



Exploratory behaviour in shrews: fast-lived *Sorex* versus slow-lived *Crocidura*

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Exploration of the environment is a key behaviour in animals. The exploratory behaviour of species or populations depends on different aspects of their ecology. New evidence suggests that differences in exploratory behaviour might also be related to life history strategies, with fast-lived animals (high metabolic rate, short life span) being faster explorers than slow-lived ones. We tested this assumption in shrews. Shrews are divided into two phylogenetic groups, which differ tremendously in life history. We compared the exploratory behaviour of three species, covering both phylogenetic groups. Shrews of the fast-lived genus *Sorex* were quicker to start exploration and to locate the first food patch. They also moved faster than the slow-lived genus *Crocidura*. Unlike many studies on exploratory behaviour that analyse only a short period of time (i.e. a single exploration bout with a fixed duration), we analysed the species-specific allocation of prolonged total exploration time into exploration bouts. Using this method, we could show that *Sorex* performed more, but shorter exploration bouts than *Crocidura*. Our results support the hypothesis of exploratory behaviour being related to life history. While the species we tested occur sympatrically, the two genera differ strongly in the climatic zones they inhabit. It is likely that also during evolution they faced different types of habitat and thus different selection pressures. These differences in evolutionary histories possibly favoured the evolution of their diversified life histories and exploration strategies.

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Exploration of the environment is a key behaviour in many animals (Barnett 1958; Hughes 1997; Russell et al. 2009). Generally, animal behaviour is motivated by direct needs: foraging is motivated by the need to feed, courtship by the need to find a mate. In contrast, exploratory behaviour can be conducted without any specific need. During exploration an animal gathers general information about the structural properties of its surroundings and about features such as where to find food (Heinrich 1995) or a possible mate (Schwagmeyer 1995). This information might be helpful later when specific needs prevail. Exploration often occurs simultaneously with other behaviours such as foraging (Winkler & Leisler 1999). This type of exploratory behaviour is defined as extrinsic exploration. In contrast, intrinsic exploration is exploratory behaviour conducted for the sole purpose of gathering information for later use (Glickman & Sroges 1966; Tebbich et al. 2009; reviewed in Hughes 1997).

The exploratory behaviour of species or populations depends on different aspects of their ecology, including diet and habitat characteristics (Greenberg 1990; Mettke-Hofmann et al. 2002; Tebbich et al. 2009). One example is the increased tendency to explore the

environment in bird species that feed on concealed food items (Mettke-Hofmann et al. 2002) or that have more diverse diets (Tebich et al. 2009) compared to species with easily accessible food or less varied diets. Both concealed food and a diverse diet necessitate a higher investment in learning where to find food and consequently more time must be devoted to exploration (Renner 1988). Furthermore, bird species living in complex habitats show higher exploration rates than species living in less complex habitats (Greenberg 1990; Mettke-Hofmann et al. 2002). In complex, variable environments investigation of possible changes via exploration is much more critical to survival than it would be in more simple, stable environments. This would explain higher exploration rates in complex environments than in simple ones.

In the context of behavioural syndromes it has been suggested that the behaviour of individuals or populations is also linked to their life history strategies (Stamps 2007; Wolf et al. 2007; Biro & Stamps 2008). Some studies specifically investigated the relation of exploratory behaviour and basic metabolic rate (BMR; reviewed in Careau et al. 2008, Biro & Stamps 2010). These studies corroborate the expectation that individuals with higher BMRs tend to be more active than individuals with lower BMRs (Mueller & Diamond 2001; Gebczynski & Konarzewski 2009; but see Lantova et al. 2011). Most of the previously mentioned studies focus on differences between individuals (i.e. within a species). However, differences in

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behavioural strategies can also be found between species (Careau et al. 2009; Haupt et al. 2010; Page et al. 2012). Careau et al. (2009) related previously published exploration data of 19 muroid rodent species (Wilson et al. 1976; Webster et al. 1979) to the life history strategies of these species. They found that species with a slow life history (high age of first reproduction and low BMR) spend more time exploring a novel environment than species with a fast life history (low age of first reproduction and high BMR). The authors termed these two strategies as thorough and superficial exploration.

It seems obvious that exploratory behaviour should be related to BMR and life history strategy: animals with higher energetic needs would benefit from the ability to explore novel surroundings and learn about possible sources of food quickly. However, apart from the literature-based rodent study by Careau et al. (2009), we know of no work investigating the relationship between exploratory behaviour and life history using a comparative multispecies approach. To our knowledge, ours is the first study to examine this relationship experimentally.

A promising but until now unexplored model for studying the influence of life history strategy on exploratory behaviour is the family Soricidae (shrews). Belonging to the smallest mammals known, shrews are divided into two phylogenetic groups: red-toothed shrews (Soricinae) and white-toothed shrews (Crocidae). Most Soricinae occur in cold and humid climates and are mainly distributed throughout the northern hemisphere. Crocidae, in contrast, generally inhabit warm and arid areas, covering the middle and southern part of the Eurasian continent and Africa. In wide parts of Europe (between 36 and 51 degrees of latitude), however, members of the Crocidae and Soricinae occur sympatrically and sometimes even syntopically (Churchfield 1990). Both groups mainly feed on insects and other small invertebrates (Churchfield 1990).

Two genera that can be found in the overlapping zone of distribution are *Sorex* (Soricinae) and *Crocidae* (Crocidae). While the BMR of shrews of the genus *Crocidae* lies within the typical range for a mammal of this size, shrews of the genus *Sorex* are known for their extraordinarily high BMR (Kleiber 1961; Taylor 1998). To avoid starvation, they must feed every few hours and eat approximately their own body weight per day (Genoud 1988). *Sorex* shrews live just over 1 year. They mostly reproduce after their first winter, but some individuals breed in their first summer (Shchipanov et al. 2005). *Crocidae* shrews, in contrast, live up to 3 years and reproduce for several seasons (Churchfield 1990). Furthermore, *Sorex* has considerably larger litter sizes than *Crocidae* (5.9 versus 3.1 pups/litter; Innes 1994). Considering BMR, life span and litter size, shrews of the genus *Sorex* are a perfect example of animals with a fast-paced life history, whereas *Crocidae* has a much slower life history strategy (Promislow & Harvey 1990).

We investigated whether the differences in life history between *Sorex* and *Crocidae* are reflected in their exploratory behaviour. As experimental species we chose common shrews, *Sorex araneus*, pygmy shrews, *Sorex minutus*, and bicoloured shrews, *Crocidae leucodon*. We analysed their tendency to explore, and manner of exploring, a novel environment in a laboratory experiment. As shrews have a highly diverse diet and will consume most palatable food they encounter while running about, it is not possible to distinguish between exploratory and foraging behaviour. Thus the type of exploration we analysed clearly falls into the category of extrinsic exploration.

We expected the shrews of the fast-lived genus *Sorex* to explore the novel environment faster and more time efficiently, that is covering more space in a shorter amount of time than the slower-lived *Crocidae leucodon*. Based on the findings that rodent species with a slow life history spend more time exploring a novel environment than species with a fast life history (Careau et al. 2009), we further

expected *Crocidae leucodon* to explore the novel environment for a longer time than the two *Sorex* species. The BMR of the smaller *S. minutus* is only about 30% higher than that of *S. araneus* (Taylor 1998). We therefore expected, if anything, a slightly faster exploratory behaviour in *S. minutus* than in *S. araneus*.

METHODS

Animals and Housing

In the main experiment, we tested seven *S. araneus* (BMR: 6.1–8.3 ml O₂/[g h] (Taylor 1998); mean body mass: 8.4 g, own data), seven *S. minutus* (7.0–12.0 ml O₂/[g h]; 4.1 g) and seven *Crocidae leucodon* (2.6 ml O₂/[g h]; 9.6 g). In a separate experiment (see [Exploration of the Home Terrarium](#)) we additionally tested five *S. araneus*, six *S. minutus* and one *Crocidae leucodon*.

All shrews were caught in Germany either in the area surrounding the Max Planck Institute for Ornithology in Seewiesen or along the river Würm in Gauting, between April 2008 and November 2009. We used wooden box live traps (Mammal Research Institute, Białowieża, Poland), whose 1.4 cm thick wooden walls provide reasonable insulation from warm or cold weather and precipitation. If there was a risk of ground frost we additionally provided cotton wool as bedding. Owing to their rather large size (17 × 8 cm and 10 cm high, 481 g) traps are unlikely to be manipulated or taken by predators; in fact, during trapping sessions we never found that our traps were manipulated or missing. Traps were baited with a few dead mealworms, *Tenebrio molitor*, and a teaspoon of minced beef heart; the amount of food provided was sufficient for a shrew to survive for the short time it would spend in the trap. We checked traps every 2–3 h to minimize the stress and hunger of trapped animals. During the breeding season, we checked the captured individuals upon retrieval from the traps for pregnancy or lactation. Females showing any sign of pregnancy or lactation were released immediately to reduce stress to the pups. As far as is known, shrew pups should not be kept without food for more than about 3 h, the same as for adult shrews of the high-metabolic genus *Sorex* (Churchfield 1990). By checking traps in very short intervals, we gave mothers the opportunity to return to their pups within 3 h. Shrews were transported inside the traps from the place of capture to the keeping facilities; this generally took between 10 and 30 min. Upon completion of our experiments, all shrews were released at the place of capture. Before releasing them, we marked the shrews to avoid multiple testing. Marking was done by bleaching a small patch of fur above the base of the tail with mild, commercially available hair bleach for humans. As we recaptured many marked individuals in the days and weeks after release, we conclude that our marking technique had no adverse short- or long-term effects on shrews. Capturing was conducted with approval from the governmental review board of the Regierung von Oberbayern (licence number: 55.1-8642-8-2007).

Shrews were housed individually, because of their solitary lifestyle (Rychlik 1998), in plastic terraria (44 × 30 cm and 32 cm high) in a climate-controlled room (16–18 °C, 60–70% humidity) at the Max Planck Institute for Ornithology. Terraria were equipped with soil and moss as litter and bowls for water and food. An upturned clay flowerpot filled with hay served as a nestbox. Each shrew was provided with 3 g of live mealworms and 4 g of minced beef heart daily; water was available ad libitum. Shrews were kept on an inverted light:dark schedule (2100 hours light on, 0900 hours light off).

Behavioural observations were conducted in a separate climate-controlled room (same temperature and humidity as the keeping room). The experimental room was evenly illuminated by four infrared LED beams (Tripol, Poland) and presumably appeared dark to the shrews. This presumption is based on the evidently poor

eyesight of shrews (Branis & Burda 1994) and their limited range of good vision (471–622 nm, Sigmund 1985; infrared light is above 700 nm). These conditions were selected to ensure that shrews of both genera felt safe to explore the arena. Housing and behavioural observation were conducted with approval from the governmental review board of the Landratsamt Starnberg (licence number: 301c.4V-sä).

As sex and age could not be reliably determined in some individuals, we could not investigate the relationship between sex or age and exploration in any of the species. All *C. leucodon* and *S. araneus* as well as most *S. minutus* were caught and tested in summer or autumn. Three *S. minutus* were caught and tested in spring. Only one *C. leucodon* and one *S. minutus* were identified as sexually active males (enlarged testis). As their data did not include any outliers, we included them in our analysis.

Set-up and Experimental Design

Behavioural observations were conducted in a large circular arena (diameter 250 cm, wall height 50 cm; Fig. 1a) made from PVC. The arena was equipped with 10 brick stones, four foraging patches and a shelter. Bricks were arranged radially, with pairs of two bricks building the rays of a five-rayed star. At the end of one of these rays, we placed a circular Perspex box (diameter 15 cm). This box served as the starting box and as a shelter during the experiment. At the ends of the other four rays, we placed small square Perspex boxes (11 × 11 cm) that served as foraging patches. Each foraging box contained a thin layer of sand as substrate and some mealworms. For shrews of the genus *Sorex*, four mealworms were available in each foraging box, for *C. leucodon* only two. A bowl of water was placed behind the starting box/shelter, for refreshment of the shrews during the experiment.

Shrews were kept in captivity for a minimum of 1 week before testing. Before the start of the experiment, the focal subject was kept without access to food in a separate terrarium for 1 h (the two *Sorex* species) or 4 h (*C. leucodon*). These time periods were meant to simulate the natural activity patterns found in *Sorex* and *Crocicidura*, respectively (Churchfield 1990; Saarikko & Hanski 1990) and induce a comparable intermediate level of hunger in each species. We assumed shrews of both genera to be similarly motivated to explore and forage without being extremely hungry. At the onset of the experiment, the nestbox of the focal subject was placed into the starting box inside the arena. The shrew was given 4 h to explore the arena. Each shrew was tested once.

As opposed to a classic open-field test (Archer 1973), our experimental approach allowed the shrews to retreat to the shelter at any time. Consequently this experiment was much less stressful to the animals than an open-field test would be and is more likely to reveal relatively natural exploration strategies.

Analysis of Movements

Movements of shrews were filmed with an IR-sensitive camera (B/W video camera C-FO432SB with high-resolution objective L-SV-0514MP, both NET, Finning, Germany), mounted 2.7 m above the centre of the arena and recorded by motion-tracking software (ANY-maze, Stoelting, Wood Dale, IL, U.S.A.; see [Supplementary Material, Movie1](#)). Shrew movements were stored as the x–y position as a function of time.

The arena was divided into four zones of interest (Fig. 1a): (1) 'shelter zone', defined as being within the shelter; (2) 'foraging zone', defined as being within any of the four foraging boxes; (3) 'wall-seeking zone', defined as being within the outermost 5 cm ring of the arena and the 5 cm around each brick, foraging box and

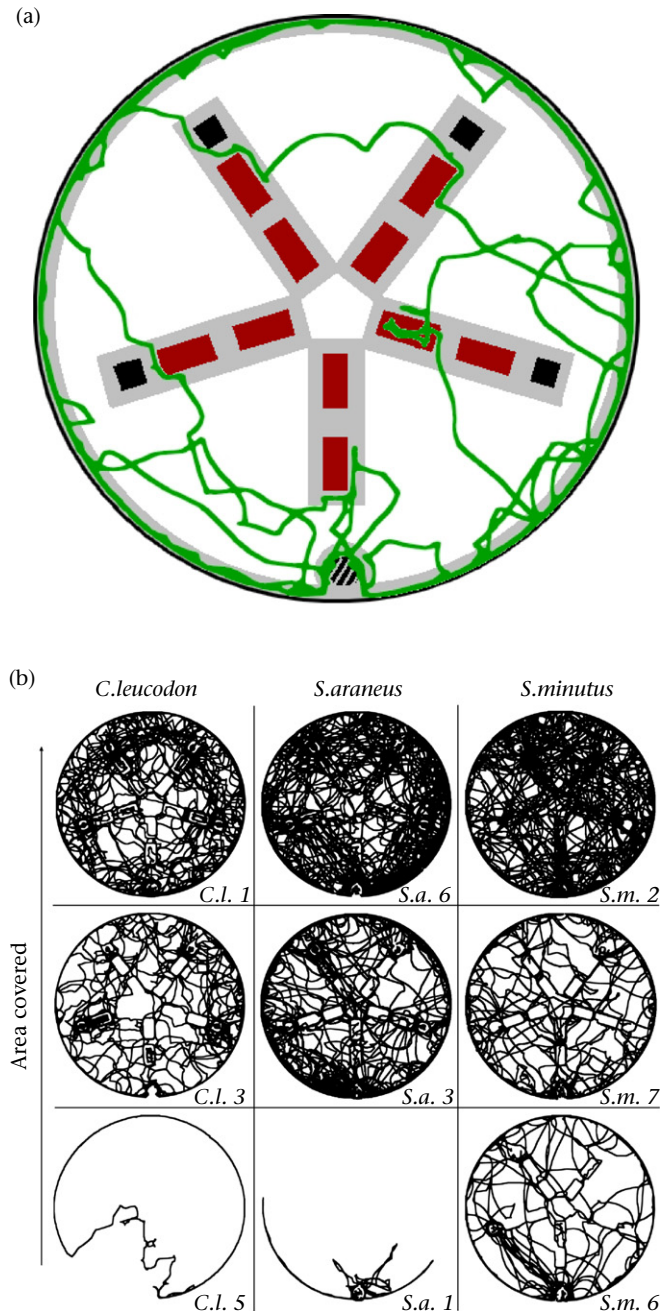


Figure 1. (a) Schematic drawing of the experimental arena (diameter 250 cm) with the shelter (striped), the four foraging boxes (black), the brick stones (red), the 'wall-seeking zone' (grey), and the rest of the arena (white). The white and red parts of the arena add up to the 'free-exploration zone' (see [Methods](#) section 'Analysis of movements' for details). Overlaid is the track line of one of the experimental shrews (a *C. leucodon*; green). (b) Example track lines for all three species. From each species, we chose three individuals: one with high, one with intermediate and one with low coverage of the arena. Track lines were broadened from ANYmaze track lines to resemble the real path width a shrew would cover with its nose and whiskers (about 7 cm).

the shelter; and (4) 'free-exploration zone', defined as being somewhere within the rest of the arena. The wall-seeking zone was used to analyse the amount of time a shrew explored the arena running alongside a wall.

Using custom Matlab routines (Matlab, MathWorks, Natick, MA, U.S.A.; routines by S.v.M.), we calculated the following parameters: (1) the latency to leave the shelter for the first time; (2) the latency

to find the first foraging box; (3) the proportion of time spent exploring the arena; (4) the number of exploration bouts; (5) the duration of single exploration bouts; the area of the arena the shrews covered (6) during single exploration bouts and (7) during the whole experimental time; (8) the area covered per second of exploration; and (9) the speed of movement. Additionally we calculated (10) the proportion of exploration time spent wall seeking. Exploration was defined as exploratory movement of the shrew inside the free-exploration zone and the wall-seeking zone. The time shrews spent inside the foraging boxes (on average 3.3 s per visit per shrew; no significant difference between genera or species; Wilcoxon two-sample test: $P > 0.9$) was excluded from all measures of exploration. Exploration bouts were defined as exploratory movement separated by the shrew's retreat into the shelter.

To analyse the area of the arena covered during exploration (parameters 6–8), movement plots were generated from the x–y positions and broadened to 7 cm, to resemble the real path width a shrew would cover with its nose and whiskers (about 7 cm; Fig. 1b). Even though *S. minutus* is smaller than the other two species, based on the typical movement of nose and whiskers during shrew locomotion, path width would vary not only between but also within species. We thus decided to use a common measure of 7 cm for all species. From these movement plots we calculated the area covered during the single exploration bouts, the overall area covered during the whole experimental time and the area covered per second of exploration.

To obtain comparable measures of speed of movement (9) between species, we only used runs in which shrews were running along the outer wall of the arena, because these were the only fully similar paths that all shrews of all species took. We divided the outermost ring of the arena into 10 virtual segments. For each shrew, we calculated the mean speed for the first six to eight runs, in which the shrew had run along the outer wall of the arena for at least three consecutive segments. We calculated and used for analysis only the speed of the middle of these three segments.

To obtain a comparable measure of wall-seeking time (10), we calculated the proportion of exploration time that a shrew's position lay inside the wall-seeking zone and not in the free-exploration zone. To ensure statistical independence of the data points, we only used position data that were independent of the shrews' previous position. To achieve this, we calculated the amount of time necessary for each individual to cross the diameter of the arena (t_{Diam}), using each individual's speed of movement. In this time span, a shrew is in theory able to reach every possible position of the arena independent of the previous position. We included in our analysis only position data that were t_{Diam} apart, starting with a randomly chosen starting point t_{Rand} , with $t_{\text{Start}} \leq t_{\text{Rand}} < (t_{\text{Start}} + t_{\text{Diam}})$, where t_{Start} is the time of the onset of exploration and ending with the end of the experimental time. We calculated 1000 bootstrapped samples of each individual's position data with randomly chosen starting points as described. From the data obtained, we calculated the proportion of exploration time in which a shrew was located in the wall-seeking zone.

Statistical Analysis

We mainly expected differences between *C. leucodon* and the two *Sorex* species, and only small or no differences between the two *Sorex* species. To test for genus and species differences, we compared each of the behavioural parameters using planned comparisons with *Sorex* versus *Crocicidura* as the first contrast, and *S. araneus* versus *S. minutus* as the second contrast. As our comparisons were planned (a priori) based on our experimental design and questions, we did not perform Bonferroni adjustments

on P values. As data for some parameters were not normally distributed (Shapiro–Wilk: $P < 0.05$) or showed unequal variances (Levene's test: $P < 0.05$), we used the nonparametric Wilcoxon two-sample test throughout. All statistical tests were performed in R 2.8.0 (R Development Core Team 2009).

We expected all three species to prefer running along walls instead of freely exploring the arena. Thus, we compared the proportion of time inside the wall-seeking zone with the probability of being inside the wall-seeking zone by chance using a one-sample Wilcoxon test. The probability of being inside the wall-seeking zone by chance is the area of the wall-seeking zone divided by the summed areas of the wall-seeking zone and the free-exploration zone.

Exploration of the Home Terrarium

With a subset of the shrews of this experiment (all seven *C. leucodon*, five *S. araneus* and three *S. minutus*) plus additional shrews (one *C. leucodon*, five *S. araneus* and six *S. minutus*), we conducted a separate experiment that measured the exploratory behaviour of freshly caught shrews inside their new home terraria (for a description of the terraria see [Animals and Housing](#)).

On the day of capture, each shrew was directly placed into the nestbox of its new terrarium. The behaviour of shrews in the terrarium was recorded from above with an IR-sensitive recording system (WAT-902H2 Ultimate camera with 1.4/3.5 mm objective, Watec, Tsuruoka, Japan; recorder: DCR-TRV 80E, Sony, Tokyo, Japan). The only exploratory measure we analysed in this experiment was the latency of the shrews to leave the nestbox for the first time and start exploring the new terrarium. We compared this measure between species using planned comparisons as in the main experiment.

RESULTS

Exploration of the Arena

Latency to leave the shelter ranged from 56 s (a *S. minutus*) to 2 h 22 min (a *C. leucodon*). Overall, this latency was almost significantly higher for *C. leucodon* than for the two *Sorex* species (Fig. 2a; all statistics are shown in the respective figures). Also, the within-species variance in latency to leave the shelter was significantly higher in *C. leucodon* than in the two *Sorex* species (Levene's test: $P = 0.012$). There was no significant difference between *S. minutus* and *S. araneus* in this or any of the other measured parameters.

Latency to find the first foraging box was significantly higher for *C. leucodon* than for the two *Sorex* species (Fig. 3a). Also, the within-species variance in latency to find the first foraging box was significantly higher in *C. leucodon* than in the two *Sorex* species (Levene's test: $P = 0.009$). In all three species we found both half-eaten mealworms and intact mealworms in both the foraging boxes and the shelter. This is probably a consequence of the shrews consuming food in both places and hoarding some food in the shelter.

There was no difference between genera or species in the proportion of time spent exploring the arena after first leaving the shelter (first contrast: *C. leucodon* versus *Sorex*: $W = 51$, $P = 0.913$; second contrast: *S. minutus* versus *S. araneus*: $W = 29$, $P = 0.620$) or in the proportion of the area of the arena that was covered during this exploration time (first contrast: *C. leucodon* versus *Sorex*: $W = 34$, $P = 0.287$; second contrast: *S. minutus* versus *S. araneus*: $W = 31$, $P = 0.456$). However, *C. leucodon* performed significantly fewer exploration bouts than the two *Sorex* species (Fig. 3b), while the mean duration of bouts (Fig. 3c) and the mean area covered during bouts (Fig. 3d) were significantly higher in *Crocicidura* than the two *Sorex* species. The area covered per second of exploration

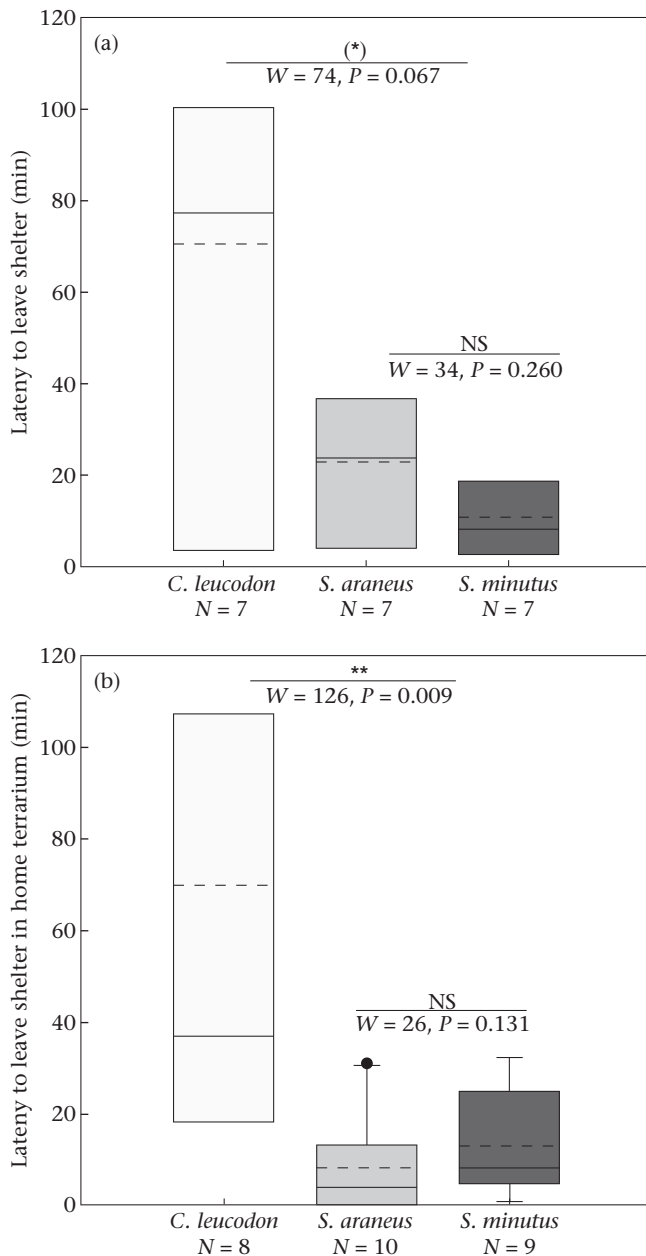


Figure 2. Latency to leave the shelter (a) in the main experiment and (b) in the home terrarium experiment. Boxes denote first, second and third percentiles; dashed lines show the species mean; whiskers show 10th and 90th percentiles. The filled circle is an outlier. Planned comparison using Wilcoxon two-sample test, all P values are two tailed; first (*C. leucodon* versus *Sorex*) and second (*S. minutus* versus *S. araneus*) contrasts are shown.

time was significantly higher in the two *Sorex* species than in *Crocicidura* (Fig. 3e).

Speed of movement ranged from 16.3 cm/s (a *C. leucodon*) to 55.8 cm/s (a *S. minutus*). It was significantly lower in *C. leucodon* than in the two *Sorex* species (Fig. 3f).

There was no significant difference between genera or species in the proportion of time spent inside the wall-seeking zone (first contrast: *C. leucodon* versus *Sorex*: $W = 45, P = 0.799$; second contrast: *S. minutus* versus *S. araneus*: $W = 24, P = 1$). However, all species spent significantly more time in wall-seeking behaviour than expected by chance (Fig. 4).

Exploration of the Home Terrarium

As in the arena experiment, the latency to leave the nestbox and begin exploration of the home terrarium was significantly higher for *C. leucodon* than for the two *Sorex* species (Fig. 2b). There was no difference between *S. minutus* and *S. araneus*. Again as in the arena experiment, the within-species variance in latency to leave the shelter was significantly higher in *C. leucodon* than in the two *Sorex* species (Levene's test: $P = 0.001$).

DISCUSSION

In two different experimental set-ups, we found clear differences between the exploratory behaviour of *C. leucodon* and the two *Sorex* species, but no differences between *S. araneus* and *S. minutus*. The two *Sorex* species were quicker to start exploration and to locate the first patch with food. They also moved faster and performed more but shorter exploration bouts than *Crocicidura*. Generally *Sorex* showed an exploration strategy that was fast and time efficient, while *Crocicidura* displayed a slower and more thorough exploration strategy.

The distinct differences in exploratory behaviour between *Crocicidura* and the two *Sorex* species matched our expectations. However, because of the slightly higher BMR of *S. minutus* than *S. araneus*, we had predicted a slightly faster exploration strategy for the former species. The fact that we could not find such a difference can probably be explained by differences in body size: by being considerably smaller than *S. araneus*, *S. minutus* requires a smaller absolute amount of food. Consequently it might not be necessary for them to cover more space in less time.

In a laboratory study on movement patterns it has been shown that *S. araneus* is more efficient in covering space systematically than a random model (Pierce 1987). Pierce's measure of efficiency was a purely spatial one (number of different places visited per distance travelled), while ours was spatiotemporal (area covered per second of exploration). In this spatiotemporal measure, *Crocicidura* was less efficient than the two *Sorex* species, covering less area per unit time. However, in the current study we did not analyse exact movement patterns or spatial efficiency. Thus, we cannot draw any conclusions regarding the space use efficiency of *Crocicidura* movements.

Exploratory Behaviour and Life History Strategies

The differences we found can probably be explained by the tremendous differences in life history strategy between the two genera (Innes 1994): shrews of the genus *Sorex* live only about half as long as shrews of the genus *Crocicidura* (Churchfield 1990), and their BMR is more than double that of *Crocicidura* (Genoud 1988; Taylor 1998). For the high-metabolic shrews of the genus *Sorex* it is particularly important to learn quickly about secure places to rest and possible sources of prey when entering a novel environment. Shrews of the genus *Crocicidura*, in contrast, can metabolically afford to take their time in thoroughly exploring a novel environment.

To reduce the possibility that *Sorex* shrews were hungrier and thus more motivated to search for prey than *C. leucodon*, we attempted to induce moderate natural levels of hunger in all individuals of both genera. Shrews of all species left intact mealworms in the foraging patches or even hoarded food inside the shelter, a behaviour found in shrews of different species (Rychlik & Jancewicz 2002), indicating that none of the species were overly hungry when exploring the arena. If we had started the experiment with both genera just fed, the two *Sorex* species would have had to start foraging within a shorter amount of time than *C. leucodon*. In this case, any genus difference could have resulted not only from

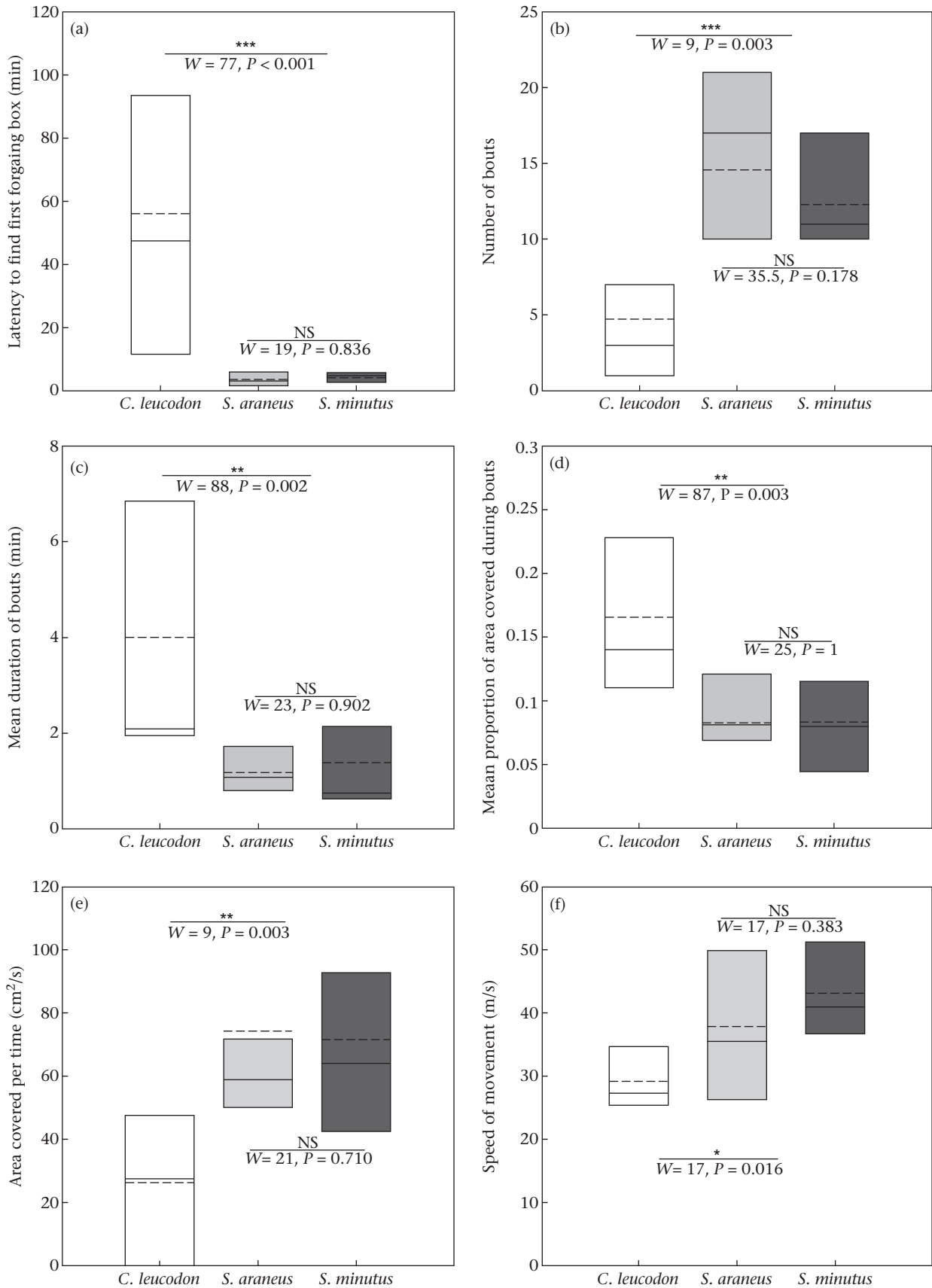


Figure 3. (a) Latency to find the first foraging box after the start of exploration; (b) number of exploration bouts conducted within the entire 4 h of exploration; (c) mean duration of single exploration bouts; (d) mean proportion of area covered during single exploration bouts; (e) area covered per amount of exploration time; (f) speed of movement during exploration. Boxes denote first, second and third percentiles; dashed lines show the species mean. Planned comparison using Wilcoxon two-sample test, all P values are two tailed; first (*C. leucodon* versus *Sorex*) and second (*S. minutus* versus *S. araneus*) contrasts are shown. For all species $N = 7$.

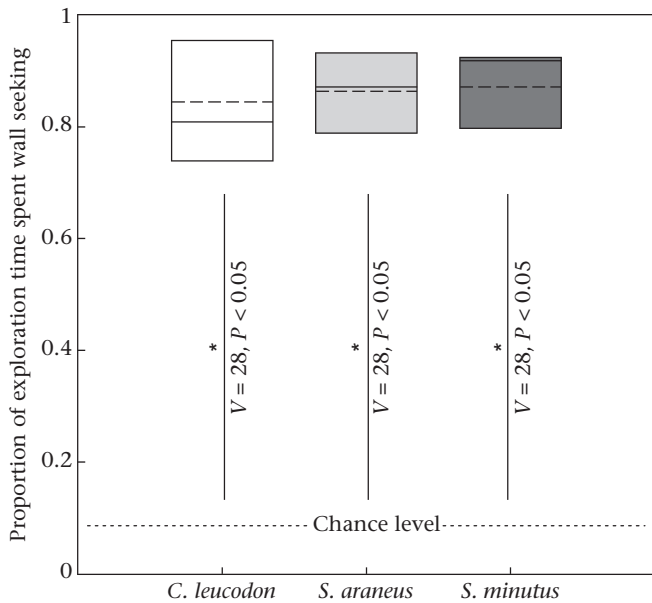


Figure 4. Proportion of the exploration time the shrews spent running along walls. Boxes denote first, second and third percentiles; dashed lines show the species mean; dotted line shows the chance level (0.09%). Statistics shown in figure: one-sample Wilcoxon test.

differences in exploratory behaviour, but also from different levels of hunger. With our design, however, the genus differences we found are very likely to be a result of true differences in exploration strategy.

Shrews of the species *C. leucodon* not only had a longer latency to start exploration than *Sorex* shrews, but also the within-species variation in latency to start exploration was much higher in *C. leucodon* than in *Sorex*. This complements a key difference in their life history strategies: shrews of the genus *Crocicidura* are not forced to eat as regularly as *Sorex*. Thus, in *C. leucodon* higher interindividual differences in exploratory behaviour are possible, while the behaviour of shrews of the genus *Sorex* must be quicker and less variable.

The interindividual variability in *Crocicidura* was higher than in *Sorex* not only in latency to start exploration in the arena, but also in several of the other exploratory parameters that we measured. Consistent interindividual differences in behaviour are receiving more and more attention in studies on animal behaviour (reviewed in Wilson et al. 1994; Dall et al. 2004; Sih et al. 2004; Réale et al. 2007; Dingemanse & Wolf 2010; Stamps & Groothuis 2010). It is suggested that within a species different individuals behave differently in the same context (foraging, novelty, social stress) but that the same individual will show similar behavioural reactions across different contexts. Typically, some individuals behave, independent of the situation, more boldly, aggressively and actively (proactive type; Koolhaas et al. 1999) and others are shyer, more docile and more inactive (reactive type). Such suites of correlated individual-specific behavioural reactions are referred to as animal personality traits (Buss 1991; Gosling & John 1999), temperament (Boissy 1995), coping style (Koolhaas et al. 1999) or behavioural syndromes (Sih et al. 2004).

To test for personality, the same individual has to be tested repeatedly to check for consistency of behavioural reactions over time and across contexts. In our study, we tested some of the individuals twice (arena and home terrarium experiment). Our sample size, however, does not allow us to make confident statements about possible personalities of our study subjects. However,

concepts of animal personality research might still prove helpful in the interpretation of the data from our cross-species comparison, namely, in an attempt to confirm and define the existence of what could be referred to as 'species personality'.

Species Personality

While most of the literature on behavioural syndromes focuses on within-species differences, some studies also consider differences between species (Glickman & Sroges 1966; Mettke-Hofmann et al. 2002; Careau et al. 2009; Page et al. 2012). Similarly, we analysed consistent behavioural differences between three species (two genera) of shrews. We found consistent behavioural differences between the two genera *Sorex* and *Crocicidura*, but not between the two *Sorex* species. The two *Sorex* species behaved more boldly and actively than *Crocicidura*. Also, *Sorex* shrews are generally more aggressive towards conspecifics (Churchfield 1990) and during handling (personal observation). This makes them typical proactive animals, while the more docile *Crocicidura* can be termed reactive.

In an evolutionary scenario it is feasible to imagine that consistent behavioural differences between individuals lead to consistent behavioural differences between populations. Several empirical studies support this idea (Dingemanse et al. 2007; Brydges et al. 2008; Wray et al. 2011). In shaping such consistent behavioural differences between populations, external factors are involved. In birds and fish the strength of predation pressure and the type of habitat can influence the behavioural trait of a population (Dingemanse et al. 2007; Brydges et al. 2008). Also in mammals an effect of predation on personality has been shown (Réale & Festa-Bianchet 2003). Ultimately strains or populations with consistent behavioural differences might split up into different species, given that other factors such as a reproductive barrier are present. In such a scenario, the emerging sister species would then be characterized by different behavioural reaction norms, or, as we might say, 'species personalities'.

Apart from such external factors, life history trade-offs seem to maintain behavioural syndromes (reviewed in Biro & Stamps 2008; theoretical work: Stamps 2007; Wolf et al. 2007; empirical data: Réale et al. 2000; Boon et al. 2007; Schürch & Heg 2010; Gyuris et al. 2011; Krause & Naguib 2011). Animals with a high growth rate, for example, have high energetic requirements to maintain this fast growth. For them it is therefore adaptive to have a bold (explorative and aggressive) personality in order to find and defend sufficient food sources. Such a bold behavioural trait, however, might also lead to higher mortality through a higher risk of predation or competitive encounters. The growth–mortality trade-off is one of the life history factors that seem to be strongly involved in maintaining personality differences (Stamps 2007; Biro & Stamps 2008). Our study supports this idea on a cross-species level: while the bold and active *Sorex* species grow, reproduce and die quickly, the more shy and inactive *Crocicidura* invests more in slow growth, later reproduction and longer life.

Better Learning through Slower Exploration?

Owing to their longer life span, *Crocicidura* shrews may be more prone to invest in knowing their environment well. Knowledge about the environment is gained by a thorough exploration of it (Renner 1988), which can be achieved, for example, by exploring the environment at a lower speed and/or for a longer period of time. Indeed, *C. leucodon* investigated the arena in our study at a lower speed than the *Sorex* shrews. However, they did not explore it for a longer period of time, as we had hypothesized based on the meta-analysis by Careau et al. (2009). In their study, rodents with a slower

life history strategy were found to spend more time exploring an open-field arena than rodents with a faster life history strategy. However, in the rodent studies (Wilson et al. 1976; Webster et al. 1979) the total experimental time was much shorter (10 min) than in our study (4 h). Furthermore, the rodents had no shelter to retreat to during experiments, while our shrews did. Thus, it seems more reasonable to compare the duration of exploration in the rodent study to the duration of single exploration bouts in our experiment. Indeed, the exploration bouts of *Crocidura* were longer than those of *Sorex*, which is in line with the results of the rodent study: animals with slow life history strategies investigate their surroundings for longer and probably more thoroughly. This is also reflected in the larger proportion of the arena covered during the single exploration bouts of the *Crocidura* shrews in our study. However, as our *Sorex* shrews performed more exploration bouts than *Crocidura*, the overall exploration time and area were the same in both genera.

The overall area shrews covered during the whole exploration time did not differ between the two genera. *Sorex* shrews, however, were exploring the novel surroundings at a higher speed and thus covering more space in a shorter amount of time. It may well be that by exploring at a slower pace *Crocidura* gains more knowledge about the environment, which can be invested for its future. A study comparing the spatial-learning ability of the two genera could help to answer this question. New evidence indeed suggests that slower-lived taxa are better learners than fast-lived ones (Page et al. 2012).

Studies on spatial exploration often compare simple parameters such as total distance moved (Bell & Stamps 2004; Stapley & Keogh 2004) or total time of exploration (Wilson et al. 1976; Gebczynski & Konarzewski 2009), mostly within short periods of time. We, however, analysed the allocation of the total exploration time into single exploration bouts within a longer period of time. Through this we were able to reveal the different exploration strategies of *Sorex* and *Crocidura*, which would not have been obvious from comparisons of the total time spent exploring the arena.

Exploratory Behaviour and Differences in Habitat

In addition to life history strategy, differences in habitat might also play a role in differences in exploratory behaviour (Greenberg 1990; Mettke-Hofmann et al. 2002) and learning (Haupt et al. 2010). Many species of the two genera of our study differ in their natural habitat: members of the genus *Sorex* often inhabit more cold and humid environments than members of the genus *Crocidura* (Churchfield 1990). Humid habitats, such as a swampy forest edge or an occasionally flooded meadow, are likely to be more complex than dryer ones, such as a savannah or an evenly irrigated crop field (August 1983). Complex habitats have been shown to favour high exploration rates (Greenberg 1990; Mettke-Hofmann et al. 2002). This behaviour has an adaptive value: in more complex and variable habitats the amount of information gained during repeated exploration bouts is higher than in simpler, more stable ones. The humid and probably complex habitat of *Sorex* thus provides an environment that favours selection for a fast exploration strategy.

While the differences in habitat hold true when comparing the two genera, there is no general habitat difference between the shrew species we compared in this study. They can all live under similar climatic conditions and their habitat and ecological niches overlap considerably (Churchfield 1990).

Evolution of Exploration Strategies

Although the biogeographical origins of Soricinae and Crocidurinae are not fully resolved, the two subfamilies presumably originated in two diverse climatic zones (Butler 1998; Dubey et al.

2007). The centre of radiation of the subfamily Soricinae (on the Eurasian continent about 13.8 million years ago; Dubey et al. 2007) was probably colder and more humid than that of the Crocidurinae (on the African or the southern Eurasian continent about 10.8 million years ago; Dubey et al. 2007).

Humid habitats are more productive than dry ones, and thus exhibit a higher predictability of food supplies (Lovegrove 2000). There is evidence that productive environments favour the evolution of a high BMR (Lovegrove 2000; Mueller & Diamond 2001; Bozinovic et al. 2007). In humid habitats with a high and predictable abundance of prey the evolution of fast life history traits, where a lot of food is required to fuel the fast metabolism, is possible. At the same time it is adaptive to evolve a fast exploration strategy to maintain such a fast life history. Indeed, it has been shown that productive environments favour the evolution of higher activity levels (Mueller & Diamond 2001). We argue that the high BMR and fast exploration strategy probably evolved together in shrews of the genus *Sorex* and were both favoured by their evolutionary origin in humid, productive habitats. Shrews of the genus *Crocidura*, in contrast, presumably evolved in more arid and thus less productive climatic zones, where a fast life history with a high BMR is not likely to arise. A less productive habitat and the resulting evolution of a moderate BMR supposedly did not provide a suitable environment for *Crocidura* to evolve a fast exploration strategy. Their slower exploration strategy might even help them to learn more about their environment and thus invest in their future.

Spending more time outside a shelter is costly because of an increased risk of predation. Shrews are a common prey item, especially for owls and raptors (von Blotzheim & Bauer 1969; Churchfield 1990). A slower exploration strategy, as we found in *Crocidura*, might reduce the risk of predation during exploration (Werner & Anholt 1993), because slow explorers are less conspicuous to predators and can invest more time and attention in vigilance. In contrast to *Sorex* shrews, which are restricted by their fast metabolism, *Crocidura* can develop different solutions to the trade-off between the gathering of information through exploration and the risk of predation. Different individual strategies for solving this trade-off may explain the high within-species variability in exploration behaviour that we found in *Crocidura*. This explanation is consistent with other studies on the influence of predation on shaping animal personalities (see *Exploratory Behaviour and Life History Strategies* above; Réale & Festa-Bianchet 2003; Dingemans et al. 2007; Brydges et al. 2008).

Wall-seeking Behaviour

A typical behavioural reaction to the risk of predation is wall seeking (Mashoodh et al. 2009). When keeping close to larger structures, small animals are less likely to be exposed to predators and thus show less anxiety-related behaviour (Harris et al. 2009). Indeed, all shrew species tested in the current study showed the same preference to run along the edges of either the arena or structures inside the arena. Wall-seeking behaviour is a common phenomenon not only in small ground-dwelling mammals but also in many other animal species, including insects, fish and blind humans (Wilson et al. 1976; Martin 2004; Kallai et al. 2007; Sharma et al. 2009). Apart from predator avoidance, using the physical guidance provided by structures in the environment is assumed to aid in spatial orientation, especially in situations in which only short-range senses are available (Sharma et al. 2009).

Conclusions

In the present study we showed that shrews of the fast-lived genus *Sorex* have a faster exploration strategy than shrews of the

slow-lived genus *Crociodura*. Our results are consistent with the hypothesis of a correlated evolution between exploratory behaviour and life history strategy. To explore this correlation further, a multispecies approach, preferably with phylogenetically independent contrasts (Harvey & Pagel 1991), is necessary. The species to choose for such a study should face comparable ecological conditions, while differing in their life history strategies.

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Supplementary Material

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