test battery and for the separate experimental blocks, control set-up and sequential task set-up, time spent exploring the open set-up, latency to approach the open and closed set-ups, latency to solve the set-ups and persistence in relation to area of origin (rural versus urban), boldness, activity, set-up number (1–7) and latency to approach the set-up. Marginal R^2 values (R_m) are based on fixed factors; conditional R^2 value (R_c) includes random effects, i.e. individual identity (ID). Reference levels are given in parentheses. Statistically significant P values are shown in bold.

Table A3
Repeatabilities of problem-solving success, latencies to approach the set-ups, time spent exploring the open set-up, latency to solve, persistence in case of failure, boldness and activity for 31 striped field mice, *Apodemus agrarius*

Variable	R	SE	CI	P
Solving success	0.30	0.10	0.096–0.492	<0.001
Latency approach set-up (open)	0.46	0.08	0.288–0.583	<0.001
Latency approach set-up (closed)	0.48	0.08	0.313–0.614	<0.001
Latency to solve	0.02	0.05	0–0.17	0.442
Persistence	0.33	0.14	0.043–0.568	0.023
Time inspecting open set-up	0.43	0.08	0.261–0.557	<0.001
Boldness	0.84	0.06	0.671–0.919	<0.001
Activity	0.36	0.16	0.047–0.654	0.024

CI: confidence interval. Statistically significant *P* values are shown in bold.

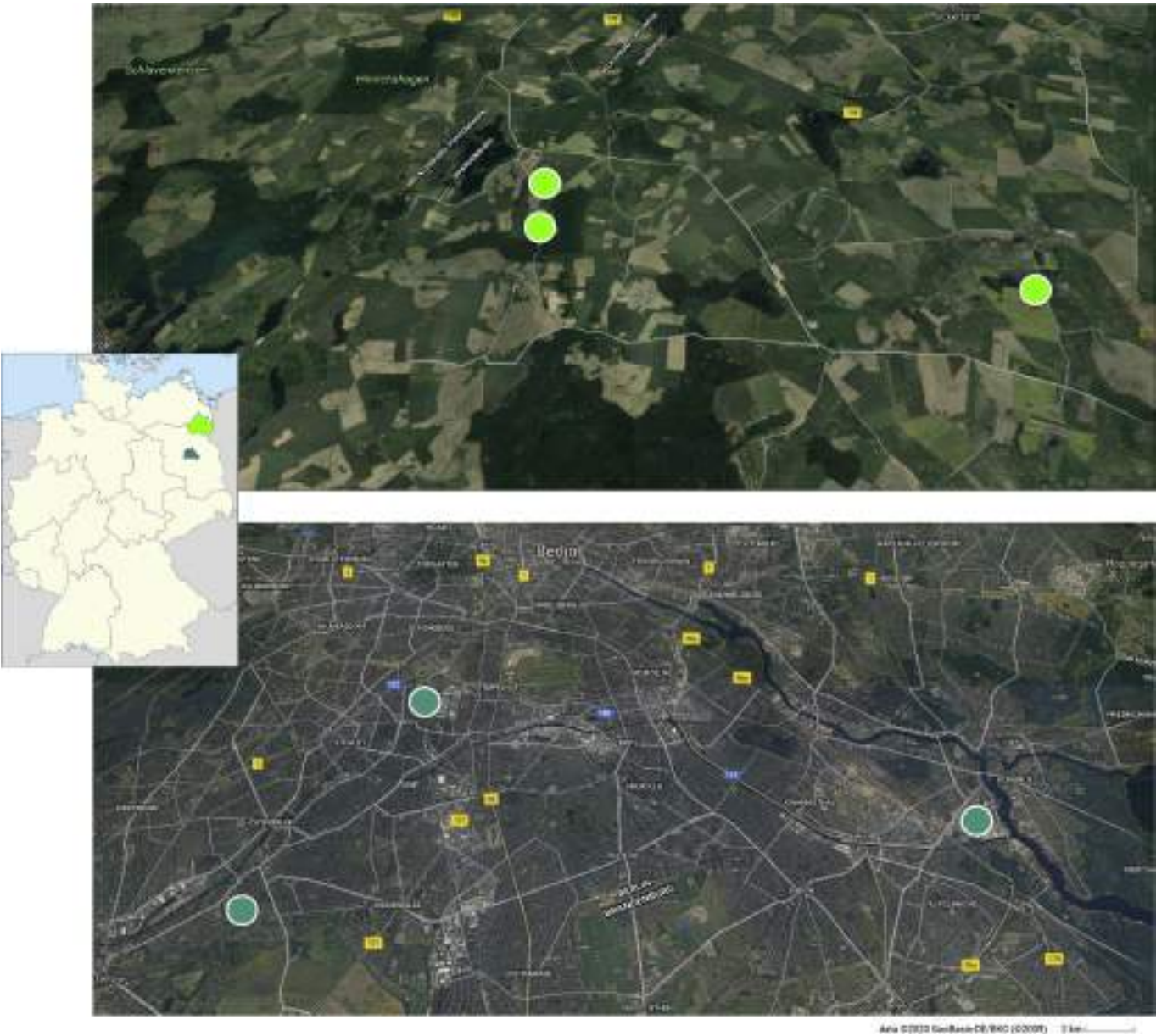


Figure A1. Locations of the rural (green, upper) and urban (blue, lower) study sites (adapted from Mazza et al., 2020).