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How to explore a new environment: exploratory tactics of the black rat (*Rattus rattus*)

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Abstract

The black rat (*Rattus rattus*) is a unique model for studying exploratory tactics due to its enormous colonizing potential. Considerable behavioral variability and consistent interindividual differences might help populations inhabit new environments and persist there even under intense pressure. Additionally, the affinity of the black rat for climbing might be another advantage, widening their potential niche. In this study, we describe the exploratory tactics of the black rats when introduced to a novel environment. In the first experiment, we tested 12 rats and calculated repeatability of their behaviors across 12 sessions of an enriched open-field test. We concluded that climbing is a highly repeatable behavior that serves as an important source of interindividual variability. In the second experiment, we tested 24 black rats in a unique L-shaped arena. Each rat was tested twice. We found that the majority of rats distributed their activity evenly, exploring each part of the apparatus for a similar amount of time, thus maximizing their chances of finding resources. Nevertheless, these "even" explorers still greatly differed in their level of activity, orderliness and affinity for climbing, generating large variability. In contrast, the minority of rats concentrated their activity only on a section of the new environment and were therefore characterized as selective explorers. Overall, we concluded that a combination of such exploratory tactics as well as a bias for even explorers enables black rats to quickly colonize new environments and persist there even under unfavorable conditions.

Key words: 3D, behavior, climbing, repeatability, strategy.

Despite the similar appearance and close phylogenetic relation (Aplin et al. 2011), the black rat (*Rattus rattus*) and the Norwegian rat (*Rattus norvegicus*) differ in their ecology and behavior. The black rat is reported to prefer warmer and drier microhabitats and is usually considered more arboreal (Aplin et al. 2003; Shiels et al. 2014). It seems to prefer structurally complex environments, preferably with dense vegetation cover (Cox and Cox 2000). Consequently, the movements of the black rat are more rapid (Barnett 1975), it is slightly more agile when climbing and can keep balance on thinner surfaces (Foster et al. 2011). Most importantly, the black rat readily explores at heights (Cox and Cox 2000), which is in contrast to the Norwegian rat which explores mostly on the ground surface. In natural forests (e.g., in New Zealand), the black rat tends to dominate the Norwegian rat (e.g., Harper et al. 2005; reviewed in Harper and Bunbury 2015). Nonetheless, when directly confronted, the Norwegian rat dominates the black rat owing to its higher aggressiveness and larger body size (Barnett 1975). This extends to an urban environment, with which the Norwegian rat is strongly associated (Feng and Himsworth 2014); the Norwegian rat might push the black rat out to higher places (for example, roofs) where food resources are scarcer, eventually resulting in complete displacement (Barnett and Spencer 1951).

The black rat is well known for its dispersal abilities and large capacity for colonizing new environments (e.g., Nolte et al. 2003). Coupled with their ability to take advantage of human transport paths (e.g., Berthier et al. 2016), this colonizing potential has had serious consequences on the indigenous flora and fauna of many Pacific islands (Aplin et al. 2003). Fast life history, omnivore diet, and relatively small body size are certainly key factors behind their success (Shiels et al. 2014). Nonetheless, certain behavioral traits may be similarly important. First, exploratory behavior allows rats to locate resources such as food, water, or shelter, and to collect information on local topography (Barnett 1956). This is crucial for successful settlement of a new environment. Second, King et al. (2011) showed that black rats might prosper in complex, structured environments due to their unique foraging strategy characterized by a nearly constant movement through space and utilization of all 3 dimensions. Affinity for climbing might make a wider range of resources available to the black rat, increasing the probability of successful colonization. Lastly, behavioral flexibility might be especially advantageous when colonizing an environment different from the natal one. Indeed, several studies show that black rats are very flexible in their behaviors, for example, feeding preferences (Quillfeldt et al. 2008) or nest building (Matsui et al. 2010). Yet, exploratory behaviors of wild-derived rats, especially vertical exploration (e.g., climbing) and use of space, as well as the variability of exploratory behavior, are seldom studied. Our study is, therefore, the first step toward

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understanding vertical exploration and use of space in the black rat. This research uses a novel approach of combining standard laboratory methods with tasks more suitable for wild animals, which should provide a better insight into their exploration behavior.

When studying exploration, researchers often use standard laboratory methods with one being particularly common—an open field test (OFT; Hall 1934; Wilson et al. 1976). For several decades now (e.g., Archer 1973) it has been discussed that rodents show stable inter-individual differences in behavior (Réale et al. 2007). Stability of these inter-individual differences in time is described by repeatability (reviewed in Žampachová et al. 2017b) and seems to be present in both wild and wild-derived animals (e.g., Petelle et al. 2013; Guenther and Trillmich 2015; Kelley et al. 2015) as well as laboratory-bred animals (e.g., Rudolfová et al. 2022). In rodents, these inter-individual differences are commonly assessed by the above-mentioned OFT (Žampachová et al. 2017b), which was previously also used for black rats; specifically, for estimating repeatability of exploratory behavior (Žampachová et al. 2017a). Utilizing OFT, Eilam and Golani (1989) described that if the animals are given enough time, they establish a "home base"—a place where the animal spends the longest time and readily returns to. From a behavioral point, home bases are also associated with a high frequency of grooming and rearing (Wallace et al., 2008). Even though some behavioral differences found in the OFT correspond well to those found under more natural conditions (e.g., Krebs et al. 2019), combining laboratory and field (or wild-like) research might yield important insights into animal behavior (Horn et al. 2022). Several previous studies have, for example, found that even not commonly reported vertical behaviors, such as jumping, may be important when studying exploration of wild-derived rodents (*Rattus rattus*, Žampachová et al., 2017a; *Mus musculus*, Frynta et al. 2018; *Mastomys natalensis*, Vanden Broecke et al. 2019; *Acomys sp*., Štolhoferová et al., 2020).

The few existing studies on exploration of a 3-dimensional environments yield interesting results. It has been shown that laboratory mice (*Mus musculus*) made more mistakes in a spatial learning task in a 3D radial maze than in a 2D setup (Wilson et al. 2015). Laboratory Norwegian rats were often found to divide complex 3D environment into horizontal levels and explore each relatively independently (Grobéty and Schenk 1992; Hagbi et al. 2020, 2022). Crucially, it has been shown that species ecology affects rodent behavior in tests of exploration (e.g., Wilson et al. 1976; Frynta et al. 2018) and that climbing is one of the most affected behaviors (Gielam et al. 2020; Hagbi and Eilam 2022). Apart from the above-mentioned study by Foster et al. (2011), studies on exploratory behavior of the black rat focusing on movement through 3D space are missing.

For this reason, we constructed a large adjustable arena, designed specifically for testing species with vertical activity. Our arena was constructed on the basis of the OFT, but we introduced 2 important modifications: 1) we added wire mesh so the animals could climb and use the third dimension of the arena as well (Štolhoferová et al. 2020); 2) the arena consists of 3 open field cubes, which can be separated or interconnected, allowing for testing in a more complex and considerably larger environment. This unique setting allowed us to test wild-derived black rats in an apparatus similar to the classic OFT (Ohl 2003) but adjusted for their ecology. Therefore, in this enriched arena, the animals were able to express their exploratory behavior over a much wider range.

In this study, we describe the exploratory behavior of the black rat in 2 separate experiments with a particular focus on climbing and vertical activity. In the first experiment, we aimed to assess the repeatability of the black rat's exploratory behaviors, including previously unreported climbing behaviors. To suppress habituation over 12 trials of the experiment, we alternated between 3 testing arenas that were stacked on top of each other, thus introducing novelty for each trial, even though the properties of the experimental arena remained the same. We chose this design to better assess repeatability of exploratory behavior that, by definition, occurs only in novel situations (e.g., in a novel environment, toward a new object; Réale et al. 2007). In the second experiment, we aimed to comprehensively describe exploratory behavior of the black rat in a more complex environment. To this end, we defined and analyzed 4 separate aspects of exploratory behavior—the absolute level of activity, affinity for climbing, spatial orderliness, and temporal orderliness. The main questions of the second experiment were: 1) What tactics (spatial distribution of activity) do black rats use during exploration of a new environment? Which tactics are common and which tactics are rare? 2) How do the absolute level of activity, affinity for climbing, spatial orderliness, and temporal orderliness relate to each other? 3) Which parts of the arena are key areas of interest? Do black rats form a home base?

Materials and Methods

Animals

The tested animals were black rats (*Rattus rattus*) from a laboratory-kept population. They represented approx. the twelfth to fifteenth generation derived from wild-caught founders of the colony (14 males and 14 females). For more details, see Žampachová et al. (2017a). The rats were reared in large family groups of 20–30 individuals. Sawdust was used as bedding, ceramic flowerpots as shelters, and cardboard boxes were added for enrichment. Branches and wire mesh ceilings provided an opportunity for climbing from young age. Standard food pellets for mice and rats (ST1, Velaz Ltd., Czech Republic) occasionally supplemented with fruits, vegetables, and dry bread were provided ad libitum. Water was available at all times.

In Experiment 1, the subjects were 12 adult males. Two months before the start of the experiments, the tested animals were separated from their natal group and housed in pairs in glass terrariums (60 × 50 × 40 cm) placed in a different room. The cage-mates came from the same family group and were of similar age. The new terrariums were smaller than the natal ones and half of their side walls and/or ceiling were made of wire mesh. Other aspects of the husbandry remained the same.

In Experiment 2, the subjects were 12 adult males and 12 adult females housed in same-sex groups of 3. One female died before the second repetition, hence only 23 rats finished the experiment. We excluded this individual from analyses comparing both repetitions (analyses of exploratory tactics) but kept it in the rest (home base and factor analyses). The husbandry of the animals was the same as in Experiment 1. No animal was used in both experiments to ensure the novelty of the situation.

Testing apparatus

The testing apparatus consisted of 3 modular cubic arenas (80 × 80 × 80 cm). The cube arenas were made of Plexiglass set into a metal skeleton (18 mm wide hems), except for the back sides made of wire mesh enabling rats to climb and the front sides made of glass.

In Experiment 1, the cubes stood on top of each other and were separated by opaque sheets of plexiglass creating 3 separate arenas. The cubes differed only in their position and are further referred to as the bottom (B), middle (M), and top (T) cubes (Figure 1A). With this stacking design, we created a novel environment by changing the height of the testing arena between each trial. We chose this design to better assess repeatability of exploratory behavior that, by definition, occurs only in novel situations (e.g., in a novel environment, towards a new object; Réale et al. 2007).

In Experiment 2, the cubes were positioned in an L shape and are further referred to as the left (L), right (R), and the upper (U) cube (Figure 1B, C). The walls (sidewalls/floor/ceiling) that would separate the cubes were removed to create one large arena. The plastic ceiling of the upper cube was replaced by a wire mesh to allow for climbing. Three additional pieces of wire mesh (20 × 80 cm) were put along the right bottom edge of each cube, creating a shelf between the R and U cubes.

Experimental procedures

Experiment 1 consisted of 12 testing days, 1 trial per day, thus 12 trials in total. The testing was divided into four 3-day

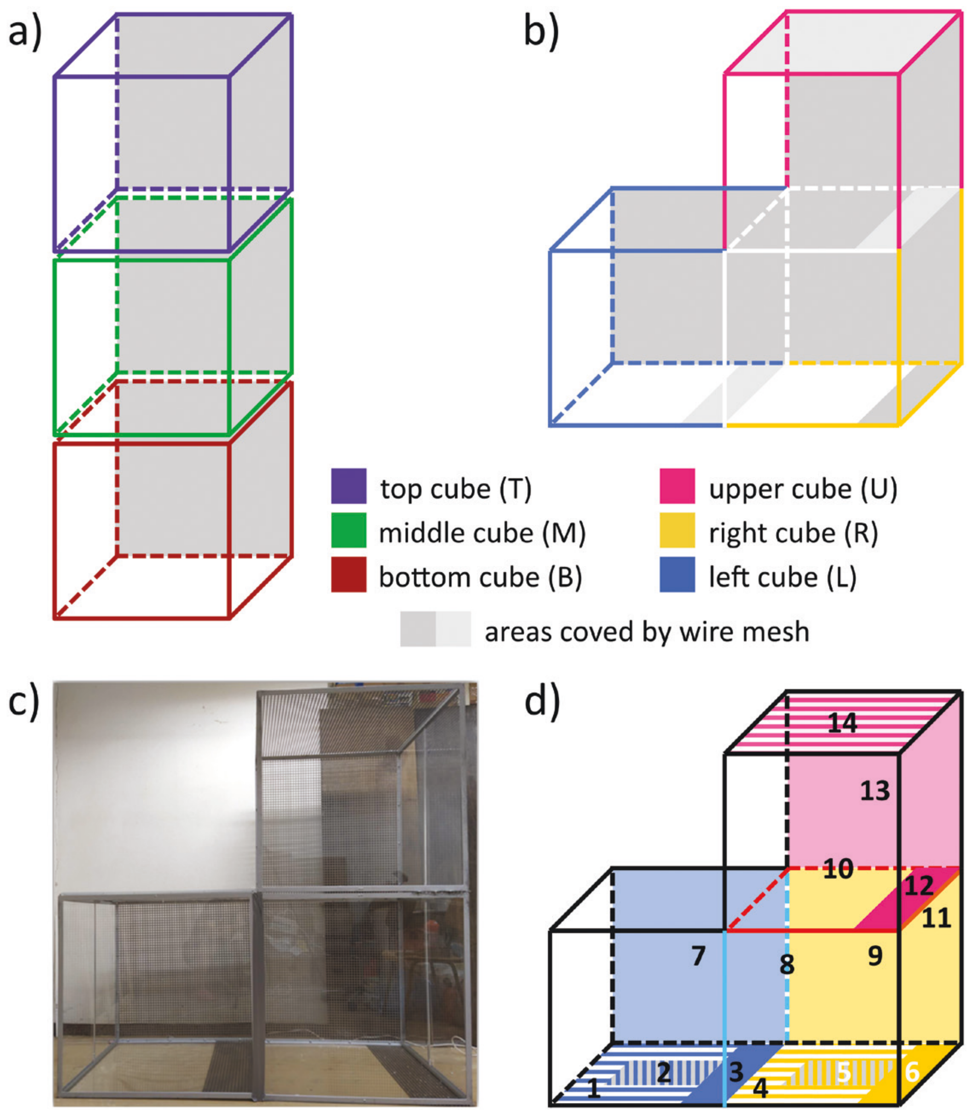

Figure 1. Testing apparatus. A) In Experiment 1, the cubes were standing on top of each other and were separated by opaque sheets of plexiglass. B) In Experiment 2, the cubes were assembled into one large, connected, L-shaped arena. Areas covered by wire mesh are in grey. C) A photo of the experimental apparatus assembled for Experiment 2. D) In Experiment 2, we defined 14 areas: 1—by-the-wall part of the L cube's floor, 2—centre of the L cube's floor, 3—wire-mesh-covered part of the L cube's floor, 4—by-the-wall part of the R cube's floor, 5—centre of the R cube's floor, 6—wire-mesh-covered part of the R cube's floor, 7—back wire mesh wall of the L cube, 8—vertical metal hems of the left and right cubes, 9—back wire mesh wall of the R cube, 10—horizontal metal hems of the upper cube, 11—wire mesh shelf of the U cube, 12—wire mesh shelf from below, 13—back wire mesh wall of the U cube, 14—ceiling of the U cube.

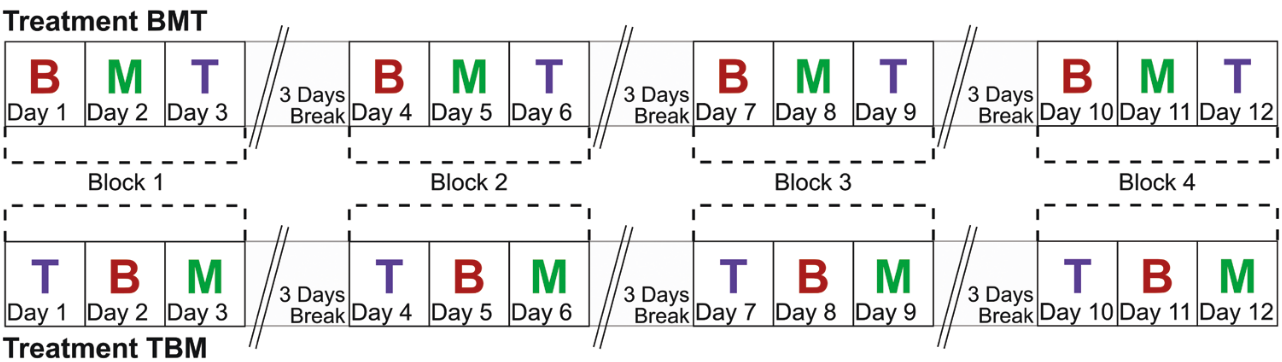

Figure 2. An example of the experimental schedule of Experiment 1. The experiment consisted of 12 testing days (Days 1–12) divided into four 3-day blocks (Blocks 1–4) separated by a 3-day break. The order of the cubes a subject was tested in is called a treatment. Because there were 3 cubes, there were 6 possible treatments randomly assigned to subjects. The figure shows the schedule for 2 treatments—treatment BMT (upper line) and TBM (lower line). B—bottom cube, M—middle cube, and T—top cube.

blocks separated by a 3-day break. During each block, a subject was tested once in each cube; subjects were randomly assigned a fixed order of cubes for the whole experiment (Figure 2). Each day, the order in which subjects were tested was decided by drawing lots. Each trial lasted for 10 min.

In Experiment 2 each animal was tested twice—the repeated testing took place after a 4-week break. The longer break between the trials was introduced to allow rats to partially forget details of the environment thus boosting the novelty essential for assessing exploration. For the first trial, subjects were tested in a semi-random order (it remained the same for the second trial). Thirty minutes per trial were analyzed.

Before being tested in either experiment, each subject was put in a transport box and left for 20 min in the keeping room; the experimenter was not present. Because rats were not used to manipulation, this offered them a chance to calm down before the experiment. Afterward, the rat was gently nudged into the testing arena. After the experiment, the subject was weighed and returned to its home cage, and the arena was cleaned using 96% ethanol to neutralize the odors. All manipulations were performed under a red light of low intensity (approx. 5 lx) and the experiments were recorded on a video camera in the experimenter's absence. The experiments were performed between 6:30 p.m. and 1 a.m., matching the peak activity period of black rats (Vobrubová et al. 2021).

Behavioral analysis

All videos taken in Experiment 1 were analyzed using ACTIVITIES software (Vrba and Donát 1993). The behavioral analysis was blinded; the experimenter was not provided with the identity of the rat or trial in the videos before the analyses were completed. We noted 12 behaviors: rearing against the wall, rearing against the wire mesh, jumping (including jumping on/off the wire mesh), climbing the wire mesh (count), locomotion, and immobility (sitting and grooming) on the ground and locomotion and immobility (pausing and grooming) on the wire mesh (duration), and latency to climb the wire mesh. The dataset generated during the experiment is available in Supplementary Table S1.

All videos taken in Experiment 2 were analyzed using the BORIS software (Friard and Gamba 2016) and the behavioral analysis was blinded. We noted the duration of 4 behaviors—locomotion, rearing, sitting (or pausing for vertical surfaces and upside-down positions), and grooming—each separately for 14 areas in the arena (Figure 1D). Additionally, we noted the number of jumps, climbing bouts, and transfers between the cubes. In this experiment, we were interested in 4 distinct aspects of exploratory behavior: level of activity, affinity for climbing, spatial orderliness, and temporal orderliness (see below). Locomotion, rearing, jumping, and the number of transfers were used for the characterization of exploratory behavior and its subsequent analysis. Sitting (pausing) and grooming were noted to identify the location of a home base. The dataset generated during the experiment is available in Supplementary Table S2.

Statistical analysis

In Experiment 1, repeatability adjusted for trial (Biro and Stamps 2015) was computed using package rptR (Stoffel et al. 2017) implemented under the software R (R Core Team 2020). For counts of rears, jumps, and climbing bouts, we used original values and Poisson error distribution (log link). For the rest (durations and latency), we used Gaussian error distribution and Box–Cox transformation (Box and Cox 1964; package car, Fox and Weisberg 2019) to improve normal distribution of the entered variables and subsequently of the residuals. The number of parametric bootstraps, as well as permutations was set to 1,000 (Stoffel et al. 2017). Additionally, repeatability adjusted for trial and cube and repeatability adjusted for trial, cube, and break before the testing day (yes/no factor) was also computed.

In Experiment 2, the statistical analyses were conducted in R, package lme4 (Bates et al. 2015). The workflow of the analyses is shown in Figure 3. Because spatial orderliness (evenness) was our prime interest in Experiment 2, we first focused on how rats distribute their activity between different parts of the arena. We chose the cube as the unit of interest because the cubes were very similar to each other (in size, accessible surfaces, and climbing opportunities), and thus directly comparable. To describe the evenness of exploratory behavior on the individual level, we used the Shannon Equitability Index (E_H). The index takes values from 0 = complete unevenness to 1 = complete evenness and can be used to compare the "size" (number of elements) of any number of groups (sets) but is usually used to compare species abundance in ecology (Sheldon 1969; Kricher 1972). In our case, we compared the number of seconds spent in each of the 3 cubes using the following formula: $E_H = \frac{-\Sigma\ (p_i\ *\ \ln(p_i))}{\ln(S)}$, where p_i refers to the proportion of seconds spent in cube i, and S to the number of cubes.

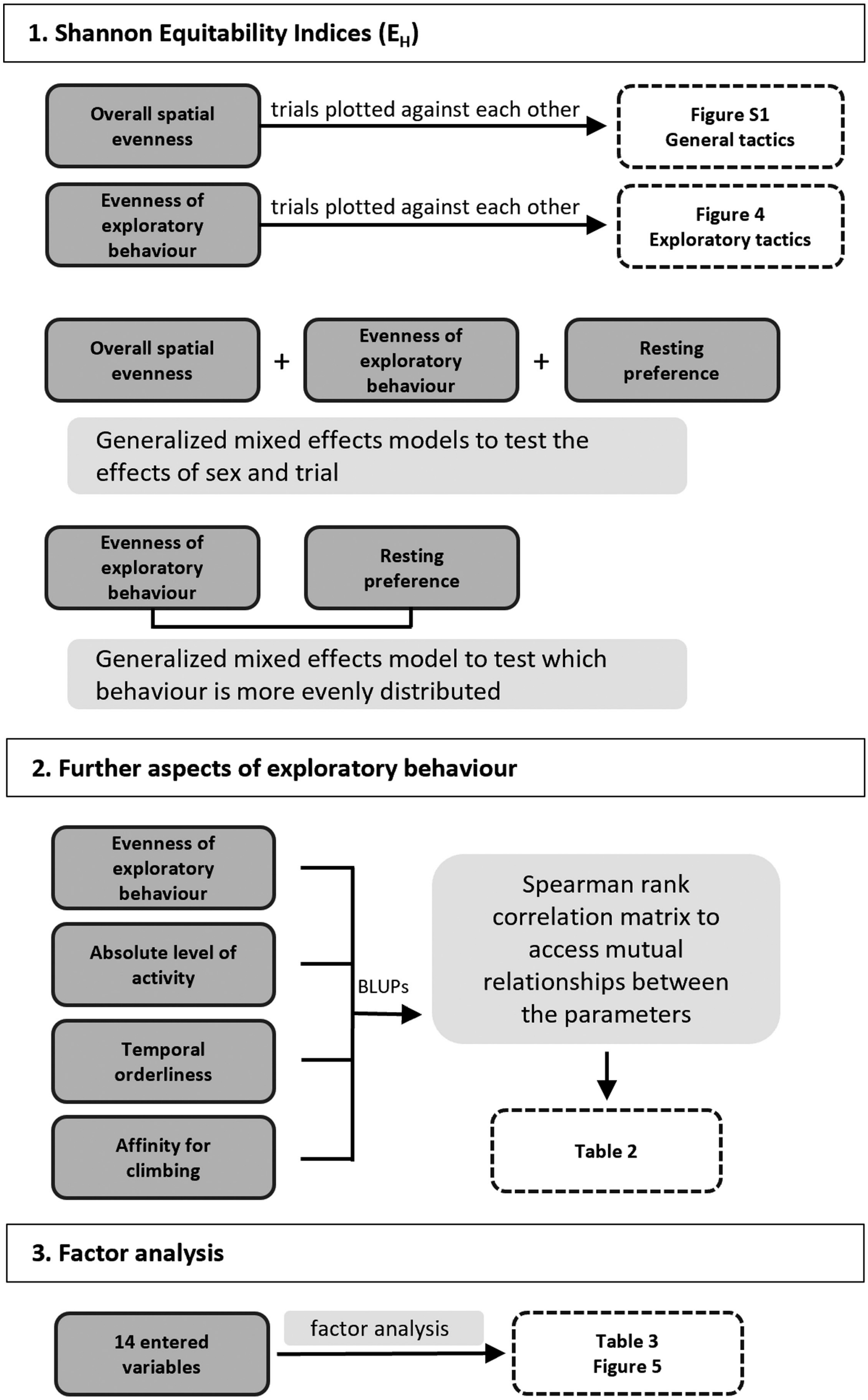

Figure 3. A workflow of the analyses in Experiment 2. The analysis can be broken down into 3 steps: (1) computation of Shannon Equitability Indices which describe spatial orderliness (evenness) of investigated behavior and their subsequent analyses, (2) mutual correlations of 4 parameters describing exploratory behavior of the rats, and (3) factor analysis of spatial relations. Dark grey boxes with full outline—variables, light grey boxes—statistical methods, and white boxes with dotted outline—outputs.

We computed E_H of total time budget, E_H of exploratory activity (total duration of locomotion and rearing), and E_H of resting preference (total duration of sitting, pausing, and grooming) separately for each observation. We paired the indices of the same individual from the first and second trail of the experiment and plotted them against each other. Based on this, we defined 4 general tactics (based on the total time budget) and similarly 4 exploratory tactics (based on exploratory activities only). The distribution of the indices was extremely negatively skewed thus, to facilitate further analyses, we recoded the indices as binary variables (1—evenness, 0—unevenness). To test the effect of sex and trial on Shannon equitability indices, we built generalized linear mixed effects models (GLME) with trial and sex as the fixed effects and rat ID as the random effect.

Next, we aimed to investigate the possible association of the evenness of exploratory activity with the other 3 parameters of exploratory behavior: the level of activity, affinity for climbing, and temporal orderliness. The level of activity was represented by the total amount of time spent engaged in exploratory activities (i.e., locomotion, including climbing, and rearing), the affinity for climbing was expressed as the time spent by climbing (locomotion and rearing in areas 7–10 and 12–14 as entered into Figure 1D), and the temporal orderliness was represented by the total number of transfers between the cubes. To avoid any potential bias stemming from sex and trial variations, as well as from repeated (non-independent) measures, we resorted to the best linear unbiased predictors (BLUPs). BLUPs extracted from GLME models provide estimates of the random effect (a single value per individual) independent of the fixed terms within the model. Hence, we built GLME models with trial and sex as the fixed effects and rat ID as the random effect; we used the binomial distribution for the evenness of exploratory activity, the Gaussian distribution for the level of activity and affinity for climbing, and the Poisson distribution for temporal orderliness. Spearman rank correlation analysis was utilized on the extracted BLUPs.

Lastly, we used factor analysis to assess the multivariate relationships between the areas in the arena. Total time spent in each of the 14 areas (as listed in Figure 1D) entered the analysis. Using the principal component extraction and Varimax normalized rotation, we extracted 3 factors, which represented various aspects of the space as viewed by the rats. To investigate the potential formation of a home base, we identified the area where the rats spent the longest and the second longest cumulative time during a trial. Because rearing and grooming relate to resting behavior, it can be used to identify home base (Eilam and Golani 1989). Therefore, we identified areas associated with the most frequent rearing and the longest cumulative grooming and checked whether they match the area where the rat spent the longest cumulative time.

Ethical note

All procedures during both experiments were performed in accordance with the Czech law implementing all corresponding EU regulations and were approved by the Institutional Animal Care and Use Committee (permit no. MSMT-33802/2021-4). To minimize the stress, all experimenter–rat interactions were kept to a minimum. Additional adjustments to minimize the stress were also implemented: The rats were reared in family groups and subsequently housed in pairs or groups of 3 with familiar individuals to socialize and reduce social stress; environmental enrichment was regularly provided. The experiments were performed during dark phase of the day and under low illumination to match natural activity of rats. When the experiments were completed, the rats were euthanized.

Results

Repeatability of climbing behavior—Experiment 1

Repeatability estimates adjusted for trial, trial + cube, and trial + cube + break were very similar (Supplementary Table S3), we therefore chose results of the simplest model. These repeatability estimates ranged from 0.218 to 0.519 (Table 1).

Evenness of exploratory activity in the cubes—Experiment 2

We computed the Shannon Equitability Index (E_H) as a measure of the evenness of the total time budget. The maximum E_H (1.00) corresponds to total evenness or a perfectly balanced time budget in our case. The evenness of total time budget was highly negatively skewed suggesting that most rats utilized the space rather evenly. We plotted E_H of the total time spent in cubes in the first trial against E_H of the total time spent in cubes in the second trial (Supplementary Figure S1). Based on the plot, we ad hoc chose $E_H = 0.94$ as the cut-off line for high evenness—it best distinguished the only clear tight cluster of observations in the plot. For a better picture, $E_H = 0.94$ translates to approximately 7, 8, and 15 min spent in the cubes respectively. Using this cut-off line, we were able to define 4 general tactics. The most frequent was the even tactic (10 rats); individuals with this tactic spent about the same amount of time in each cube during both trials of the test. The second most frequent was the combined tactic (8 rats); these rats spent about the same amount of time in all cubes during the first trial but showed a clear preference for one cube in the second trial. The opposite, the reversed combined tactic, was identified only in one rat. Lastly, 4 rats with a selective tactic preferred to spend time in one cube during both trials (Supplementary Figure S1). Specifically, 3 out of 4 preferred the upper cube in both trials whereas the last one preferred the upper cube in the first trial but the right cube in the second.

Further, we computed E_H of exploratory activity (i.e., running. climbing. and rearing) and resting preference (i.e., sitting, pausing, and grooming). Similarly to plotting the evenness of the total time budget, we plotted E_H index for exploratory activity to access frequencies of rat exploratory tactics (Figure 4). Applying the same cut-off line of 0.94, 15 out of 23 rats adopted the even exploratory tactic, 2 and 3 rats followed the combined and reversed combined tactic, respectively, and 3 rats were characterized by the selective exploratory tactic with one always preferring to explore in the right cube, one in the upper cube, and one preferring the upper cube in the first trail but the right cube in the second trial. Frequencies of general and exploratory tactics are summarized in Supplementary Figure S2.

Next, we investigated the effects of trial and sex on the computed indices of evenness. The effect of the trial was not significant on any of the tested indices (evenness of total time budget: $F = 4.58$, $P = 0.052$; evenness of exploratory activity: $F = 0.20$, $P = 0.652$; resting preference: $F = 1.24$, $P = 0.164$). The effect of sex was not significant neither on the evenness of the total time budget ($F = 3.70$, $P = 0.110$) or the evenness of exploratory activity ($F = 1.79$, $P = 0.231$) but it was significant on the resting preference ($F = 4.53$, $P = 0.036$) with males being the more selective sex (male estimate = −1.95 and 0.13, female estimate = −0.37 and 0.41 on logit and original scale, respectively). We additionally tested whether exploration was distributed as evenly as resting. The GLME model with index type as a fixed factor and rat ID as a random factor supported that

Table 1. Estimated repeatability *R* (adjusted for trial) for exploratory behaviors observed in Experiment 1 (modified open field test). For the numbers of rears, jumps, and climbing bouts (*), we used Poisson error distribution (log link), link-scale approximations are shown. For the remaining behaviors, we used Gaussian error distribution; note that these original variables were Box–Cox transformed. *P*-values were assessed by likelihood ratio test. Var_{inter}—estimate of inter-individual variability, var_{resid}—estimate of residual variability, R—repeatability estimate, 95% CI—95% confidence interval, *P*—*P*-value.

Observed behavior	var_{inter} (95% CI)	var_{resid} (95% CI)	*R* (95% CI)
Number of rears against walls *	0.049 (0.005, 0.099) $P < 0.001$	0.175 (0.132, 0.221)	0.218(0.035, 0.385) $P < 0.001$
Number of rears against wire mesh *	0.155 (0.039, 0.300) $P < 0.001$	0.213 (0.158, 0.268)	0.421 (0.144, 0.611) $P < 0.001$
Number of unsupported rears *	0.684 (0.124, 1.286) $P < 0.001$	0.872 (0.609, 1.158)	0.440 (0.120, 0.641) $P < 0.001$
Total number of rears *	0.059 (0.009, 0.117) $P < 0.001$	0.167 (0.127, 0.212)	0.262 (0.060, 0.432) $P < 0.001$
Total number of jumps *	0.724 (0.176, 1.343) $P < 0.001$	0.758 (0.548, 0.991)	0.489 (0.160, 0.683) $P < 0.001$
Number of climbing bouts on the wire mesh *	0.388 (0.092, 0.721) $P < 0.001$	0.359 (0.261, 0.479)	0.519 (0.203, 0.708) $P < 0.001$
Time of locomotion on the ground	1.554 (0.383, 3.344) $P < 0.001$	3.625 (2.803, 4.533)	0.300 (0.083, 0.508) $P < 0.001$
Time of locomotion on the wire mesh	4.192 (1.200, 8.618) $P < 0.001$	4.392 (3.318, 5.513)	0.488 (0.199, 0.686) $P < 0.001$
Time of immobility on the ground	5401 (1742, 11994) $P < 0.001$	6922 (5260, 8688)	0.438 (0.170, 0.623) $P < 0.001$
Time of immobility on the wire mesh	0.908 (0.242, 1.994) $P < 0.001$	1.353 (1.041, 1.678)	0.402 (0.147, 0.606) $P < 0.001$
Total time of activity	3197 (757.3, 6545) $P < 0.001$	5860 (4467, 7282)	0.353 (0.109, 0.560) $P < 0.001$
Latency to climb the wire mesh	1.082 (0.309, 2.331) $P < 0.001$	1.520 (1.176, 1.896)	0.416 (0.163, 0.617) $P < 0.001$

exploratory activity was more evenly distributed between the cubes than sitting, pausing, and grooming ($F = 25.79$, $P < 0.001$; exploratory activity estimate = 1.34 and 0.79, resting preference estimate = −1.21 and 0.23 on logit and original scale, respectively).

Lastly, we investigated whether the focal aspects of exploratory behavior are interconnected. To this end, we assessed a Spearman correlation matrix for BLUPs of evenness of exploratory behavior, the absolute amount of exploratory behavior, the number of transfers between the cubes, and the time spent by climbing. The results are shown in Table 2.

Spatial relationships: home base and factor analysis—Experiment 2

To investigate the potential formation of a home base, we identified the area where the rats spent the longest cumulative time during a trial (a descriptive statistic not backed by any specific statistical test). In most cases (31/47), the preferred place was the shelf between the R and U cubes. In the 7 and 3 cases, it was the wire-mesh-covered part of the R cube‘s floor and L cube’s floor, respectively. In 4 cases, it was the by-the-wall part of the L cube‘s floor. Finally, in 2 cases, it was the back wire mesh wall of the U cube. Generally, rats showed a strong preference for their favorite area where they spent 587 seconds on average, almost twice as much compared with their second favorite area (295 s on average). In 28 cases, each individual’s preferred area was additionally associated with the most frequent rearing and in 35 cases with the longest grooming.

Next, we computed factor analysis to determine which were the key areas of interest for rats based on their time budget. We extracted 3 factors using the principal component extraction method and Varimax normalized rotation. In total, these factors explained 55.9% of the variance; factor loading is shown in Table 3. We interpret factor 1 as a level preference: rats preferring the ground level scored high, whereas rats preferring the upper level of the arena scored low. Factor 2 can be interpreted as climbing proficiency: areas correlated with this factor were difficult to climb on and required a higher level of balance and coordination. Finally, factor 3 can be interpreted as a climbing activity. Areas correlated with this factor (back walls of the lower cubes) were used more for climbing than for sitting and pausing which contrasts with the back wall of the upper cube (factor 1) and metal hems (factor 2), where rats on average spent more time sitting and pausing than climbing.

Based on the factor analysis, we divided the experimental arena into 4 zones to better visualize the rat’s view of the apparatus (Figure 5). The first zone was the floor, that is, the areas positively correlated with factor 1. The second zone consisted of areas negatively correlated with factor 1 and corresponded to easily accessible space above the ground. The third zone was represented by metal hems and the ceiling (areas correlated with factor 2) and the fourth zone corresponded to the wire mesh of the lower cubes and the shelf from below (areas correlated with factor 3).

Discussion

Repeatability of observed behaviors

In the first experiment, we assessed the repeatabilities of several behaviors including previously unreported repeatabilities of climbing (Table 1). The estimated values ranged

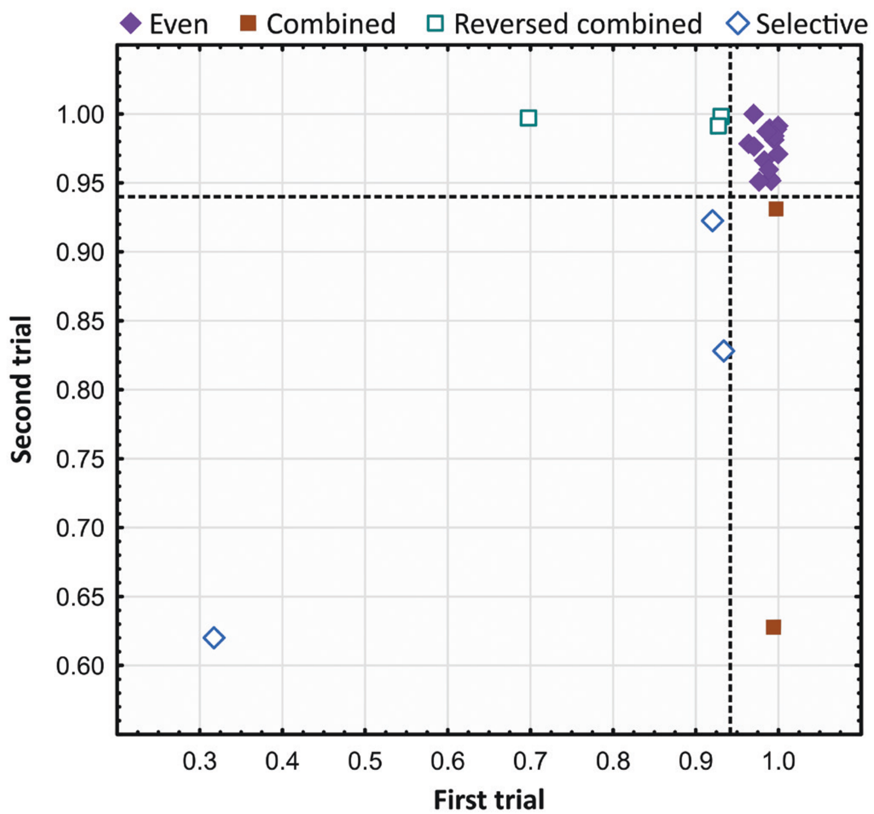

Figure 4. Exploratory tactics of the black rat in Experiment 2. After plotting the Shannon Equitability Index (E_H) of total time spent in cubes during the first trial against the second trial, we applied the previously chosen cut-off line 0.94 (dotted lines) to define 4 exploratory tactics, each corresponding to one quadrant created by this line.

Table 2. Spearman rank correlation between BLUPs extracted from GLME models of 4 key variables describing exploratory behavior in Experiment 2. Evenness—evenness of exploratory activity (BLUPs), exploration—absolute time of exploratory behavior (BLUPs), transfers—number of transfers between the cubes (BLUPs), climbing—time spent by climbing (BLUPs), R_S—Spearman rank correlation coefficient, *P*—*P*-value; *P*-values < 0.05 are in bold.

	Exploration	Transfers	Climbing
Evenness	R_S = 0.24 *P* = 0.107	R_S = 0.19 *P* = 0.202	**R_S = 0.41** ***P* = 0.004**
Exploration	–	**R_S = 0.70** ***P* < 0.001**	R_S = 0.32 *P* = 0.142
Transfers		–	**R_S = 0.50** ***P* = 0.016**

from 0.218 to 0.519 and were thus similar to previously published repeatabilities of behavior and exploratory behavior (0.37—Bell et al. 2009, 0.34 –; Žampachová et al. 2017b). This supports the notion of consistent individual differences in the exploratory behavior of the black rats, even in a relatively small and homogenous sample. The medium to high repeatability of several vertical behaviors (i.e., jumping, wire mesh-related behavior) suggests that some individuals consistently climb more than others and overall use the vertical axis more extensively. Individual animals might, therefore, specialize in a certain micro-niche and a related type of movement; they choose between movement high above the ground, which is more energetically demanding and entails high coordination and skill, and movement on the ground, which may be riskier. Vertical behavior is thus an important part of behavioral repertoire of the black rat, as could be expected in a semiarboreal animal.

Exploratory tactics

In Experiment 2, we tested exploratory behavior in a larger arena with the aim to investigate the exploratory tactics of the black rats (Figure 4). We primarily focused on how rats move and organize their exploration in space, taking advantage of the unusually large arena. We found that the majority of rats (15/23) distributed their activity evenly and explored all 3 cubes for a similar amount of time during both repetitions of the experiment. A similar pattern has been shown in wild black rats—they move through the environment rather rapidly, only partially harvest each patch, and often return to it later, which may be advantageous in an environment with many diverse distant food patches (King et al. 2011). In contrast, 3 individuals focused their exploration on only some parts of the experimental arena during both repetitions, thus employing a selective exploratory tactic. The rest (5/23) explored evenly during one trial but showed a preference for certain cubes during the other. Specifically, 2 rats were explored evenly only during the first trial. Such a tactic suggests habituation to the apparatus. The black rats probably discovered that there are no rewards or hideouts in the arena and for the second trial, they chose to spend time in one preferred part of the arena. Finally, 3 individuals explored evenly only during the second trial. Such variability of exploration when tested repeatedly may be a result of behavioral flexibility, which may enable thorough exploration in a safer

Table 3. Factor loadings and communalities from factor 3 for each of the investigated areas in the arena. Factor loadings above |0.5| are in bold.

Area	Factor 1	Factor 2	Factor 3	Communalities
Centre of the left cube's floor	**0.69**	−0.34	−0.01	0.591
Wire-mesh-covered part of the left cube's floor	**0.59**	−0.27	−0.32	0.532
By-the-wall part (the rest) of the left cube's floor	**0.51**	−0.41	0.08	0.438
Centre of the right cube's floor	**0.71**	−0.09	0.07	0.511
Wire-mesh-covered part of the right cube's floor	**0.67**	−0.05	0.04	0.453
By-the-wall part (the rest) of the right cube's floor	**0.66**	0.28	0.24	0.568
Back wire mesh wall of the left cube	0.24	0.23	**0.67**	0.556
Back wire mesh wall of the right cube	−0.06	0.28	**0.72**	0.608
Back wire mesh wall of the upper cube	**−0.52**	0.25	−0.48	0.558
Wire mesh shelf in the upper cube	**−0.85**	−0.18	0.13	0.780
Wire mesh shelf from below	−0.42	−0.32	**0.56**	0.594
Vertical metal hems of the left and right cubes	0.02	**0.72**	0.18	0.549
Horizontal metal hems of the upper cube	−0.19	**0.82**	0.03	0.710
Ceiling of the upper cube	−0.01	**0.61**	0.08	0.383
Sum of squares	3.74	2.35	1.74	
Proportion of explained variance	26.71	16.77	12.46	

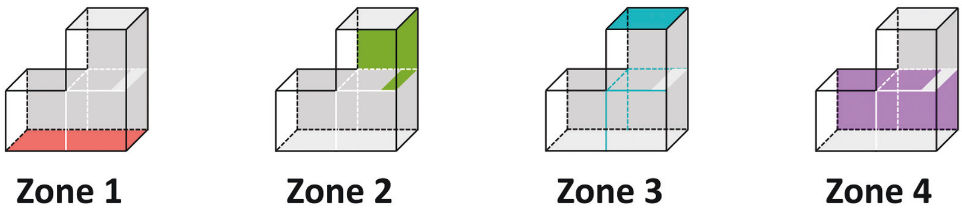

Figure 5. Rats' view of the arena—visualization of the zones based on results of factor analysis.

environment although increasing safety under more risky conditions. A similar strategy was previously described in mice (Augustsson and Mayerson 2004). Nevertheless, it is worth remembering that the cut-off line for "even" exploration was chosen arbitrarily.

The black rat is an opportunistic species with a great colonizing potential (e.g., Berthier et al. 2016; reviewed in Shiels et al. 2014). In the absence of true specialists, it prospers in complex habitats where it can outcompete otherwise stronger competitors, e.g., the Norwegian rat (King et al. 2011). King et al. (2011) suggested that the colonizing potential of the black rats is facilitated by their unique exploratory/foraging pattern—even though Norwegian rats are also quite competent climbers (Foster et al. 2011), they tend to forage slowly and thoroughly, usually exhausting the current food patch before moving on. Even in the urban environment, the difference between the 2 species still manifests in the size of a core home range (i.e., a region where an animal spends 50% of its time). In the case of the Norwegian rat, it comprises about 11% of the total home range, whereas it is 31 % for the black rat (Byers et al. 2019). This suggests that black rats distribute their activity more evenly on a daily basis.

Stable exploratory strategies may prove advantageous either in an extremely stable environment (forming a routine and sticking to it reduces both energy expenditure and risks) or, on the other hand, in an extremely unstable environment where it is useless to try to adapt. In contrast, in a moderately variable environment, it would be advantageous for behaviors, such as exploration, to be more plastic (Niemelä et al. 2013). Black rats are able to colonize and successfully live in complex, rather stable habitats (King et al. 2011), but they are, on the other hand, also strongly opportunistic and may live in ruderal environments and unpredictable resource-poor localities. They are able to survive on small atolls (Russel et al. 2015), forage deep in caves (Howarth and Stone 2020), or collect seeds from disturbed parts of the rain forest (Shiels and Ramírez de Arellano 2019). In other words, they are capable of inhabiting a wide range of environments; a polymorphism in exploratory strategies hinted at by this study might be a contributing factor. Nonetheless, a follow-up genetic study is necessary to determine whether described exploratory tactics (observed behavior under certain conditions) translate to exploratory strategies (genetically fixed patterns). If genetically based and heritable, the coexistence of several strategies in a relatively small, laboratory-bred population might seem surprising. However, keeping the black rats in extended social groups largely increases the level of environmental complexity and variability. The social conditions and therefore the environment may change even within one generation.

Even though the vast majority of rats explore the whole environment evenly, these individuals may still differ greatly in their level of activity, temporal orderliness, or affinity for climbing (Table 2), thus creating a highly variable population. It's particularly interesting that the absolute amount of activity does not correlate with the evenness of exploration suggesting that the evenness of exploration is not a mere byproduct of variation in activity. Thus, the evenness of exploration is indeed a specific tactic characteristic of black rats and perhaps other opportunistic species. Importantly, it has been suggested that the intensity of a response to a novel space (which might be reflected especially in the level of activity and affinity for climbing) might play a crucial role when adapting to novel environments (Mazza et al. 2020, 2021). Large population-level variability of exploratory behavior may, therefore, be another reason behind the black rat's success in settling new environments.

Rats' view of the L-shaped arena

When exploring a 3D space, laboratory rats tend to move in the vertical and horizontal axes, avoiding diagonal movements (Grobéty and Schenk 1992; Jovalekic 2011) and use the vertical axis only to ascend to another horizontal level (Hagbi et al. 2020, 2022). Similarly, the black rats in our experiment seemed to face a choice between spending time on the ground or in the upper cube, especially the shelf (zones 1 and 2; Figure 5). These 2 zones (the ground and the upper cube) belonged to the same factor but were opposite in direction (Table 3) indicating that rats spent time in one of the zones at the expense of the other.

This trend was especially noticeable for resting (sitting, pausing, and grooming) as E_H for resting preference was significantly lower than E_H for exploratory activity suggesting that many black rats preferred mainly one cube for resting. A simple data check revealed that in about two-thirds of cases (31/47), the rats spent the longest cumulative time during a trial on the shelf. The position on the shelf allowed the rats to be "safely" above ground while sitting horizontally (and offered the rats an overview of almost the entire arena). Similarly to other studies (e.g., Eilam and Golani 1989), the shelf area was also often associated with the longest grooming or the most frequent rearing suggesting the home base of many rats was established there.

Areas belonging to the third zone were the most difficult to access—very slim (18 mm) and smooth hems (which were surprisingly used for climbing, pausing, sitting, and even rearing) and the ceiling, which required rats to climb high (1.6 m) above the ground. The motivation or ability of the black rats to visit this demanding zone varied with some rats not visiting it at all and some spending several minutes there. We observed that black rats used their tails to lean against a wall (or wrap them around an object), or they used it as a helm when jumping. Such use of the tail was not documented in wild Norwegian rats (Foster et al. 2011), maybe because their tail is relatively shorter (Ewer 1971). Studies in Norwegian rats show that energetically demanding movements tend to be postponed until necessary (Grobéty and Schenk 1992; Jovalekic 2011). In contrast, the fourth zone (back wall of the 2 lower cubes) seems to be viewed as an intersection allowing access to other parts of the arena—it was visited quite often but the rats usually climbed through it without stopping. Interestingly, when investigating the climbing of wild Norwegian rats, Foster et al. (2011) noted that before launching a climb they often stopped and hesitated.

In this study, we found that black rats divide the space into horizontal levels and prefer to spend time in these (similarly to laboratory Norwegian rats)—the transitions between the 2 bottom cubes were on average twice as frequent as transitions in the vertical axis. However, this division is not strict because the vertical climbing wire mesh of the upper cube also belongs to the preferred areas. Further, the mean number of climbing bouts in Experiment 2 was 19 (6 in the first experiment), we, therefore, argue that although black rats prefer to explore at horizontal levels, they are not hesitant to switch to vertical exploration and do so deliberately rather than out of necessity. Importantly, the black rats are considerably smaller and lighter than Norwegian rats—adult black rats weigh approximately 150–200 g (Marsh 1994; Clapperton et al. 2019) and are therefore better suited for climbing.

In summary, most exploratory behaviors were highly repeatable, we also provide repeatability estimates of vertical behaviors (e.g., climbing), which seem to be an important component of behavioral repertoire of the black rat. The exploratory behavior of the black rats can be characterized by several parameters including the general level of activity, affinity for climbing, spatial orderliness, and temporal orderliness. By utilizing a custom-made arena we were able to detect various exploratory tactics in the black rats: 1) The first one is represented by "even explorers" that search the environment evenly, although they might differ from each other in their thoroughness, affinity for elevated places, or the actual amount of exploratory activity. 2) The second tactic is represented by "selective explorers" who concentrate their activity only on a section of the available environment. 3) The third group of animals uses a combined tactic behaving like "even explorers" on one occasion but choosing the selective exploratory tactic when tested repeatedly. These 3 groups are not evenly represented in the population, and we suggest that bias for "even explorers" and flexible individuals with combined exploratory tactics enables black rats to quickly colonize new environments and exploit their resources, although the minority of selective explorers might be important for the survival of the population under unfavorable conditions, such as intense predation. Even though our study has its limitations, mainly a small number of tested individuals and descriptive character, it is important and innovative as it represents the first attempt at a more detailed investigation of the exploratory behavior of the black rat in 3-dimensional space.

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Conflict of Interest statement

The authors declare no conflict of interests.

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Author Contributions

Conceptualization: all authors; data curation: I.Š., H.S.; formal analysis: all authors; funding: I.Š., B.V.; investigation: all authors; supervision: D.F.; visualization: I.Š.; writing—original draft. I.Š., V.R. writing—review & editing: I.Š., V.R. All authors read and approved the final manuscript.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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