

Expanding through the Emerald Isle: exploration and spatial orientation of non-native bank voles in Ireland

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Abstract

Whether introduced into a completely novel habitat or slowly expanding their current range, the degree to which animals can efficiently explore and navigate new environments can be key to survival, ultimately determining population establishment and colonization success. We tested whether spatial orientation and exploratory behavior are associated with non-native spread in free-living bank voles (*Myodes glareolus*, $N = 43$) from a population accidentally introduced to Ireland a century ago. We measured spatial orientation and navigation in a radial arm maze, and behaviors associated to exploratory tendencies and risk-taking in repeated open-field tests, at the expansion edge and in the source population. Bank voles at the expansion edge re-visited unrewarded arms of the maze more, waited longer before leaving it, took longer to start exploring both the radial arm maze and the open field, and were more risk-averse compared to conspecifics in the source population. Taken together, results suggest that for this small mammal under heavy predation pressure, a careful and thorough exploration strategy might be favored when expanding into novel environments.

Key words: animal personality, biological invasions, exploration behavior, *Myodes glareolus*, range expansion, spatial orientation.

Biological invasions are the product of a multi-stage process, which requires the invader to negotiate successfully a series of sequential, selective filters (Blackburn et al. 2011; Chapple et al. 2022). To successfully settle and spread in a non-native environment, individuals have to navigate their way through all stages of the colonization process (i.e., introduction, establishment, spread), where each stage poses its own set of challenges (e.g., Sol et al. 2013; Chapple and Wong 2016).

After surviving the first stage of transport, arrival and establishment around the point of introduction, the next critical challenge for non-native animals is represented by effectively spreading into the novel environment (e.g., Burton et al. 2010; Blackburn et al. 2011; Sol et al. 2013; Chapple and Wong 2016). Expanding the current range is thus a critical point in determining whether introduced animals may become non-native, and potentially invasive, inhabitants of a new habitat. Not all species spread beyond the site of introduction, and not all populations expand their range after being established, but studying those that do can reveal a great deal about species' range limits and how they will respond to environmental change (e.g., Moran and Alexander 2014).

Range expansion in non-native species is posited to involve a run-away, selection-neutral process based on differential dispersal potential, known as spatial sorting (Shine et al. 2011). Spatial sorting can result from several phenotypic differences that allow some individuals to navigate more efficiently than others across the landscape (e.g., Shine et al. 2011; Burstal et al. 2020). These individuals will accumulate at the edge of the

expansion, mate assortatively, and select for higher expression of the traits favoring the dispersal and colonization (Shine et al. 2011). A notable example of this process is represented by invasive cane toads *Rhinella marina* in Australia. Dispersal rates of cane toads at the expansion edge have increased in successive generations, due to interbreeding of individuals that have longer legs, higher endurance, and travel further than conspecifics in settled populations (Phillips et al. 2006, 2007; Llewelyn et al. 2010).

In addition to morphology and physiology, behavior and cognition contribute to successful animal invasions and range expansions (e.g., Ruland and Jeschke 2020) because they constitute the interface through which animals interact with their surroundings (Shettleworth 2009). Being more plastic than other traits, behavioral and cognitive responses to novel or altered environmental circumstances can occur faster compared to adaptive changes in morphology or physiology (e.g., Duckworth 2009), resulting in effective and timely adjustments to current conditions (e.g., Ruland and Jeschke 2020).

Non-native animals introduced into a new environment lack the up-to-date knowledge necessary to locate and recognize resources that are key to their survival and reproduction, like, for example, local information about food sources, nesting material and opportunities, as well as local dangers like predators, poisons, and climatic exposure (Griffin et al. 2016). Efficient gathering and using of environmental information thus becomes of primary importance for non-native animals, and especially for individuals at the edge of

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an expansion front, spreading into a novel environment for which they lack eco-evolutionary experience (Saul et al. 2013; Heger et al. 2019).

At the edge of an ongoing expansion, pioneer individuals encounter novel ecological and evolutionary pressures that may not be experienced by conspecifics settled in long-colonized areas (Gruber et al. 2018). The ecological challenges that they meet are often best dealt with by specific behaviors such as a propensity to take risks, engage with novel stimuli, efficiently gather and store information for subsequent decision-making (Gruber et al. 2018), enabling them to overcome the initial naïveté. Whereas in areas where the population is already established, the costs of maintaining dispersal-promoting traits, or perhaps the presence of different selective pressures like enhanced intraspecific competition, are predicted to favor different combinations of traits (like e.g., lower aggression and better parental care, Duckworth and Badayev 2007), resulting in a non-random distribution of behavioral phenotypes between expansion edge and established population (e.g., Duckworth and Badyaev 2007; Burton et al. 2010; Canestrelli et al. 2016). By enhancing an individual's ability to find food and shelter as well as increasing its capacity to navigate novel environments, behavioral and cognitive traits such as risk-taking, exploration, and spatial orientation are thus expected to be more highly expressed at the expansion edge than in established populations (e.g., Gruber et al. 2018; Griffin et al. 2022). Differences among conspecifics in exploration, dispersal and risk-taking tendencies, might also promote the accumulation of certain phenotypes at an expanding edge, causing spatial sorting (e.g., Canestrelli et al. 2016; Chapple and Wong 2016; Gruber et al. 2017; Burstal et al. 2020). Studying ongoing processes of range expansion into non-native habitats can thus yield insights into the drivers of biological invasions as well as the role of behavior and cognition in dealing with novel environments, an emerging field of research that is raising increasing interest (e.g., Weis and Sol 2016; Jeschke and Heger 2018; Griffin et al. 2022).

Here, we address the question of whether exploration and spatial orientation are associated with non-native spread of bank voles *Myodes glareolus* in Ireland, making use of a rare opportunity where a non-native rodent species' spread is still ongoing. While rodents are the most widely introduced alien vertebrates worldwide, and often make extremely successful invaders, their colonization processes were often completed long before they could be systematically studied (e.g., Drake and Hunt 2009; Hofman and Rick 2018). A rare exception is represented by the ongoing spread of bank voles in Ireland. Voles from Central Europe were accidentally introduced at Foynes port, in the west of Ireland, during the construction of the Ardnachusha hydroelectric dam, about a century ago (Stuart et al. 2007). A source population was then established at the West coast, and has been estimated to expand its range at about 2.5 km a year (White et al. 2012), 5 times faster compared to dispersal within an occupied area with normal density (e.g., Smal and Fairley 1984; Tegelström and Jaarola 1998; Gliwicz and Ims 2000). Genetic comparison among source and edge populations indicated spatial sorting, although the phenotypic differences remained unclear (White et al. 2013).

We investigated among-individual variation in exploration and spatial orientation, as two complementary aspects of environmental information gathering and use, which are crucial when navigating novel environments. Here, we define

exploration as the gathering of environmental information (e.g., Réale et al. 2007; Mettke-Hofmann et al. 2009; Huang et al. 2016; Burstal et al. 2020), and spatial orientation as the process of positioning oneself in relation to the environment, and to guide movements through it (e.g., in search of food, mates, shelter, or better habitats) (e.g., Dyer 1998; Wallace et al. 2010; Grob et al. 2021; Kappeler 2021). Also, because among-individual variation in risk-taking and exploration form a behavioral syndrome in bank voles (e.g., Mazza et al. 2018), we also quantified boldness (Réale et al. 2007), as a measure of how animals face the inherent challenges and risks entailed by the expansion into a novel habitat.

Here, we tested whether free-ranging bank voles at the edge of their current range display differences in expansion/dispersal-relevant behaviors, namely exploration and orientation, relative to conspecifics from the longer-established source area. We expected the individuals living at the expansion edge to show higher levels of exploration and spatial orientation compared to conspecifics in the source population. We also expected boldness and exploration to be consistent when measured in different contexts and correlated with each other and with spatial orientation at the phenotypic level.

Materials and Methods

Study sites and experimental procedure

This study was conducted in September 2019, when bank voles' expansion edge had moved 200-250 km East of the source population in SW-Ireland over a 100-year period (Figure 1). The source population inhabits the area around the point of first introduction, in Foynes Port, Limerick (Stuart et al. 2007).

The current expansion edge of the Irish bank vole population was determined during the previous months in the course of a larger study (Eccard et al. 2023). To pinpoint the most recent areas reached by bank vole expansion, we consulted previous records of bank vole occurrence at the edge of their range (<https://biodiversityireland.ie/>; (Stuart et al. 2020), used the rate of spread of bank vole population in Ireland of approximately 2.5 km per year (White et al. 2012; Stuart et al. 2020) to calculate how far they could have traveled since the last record, and finally we conducted extensive trapping in the suitable woodlands of each area until woods without bank voles or with the lowest bank vole density were identified (Stuart et al. 2020; Eccard et al. 2023). Study sites were then established both at the source and at the expansion edge of the population.

We trapped and tested animals in 3 different sites at the expansion edge (53°16'14.8"N 6°57'00.7"W) and in 2 sites in the core area of the source population (52°36'46.3"N 8°52'30.1"W). Edge and source trapping sites were on average 91.6 ± 69.9 km apart. Edge sites were, on average, 13.6 ± 7.9 km apart from each other, while core sites were 2.3 km apart. Trapping sites were all located in large forest fragments (approx. size 69,453 ± 45,963 m²) characterized by beech, ash and oak trees and thick undergrowth.

We captured animals using Longworth traps (Penlon Ltd., Oxford, UK), equipped with a seed mixture from commercial bird food as bait, a piece of vegetable as water source, and hay to provide thermal insulation. At each site, 48 traps were set in lines with 10 m spacing between traps. Traps were pre-baited with oat flakes and apples for 2 nights. Once activated, they were checked every morning and afternoon. Trapping

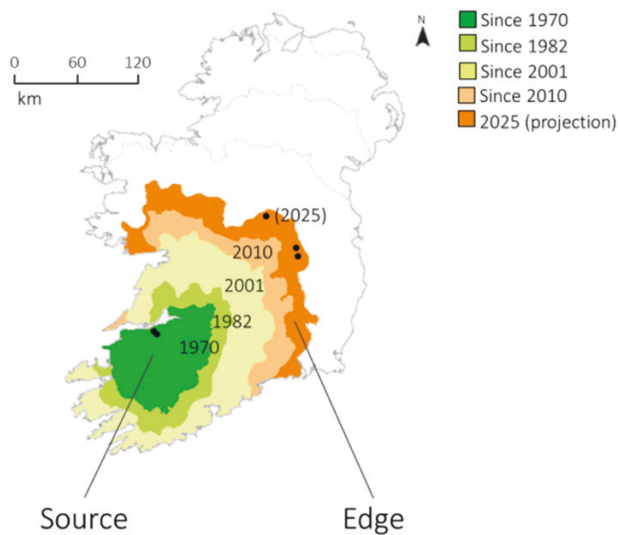


Figure 1. Representation of bank voles' dispersal pattern after introduction to Ireland. Map lines delineate boundaries of modeled expansion ranges according to White et al. 2010. Black dots illustrate location of study sites in reference to the bank vole expansion. Figure adjusted from Eccard et al. (2023), based on White et al. 2010.

was performed on each site for 2–4 days. Trapping procedures were designed to maximize trapping success and reduce bias concerning trap avoidance, even though trappability was found to be not repeatable and not connected to personality in several species of small mammals (Brehm and Mortelliti 2018). Pre-baiting, that is, leaving traps baited but inactive for a couple of nights increases the probability that animals will encounter the trap and re-visit it, since they find accessible food and no harm occurs to them. Further, if on the first night of trapping more explorative (or hungry) animals are caught, prolonged trapping does ensure that a representative sample is trapped. Therefore, we are confident that we captured a representative portion of the population of each site. Finding behavioral differences in the trappable part of the population among zones would be a conservative estimate of differences among entire populations.

All captured individuals were placed into the arena for behavioral assessment without direct handling. Afterward they were sexed, weighed, checked for reproductive status, and marked individually with a unique fur marking, and photographed. If animals had already a fur mark, they were sexed and photographed for later identification. Afterwards, animals were put back into the familiar trap, and after ca. 1 h they were tested for spatial orientation, exploration, and behavior at release, at the point of capture. Recaptured animals were tested again both for behavior and spatial orientation.

Behavioral tests

We used a combination of 2 standard laboratory tests that are commonly used in personality studies of small mammals to quantify risk-taking propensity and exploration tendencies—the dark light test and the open-field test (Archer 1973; Schirmer et al. 2019; Mazza et al. 2020). The dark-light test measures the willingness of individuals to leave a dark and enclosed shelter to enter an unknown, bright and potentially dangerous area. As most other small mammals, bank voles are vulnerable to both terrestrial and avian predators (e.g., Jędrzejewska and Jędrzejewski 1990; Jędrzejewski et al.

1993). Leaving a dark, enclosed, protected shelter to enter an open and bright space where they are visible and exposed, is an indication of an individual's propensity to take risks. 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 (e.g., Mazza et al. 2018) and by assessing the extent to which the individual explores the different parts of the arena. The set-up was structured to be executable directly on site. The test set-up consisted of a dark plastic tube (10.5 × 32 cm Ø) connected to a round PVC open-field arena (130 cm Ø, 30 cm high). Test arenas were set in shady locations or under canvas roofs to avoid direct sunlight or shade patterns. All tests were conducted between 1000 and 1800, under natural light conditions. At the start of each test, animals were transferred without direct handling from the trap into a shuttle tube that could be inserted into the dark-light tube of the apparatus (Eccard et al. 2023). After 1 min for acclimatization, the door leading to the open-field arena was opened, and we measured (1) the vole's latency to enter into the open-field arena with the full body without tail ("latency to emerge OF"), as a proxy for risk-taking. If the animals did not leave the dark tube within 5 min, they were gently guided out of the tube into the arena by pushing the sponge floor of the shuttle tube, and the latency was set to 300 s (66% of all performed tests, Eccard et al. 2023). When the animal entered the circular arena, we closed the door and recorded (2) the latency to enter the central, more exposed, part of the arena ("latency centre"), as a proxy for exploration tendency; and (3) the proportion of time spent moving around the arena ("activity"), with instantaneous 1-0 sampling, a method of time sampling in which behaviors are marked as occurring (1) or not occurring (0) at any point within a given interval (e.g., Martin and Bateson 1993), every 10 s for 5 min. After testing, animals were removed from the arena by offering a hiding place (either by opening the door to the shuttle tube or by placing their familiar trap in front of them). The arena and tubes were then cleaned with 70% alcohol.

Radial arm maze

We measured bank voles' spatial exploration and orientation using a modified version of the standard laboratory radial arm maze, which is commonly used in cognitive studies of rats and mice, where animals have to explore the maze and remember which arms had already been visited (e.g., Olton and Samuelson 1976; Crusio and Schwegler 2005). We adjusted this set-up for bank voles, to be executable directly on the field, and without prior handling, thus precluding possible influences of handling stress on cognitive performance and behavioral expression during the test. The first version of this field-ready set-up was used to observe spatial learning abilities of Eastern chipmunks *Tamias striatus* (Dammhahn and Réale, in preparation).

Our apparatus consisted of a central circular arena (26 cm diameter, 40 cm height) with 4 arms (5 cm diameter × 10 cm length) attached (Figure 2). Arms were enclosed, opaque, and bent so that the end of the arm was not visible from the point of entrance into the arm or from the central area. The arm exits were closed with removable sponge caps. Each arm was marked with a symbol above the entrance (a triangle, a circle, a square and a cross), as potential visual cues to mark each arm. We did not aim to investigate whether or not the animals actually used such cues at this stage, but provided them

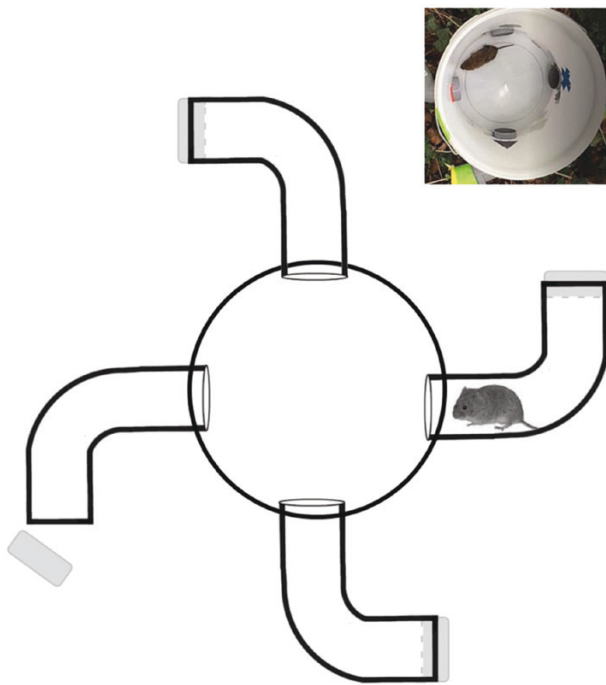


Figure 2. Schematic representation of the modified radial arm maze used in this experiment. The exit at the end each arm was blocked with a sponge, but the vole could not see the exit when entering the curved arm. Whichever last arm was left unvisited by the vole, was opened manually by the researchers so that the vole could escape. In the upper right corner a picture of the set-up with a bank vole moving in the central part.

as additional information to aid the exploration process. We used the possibility to leave the maze and return to their natural environment as reward and final outcome of the maze exploration, as in our experience wild bank voles placed in experimental arenas are more motivated to look for an escape than interested in any type of food reward (e.g., Mazza et al. 2018).

At the beginning of each test, the vole was transferred from the trap directly into one of the arms, whose both ends were then blocked. After 1 min of acclimatization, we opened the inner door and the vole could enter and explore the maze. Once the vole had entered 3 arms, we removed the cap blocking the exit of the unvisited one, thus making this the final release point for the vole (reward). Thus, the rewarded arm was always the last one that the vole entered, the one open to the outside and providing access to the familiar habitat. By direct observation, we quantified (1) the latency to emerge (with the whole body without the tail) from each arm of the maze after visiting it for the first time, (2) the number of visits to each arm (full body excluding tail), from which we later calculated the overall number of re-visits, that is, the number of times the vole entered any already-accessed arm of the maze; and (3) the latency to leave the rewarded arm of the maze and be released. If an animal lingered in one of the first 3 arms for more than 120 s, it was gently pushed out (23% of all first visits to an arm) because pilot tests (not included in this dataset) indicated that animals that did not leave the arm within this time were unlikely to do so even when given more time (5–30 min). When a vole left the maze, we kept still until we saw or heard it walk away from the testing area, then cleaned the apparatus with 70% alcohol, and moved to

the next release point, that is, the respective point of capture of the next animal.

Statistical analyses

We investigated among-individual differences in exploration and orientation between bank voles at the expansion edge and in the established source area. Generalized linear mixed models (GLMMs), including vole ID as a random factor were fitted by restricted maximum likelihood to the number of re-visits to each arm. Expansion zone (source vs. edge), sex, and personality were included as fixed factors in all models. We ensured that there was no strong collinearity between model predictor variables (i.e., an $R^2 > 0.70$) before analyses. For this reason, we ran separate models for the different personality measures (emergence in the OF, latency to explore the central part of the OF arena, and OF activity).

We also included the repeated tests for spatial orientation in the analyses, since performance did not differ in the different test rounds. As a preliminary step, we tested whether repeats changed trait values into a consistent direction with pairwise *t*-tests because most of the 10 repeats were conducted at the source (i.e., 40% of tests at the source were repeats, but only 6% of tests at the edge—2 tests for 2 individuals at the edge, 8 tests for 5 individuals at the core). Mean trait values did not change with repeated testing (Supplementary Table S2), and therefore we included repeated tests into the analyses and corrected for repeated testing of the same animal by using animal ID as a random factor. The test round was initially included as fixed factor and excluded from all models based on its lack of explanatory importance (Zuur 2009).

In prior analyses, we included trapping site as an additional random factor. Since this factor did not improve model fit, according to associated likelihood ratio tests, we retained more parsimonious models without trapping site (Zuur 2009). Interactions between expansion zone and sex were initially included and then dropped when non-significant.

We also compared the latencies to emerge from the different arms, fitting separate (G)GLMMs for each arm, and including expansion zone (source vs. edge), sex, and personality as fixed factors. The latency to leave the first arm of the maze for the first time was turned into a binary variable (emerging immediately into the central arena or not at all). The latencies for the other arms were log-transformed to meet the normality assumption. Latency to emerge and latency to explore the OF center were rescaled and mean-centered prior to running the models (e.g., Schielzeth 2010). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. We used the R package *lme4* (Bates et al. 2015).

Calculation of repeatability indexes for the performance in the radial arm maze was not possible due to the very low number of repeated tests (10 tests for 7 individuals). Repeatability of the behaviors recorded in the dark–light/open-field arena was calculated using the wider dataset obtained by combining the data obtained here with the data obtained from a larger study (Eccard et al. 2023), in order to gain a more informative representation of the sampled population (314 tests for 189 individual bank voles), since repeatability is a property of the population (Bell et al. 2009). Repeatabilities were calculated for the latency to emerge from the dark–light tube into the open-field area, the latency to enter the central part of the open-field arena, and the proportion of time spent moving in the open-field arena.

We used the *rtpr* package (Nakagawa and Schielzeth 2010; Stoffel et al. 2017), and 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 (R Core Team).

Results

We tested 43 bank voles, 33 (17 females, 16 males) of which at the expansion edge and 10 (5 females, 5 males) in the source population. Seven individuals (2 at the edge, 5 at the core) were trapped and tested multiple times in the radial arm maze (average \pm SD number of tests per individual: 1.49 ± 0.77), for a total of 53 tests.

Bank voles living at the edge of the expansion range revisited more often previously visited arms of the maze compared to voles in the source population (Figure 3, Table 1).

Voies at the expansion edge not only took longer to enter the maze from the first arm in which they were placed, but, once they found the way out, also took longer to leave it and regain freedom compared to conspecifics in the source population (Figure 4, Table 1).

We did not detect sex differences in any of the measured variables, except for the latency to leave the maze, where males took longer than females to leave the last arm of the maze and be released at the point of capture (Table 1).

Personality tests were conducted in the frame of a larger-scale experiment (Eccard et al. 2023); repeatability of the behaviors quantified in the open-field test could be calculated on a bigger portion of the population (314 tests for 189 individual bank voles), and are reported in Supplementary Table S1.

For the animals of this study, that had undergone both radial arm maze and open-field test, the number of revisits was correlated with the latency to explore the central part of the open-field arena ($r_s = 0.37$, $P = 0.009$; Figure 5A), with voles that revisited more often already-explored parts of the maze taking longer to reach the center of the open field. The latencies to emerge from the first and last arms of the radial arm maze positively correlated with the latency to leave the dark-light shelter (arm 1: $r_s = 0.50$, $P < 0.001$; arm 4: $r_s = 0.33$, $P = 0.02$; Figure 5B–D), as well as with each other ($r_s = 0.51$, $P < 0.001$; Figure 5C).

Discussion

Based on two different behavioral assays for exploration, spatial orientation and risk-taking propensity, we found evidence of non-random sorting of individuals between expansion edge and established source population of non-native bank voles in Ireland. Bank voles at the expansion edge revisited unrewarded arms of the maze more often compared to conspecifics in the source population, indicating a more thorough gathering of spatial information. They also displayed longer latencies to enter and leave both the radial arm maze and the open-field arena, indicating a slower, more careful exploration strategy and higher risk aversion compared to voles at the source. Taken together, these findings suggest that bank voles in different stages of colonization of a non-native

habitat employed different strategies to gather information about the novel situation we placed them in.

Slow explorers at the expansion edge

In line with our hypothesis, we found that bank voles at the expansion edge differed in the way they approached the exploration of a novel space, how they used spatial information, and also in their propensity to take risks. Different exploration strategies can reflect the demands posed by the different stages of the expansion process. In expanding populations, one major challenge is represented by the mapping of new territory without the help of conspecific cues or eco-evolutionary experience, while in long-established populations, environmental information can also be gathered from conspecifics, and intra-specific competition may be higher (e.g., Saul et al. 2013; Hudina et al. 2014; Heger et al. 2019). Phenotypes with a combination of the favored traits may thus be more common in a specific colonization stage (e.g., Shine et al. 2011). Our findings are in line with previous studies reporting spatial sorting for behavioral and cognitive traits between expansion edge and long-established populations (e.g., Gruber et al. 2017, 2018; Bensky and Bell 2020; Burstal et al. 2020; Magory Cohen et al. 2020; McCune et al. 2020; Bisconti et al. 2022).

Longer latencies to enter unfamiliar parts of the set-ups and more frequent sampling of previously visited arms of the maze suggest that bank voles at the expansion edge acquired more information about their surroundings before moving into new/unfamiliar ones. Contrary to previous studies portraying pioneer individuals as bold, fast-exploring, and aggressive (e.g., Duckworth and Badyaev 2007; Cote, Fogarty, et al. 2010; Hudina et al. 2014; Myles-Gonzalez et al. 2015; Damas-Moreira et al. 2019; Bensky and Bell 2020; Burstal et al. 2020), we found that bank voles at the expansion edge were more risk-averse, slower explorers compared to conspecifics in the source population. Colonizing an area that is void of conspecifics, and for which there is no previous eco-evolutionary experience, calls for more or more detailed environmental information, which in turn requires a careful and thorough strategy of information acquisition that favors accuracy over speed (e.g., Hall and Kramer 2008; Carvalho et al. 2013). Different behavioral and cognitive make-ups may then be favored in different stages of the colonization process based on the novelty and (un)familiarity of the environment animals are expanding into (habitat-dependent hypothesis, Réale et al. 2007). The coping style theory posits that slow and accurate explorers are more sensitive to changes in environmental information, while fast explorers tend to rely on routines formed on shallow sampling (e.g., Benus et al. 1990; Verbeek et al. 1994; Koolhaas et al. 1999, 2010; Coppens et al. 2010; Sih and Del Giudice 2012). Fast exploring individuals may then fare better in a familiar, predictable environment, where they can form stable behavioral routines, while slow explorers are expected to be favored in unfamiliar or unpredictable environments, because they are more sensitive (and thus adaptable) to changes in their surroundings (e.g., Carere et al. 2010; Guillelte et al. 2011; Šlipogor et al. 2022). A careful and thorough information acquisition strategy should be favored when environmental conditions change frequently, or the costs of neglecting some key environmental features exceed the benefits of gaining incomplete experience of

a wider area in less time (e.g., Carere and Locurto 2011; Guillette et al. 2011; Sih and DelGiudice 2012; Udino et al. 2017). For example, accurately checking for predator cues and mapping a territory for shelter may take a comparatively long time but result in heightened safety in case of future predator encounters. Conversely, a shallow search, for example, for a suitable food patch, may be fast and lead to short-term gains, but also present a high risk in case of danger, because other sources of information (e.g., shelter opportunities, indirect predator cues) are neglected. Fast explorers may incur in heightened dangers entailed in incomplete information acquisition or less frequent information update (e.g., Carere and Locurto 2011; Sih and Del Giudice 2012). This could explain why individuals in the long-established source population were bolder, and

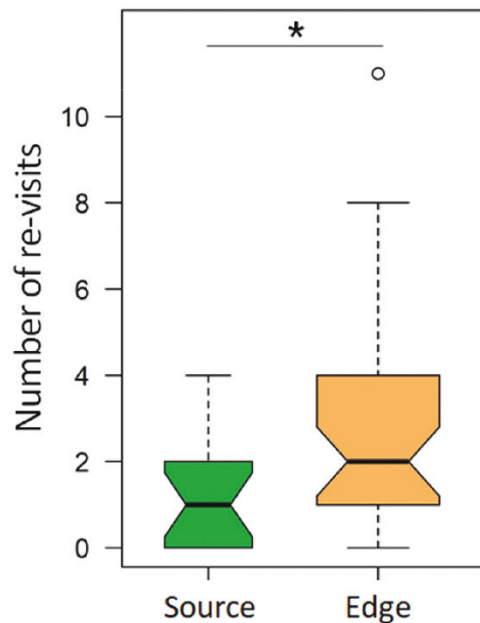


Figure 3. Number of re-visits to already visited arms in the radial arm maze for 43 individual bank voles *Myodes glareolus* in the source population and at the edge of the expansion. Asterisk indicates significant differences from zero with $P < 0.05$, width of box indicates relative sample size.

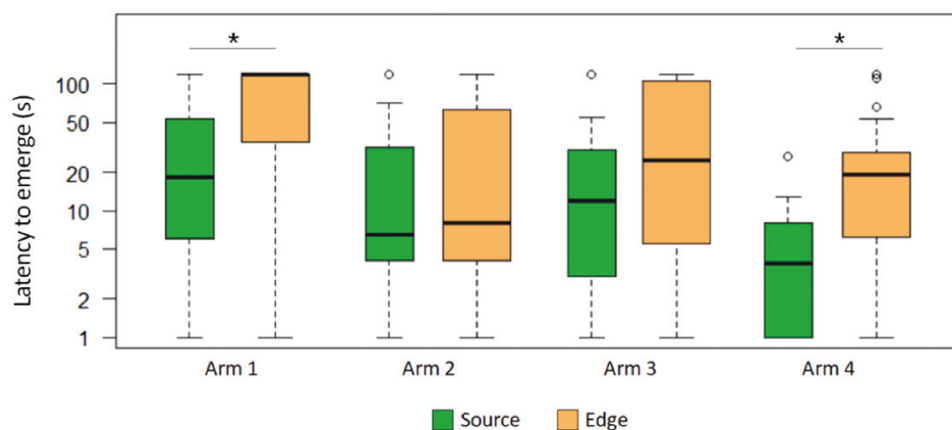


Figure 4. Latencies to leave the 4 arms of the radial arm maze for the first time, i.e. after the first visit for 43 individual bank voles *Myodes glareolus* in the source population and at the edge of the expansion. The y-axis is log scaled. Width of the boxes indicates relative sample size. Asterisks indicate significant differences from zero with $P < 0.05$.

more ready to leave the sheltered parts of the experimental set-ups to enter open, potentially risky environments, compared to conspecifics at the expansion edge. Gathering information quickly, on the other hand, may reward individuals from long-established populations, allowing them to discover or reach resources faster than conspecifics. This could be particularly favored in established populations where densities, and thereby intraspecific competition for resources and mates, are high (Burton et al. 2010).

Differences in exploration strategies or propensity to take risks can also reflect differences in local habitat conditions or population structure (e.g., Réale et al. 2007; Stamps and Groothuis 2010). However, we are confident that in this instance micro-habitat conditions carry negligible weight because we have (1) selected comparable sites in terms of both size, vegetation structure, and disturbance; and (2) conducted a previous comparison of the zones that showed no difference in demography (Eccard et al. 2023).

More information versus faster rewards

More revisits in the laboratory radial arm maze are commonly taken to indicate worse orientation, because in the laboratory version re-visits mean that test subjects could not keep track of the locations where the food had been eaten (e.g., Olton and Samuelson 1976; Crusio and Schwegler 2005). However, in the laboratory version of this test, rodents are trained to go through the maze several times (e.g., Crusio and Schwegler 2005). In our study, we recorded responses to the maze on the first to third time the animals were introduced to it, so several visits to the same arm may indeed indicate a more thorough information-gathering strategy for later use (e.g., Jardim et al. 2021). Similarly, more exploratory mound-building mice (*Mus spicilegus*) faced with an unfamiliar maze set-up showed a motivational conflict between the gathering of more information about the novel environment and the seeking of the reward, which ultimately lead to longer relative latencies to attain the reward (Jardim et al. 2021).

Exploration and risk-taking across contexts

From the repeated open-field tests, we showed that both the latency to leave the shelter and the latency to explore the central part of the arena were repeatable. We also showed that exploration strategies and risk-taking propensity were maintained in

Table 1. Number of re-visits to an already-visited arm of the maze, latency to enter the maze from the first arm and to leave it from the last visited arm in relation to expansion zone (source vs. edge), sex, and personality, for 43 individual bank voles *Myodes glareolus* across 53 tests

Variable	Fixed effects	Estimate	SE	<i>z</i>	<i>P</i>	<i>R</i> _c	<i>R</i> _m	Effect size
Number of re-visits (Poisson)	Intercept	0.124	0.309	0.401	0.689	0.23	0.51	0.76
	Area (Edge)	0.902	0.331	2.727	0.006			
	Sex (M)	-0.177	0.257	-0.689	0.491			
	Latency to emerge OF	0.191	0.135	1.414	0.158	0.34	0.52	
	Intercept	0.060	0.293	0.205	0.838			
	Area (Edge)	0.908	0.308	2.945	0.003			
	Sex (M)	-0.078	0.234	-0.334	0.739	0.27	0.51	
	Latency center OF	0.358	0.121	2.956	0.003			
	Intercept	0.420	0.324	1.295	0.195			
	Area (Edge)	1.035	0.334	3.103	0.002	0.71	0.71	-0.92
	Sex (M)	-0.157	0.245	-0.640	0.522			
	Activity OF	-0.671	0.331	-2.026	0.043			
	Intercept	2.303	0.899	2.561	0.010	0.19	0.19	
	Area (Edge)	-2.737	0.906	-3.021	0.003			
	Sex (M)	0.664	0.837	0.793	0.428			
	Latency to emerge OF	-2.700	1.363	-1.981	0.048	0.19	0.19	
	Intercept	1.397	0.680	2.054	0.040			
	Area (Edge)	-1.859	0.740	-2.511	0.012			
	Sex (M)	-0.037	0.632	-0.058	0.954	0.42	0.42	0.79
	Latency center OF	0.046	0.318	0.145	0.885			
	Intercept	1.230	0.777	1.584	0.113			
	Area (Edge)	-1.947	0.776	-2.510	0.012	0.30	0.30	
	Sex (M)	-0.035	0.631	-0.055	0.956			
	Activity OF	0.378	0.871	0.434	0.664			
	Intercept	0.859	0.274	3.138	0.002	0.29	0.29	
	Area (Edge)	1.251	0.311	4.015	<0.001			
	Sex (M)	0.630	0.289	2.178	0.029			
	Latency to emerge OF	0.510	0.144	3.540	<0.001	w		
	Intercept	0.878	0.302	2.909	0.004			
	Area (Edge)	1.151	0.342	3.370	0.001			
Sex (M)	0.747	0.320	2.337	0.019	0.29	0.29		
Latency center OF	0.245	0.159	1.546	0.122				
Intercept	1.158	0.364	3.184	0.001				
Area (Edge)	1.250	0.355	3.522	<0.001	w			
Sex (M)	0.691	0.321	2.154	0.031				
Activity OF	-0.537	0.427	-1.260	0.208				

The distribution of each variable, as specified in the models, is reported in () in the first column. Reference levels for fixed factors are given in (). *R*_m and *R*_c indicate variation explained without (marginal) and with (conditional) random factors. Effect sizes were calculated as $(\text{mean}_{\text{edge}} - \text{mean}_{\text{core}}) / \text{SD}$. Significant effects are marked in bold font.

the 2 experimental contexts we provided. Behavioral responses in the 2 tests were highly correlated at the phenotypic level, with voles that explored the radial arm maze more thoroughly (with more revisits to the same arms) also taking more time in the peripheral part of the open field before entering the central part of the arena. Further, our boldness measures, the latency to leave the dark-light tunnel to enter the open field and the latency to enter the maze, were also highly and positively correlated. The latencies to leave the first and last arm, that is, entering and leaving the maze, were analyzed and considered separately because they capture somewhat different aspects of the voles' strategies and risk-taking propensity. The vole was introduced to the maze through the first arm, a condition that mirrors the dark-light test

because the animal can choose to emerge from a dark enclosed shelter into an illuminated, novel, and empty arena. Leaving the fourth and last arm of the maze did not lead to the arena but back to freedom. Longer latencies to both enter and even leave the maze point toward a slower and more risk-averse phenotype, that favors safety over the potential gains of achieving something faster—even when faced with the opportunity of leaving the maze and be released into familiar environment, which was more likely to be displayed by animals at the expansion edge.

There were not enough repeated tests to measure learning or memory, nor which cues were used (e.g., the marks in the maze or the orientation of the maze); further studies are needed to clarify whether the initial pattern of maze

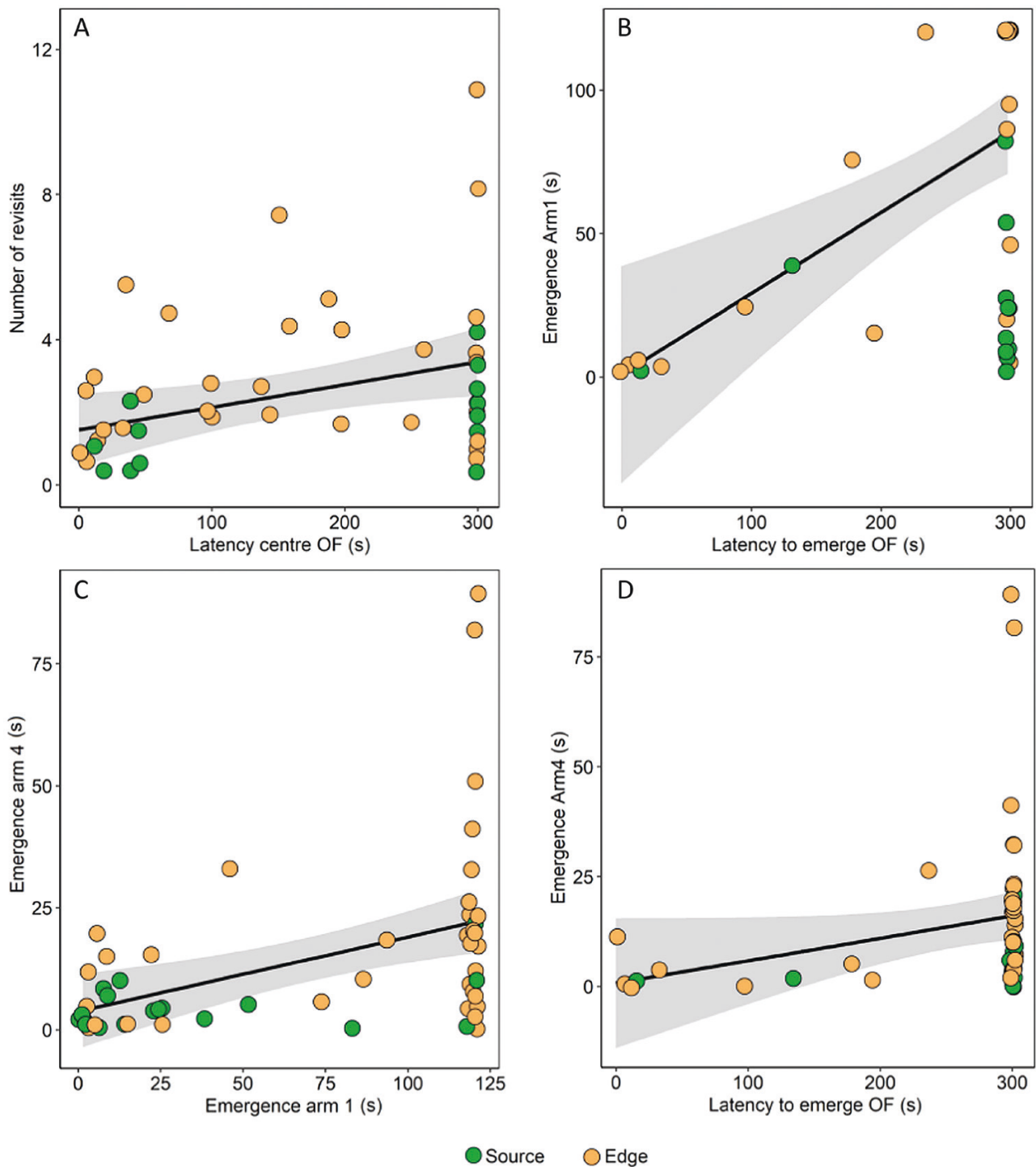


Figure 5. Number of revisits to already visited arms of the radial arm maze in relation to latency to explore the central part of the open-field arena (A); latency to emerge from the first (B) and last (D) arms of the radial arm maze in relation to the latency to leave the dark-light shelter; and in relation to each other (C). Shown are prediction lines with 95% confidence bands (gray shading) from linear models for visual representation and jittered raw data points for 43 individual bank voles *Myodes glareolus*.

exploration is maintained, and whether learning curves differ between expanding and settled populations.

Risk-aversion and the colonization of novel environments

Like most small mammals, bank voles face heavy predation pressure, and constitute the staple of the diet of several predators, both aerial and terrestrial (e.g., Jędrzejewska and

Jędrzejewski 1990; Jędrzejewski et al. 1993). The dangerous niche hypothesis posits that enhanced risk aversion is adaptive when novel stimuli are likely dangerous, for example, if toxic foods or a high level of predation risk characterize an individual's environment (Greenberg 2003). Differential selective pressure in different stages of colonization might explain the shift in strategies between populations at the source and edge of the bank vole expansion (e.g., Greenberg

and Mettke-Hofmann 2001; Greenberg 2003; Bókonyi et al. 2012). Taken together, our results suggest that for this heavily predated upon small mammal, a careful and thorough exploration strategy might be favored when expanding into novel environments. This is in line with a few previous studies on small prey species (e.g., Hudina et al. 2015; Ashenden et al. 2017), but contrasts with other findings concerning mostly birds or fish taxa where pioneers at the edge of a non-native expansion are often bold fast-explorers (e.g., Duckworth and Badyaev 2007; Cote, Fogarty, et al. 2010; Hudina et al. 2014; Myles-Gonzalez et al. 2015; Bensky and Bell 2020; Burstal et al. 2020; Morton et al. 2023). This is only an apparent contradiction, though, because for such taxa the most pressing demands concern efficient resource discovery and acquisition, challenges that are best met by bold behavioral types and fast information-gathering strategies. Small prey species instead have ecological needs that prioritize not being eaten, ensuring safety and crypticity, which is of course done best by careful, thorough individuals, thus making them the most suited to lead the expansion front in a non-native habitat (e.g., Jarić et al. 2019).

Sex differences

Contrary to Eccard et al. (2023), who found males to be more risk-averse than females at the expansion edge, we did not detect sex differences in behavior related to the expansion zone. The animals tested in this study were a subsample of a larger population that was measured for personality only by Eccard et al. (2023). It is then possible that our sample, while balanced for sex, was not big enough to capture sex differences in risk-taking propensity in relation to range expansion. The only detected sex difference was that in both zones males took longer than females to leave the maze while being released at the point of capture. This risk-averse response may refer to sex-related functional traits, with males being the dispersing sex in most mammals (Greenwood 1980). Avoiding risks may be a trait that is under strong selection during any form of dispersal (e.g., Simmons and Thomas 2004; Cote, Clobert, et al. 2010), and may thus be expressed most strongly in the dispersing sex (e.g., Michelangeli et al. 2020). We also did not detect sex differences in exploration strategy and spatial orientation. The cognitive performance of males and female bank voles was also comparable in our previous studies on associative learning, reversal learning, and decision-making (Mazza et al. 2018, 2019). The sexes may thus not face ecological challenges that differ enough to affect their cognitive performance or exploration strategies, compared to the challenges presented by colonization stage (e.g., Burstal et al. 2020).

In conclusion, behavior and cognition are labile traits whose remarkable responsiveness to environmental challenges can play a key role in evolution, and in facing novel or rapidly changing environments (e.g., Sol 2009; Foster 2013; Sih 2013). Our study shows that expanding and settled populations of non-native bank voles differ in exploration and spatial orientation, 2 complementary aspects of environmental information gathering and use. Individuals at the expansion edge were slower and more thorough in the approach to a novel space compared to conspecifics in the source population. These different strategies thus appear to represent adaptive adjustments for coping with range expansion in a

non-native environment, a colonization stage that seems to require heightened caution in a prey species. These findings highlight the importance of considering species' ecology when formulating predictions about the determinants of successful range expansions and biological invasions. Also, behavioral performance used to investigate cognitive processes needs to be contextualized within the ecological requirements of a species before drawing conclusions on specific phenotypes being more suited to novel or altered environmental conditions (e.g., Horn et al. 2022). Future studies addressing the connection between exploration, orientation and (spatial) learning and reversal learning, as well as the propensity to identify and use novel resources along the entire expansion gradient, are needed to further illuminate the role of behavior and cognition in coping with novel environments.

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Ethical Approval

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. Animal capture and behavioral tests were conducted under the permission of the Animal Research Ethics Committee of Trinity College (Ref. 130219). Site use was permitted by the respective county or local park authorities. We took great care in ensuring the animals' welfare throughout the experimental procedure. Traps contained plenty of food and vegetables as water supply; hay provided thermal insulation and the opportunity to build a nest. We covered the traps with grass, branches and leaves to provide shade and avoid overheating during daytime trapping. The use of single-capture Longworth traps ensured that there would be no stressful interactions among trap occupants. Traps were checked after max. 8 h. Occupied traps were refilled with food and water sources, and kept in the shade until testing. Handling was done with care and only on first capture. Individual markings were based on non-invasive fur cutting. Animals were released at the capture site immediately after testing.

Author Contributions

V.M. and J.A.E. designed the study and collected the data; V.M. analyzed the data and wrote the manuscript; both authors contributed to the final draft and gave final approval for publication.

Conflict of Interest

The authors declare no competing interests.

Data Availability

The data that support the findings of this study are available in the supplementary material of this article.

Supplementary Material

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

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