

Associative memory or algorithmic search: a comparative study on learning strategies of bats and shrews

Rachel A. Page · Sophie von Merten · Björn M. Siemers

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Abstract Two common strategies for successful foraging are learning to associate specific sensory cues with patches of prey (“associative learning”) and using set decision-making rules to systematically scan for prey (“algorithmic search”). We investigated whether an animal’s life history affects which of these two foraging strategies it is likely to use. Natterer’s bats (*Myotis nattereri*) have slow life-history traits and we predicted they would be more likely to use associative learning. Common shrews (*Sorex araneus*) have fast life-history traits and we predicted that they would rely more heavily on routine-based search. Apart from their marked differences in life-history traits, these two mammals are similar in body size, brain weight, habitat, and diet. We assessed foraging strategy, associative learning ability, and retention time with a four-arm maze; one arm contained a food reward and was marked with four sensory stimuli. Bats and shrews differed significantly in their foraging strategies. Most bats learned to associate the sensory stimuli with the reward and remembered this association over time. Most shrews searched the maze using consistent decision-making rules, but did not learn or remember the association. We discuss these results in terms of life-history traits and other key differences between these

species. Our results suggest a link between an animal’s life-history strategy and its use of associative learning.

Keywords Bats · Shrews · Learning · Memory · Life-history traits

Introduction

Species vary greatly in their cognitive abilities. While some animals are quick to learn and able to rapidly alter their behavior in response to novel stimuli, others are more stereotyped and are relatively locked into fixed patterns of behavior (Sih et al. 2004). Why are some species cognitively plastic while others respond slowly to novelty and change?

Animals differ in the resources they allot to different activities at different times. Life-history theory predicts that evolutionary trade-offs govern such resource allocations, and animals have evolved a continuum of strategies to best cope with conflicting demands (Promislow and Harvey 1990). Animals with fast life-history strategies often have high metabolic rates and short lifespans. They tend to reproduce early, have many litters, and many young per litter. On the opposite extreme are animals with slow life-history strategies. They have lower metabolic rates, live longer, and have fewer young later in life. Common life-history trade-offs include growth versus survivorship, fecundity versus survivorship, and early versus late reproduction (e.g., Bennet and Harvey 1988; Biro et al. 2006; Maklakov et al. 2007).

Theoretical studies suggest that behavior can mediate life-history trade-offs (Stamps 2007; Wolf et al. 2007), and recent empirical studies have found a link between life-history strategies and behavioral characteristics (Careau et al.

Rachel A. Page and Sophie von Merten contributed equally to this work.

R. A. Page (✉) · S. von Merten · B. M. Siemers
Sensory Ecology Group, Max Planck Institute for Ornithology,
Eberhard-Gwinner-Straße, 82319 Seewiesen, Germany
e-mail: PageR@si.edu

Present Address:

R. A. Page
Smithsonian Tropical Research Institute, MRC 0580-06,
Apartado, 0843-03092 Panama, Republic of Panama

2009; Schürch and Heg 2010; von Merten 2011). Careau et al. (2009) investigated the exploratory behavior of 19 species of muroid rodents as a function of metabolic rate and age of first reproduction. They found that species with fast life-history traits (high metabolic rate and early first reproduction) explore their environment superficially, while species with slower life-history traits explore their environment more thoroughly. There is mounting evidence that behavioral traits such as boldness, aggression, and exploratory behavior are also linked to life-history characteristics (Biro and Stamps 2008; Stamps 2007; Wolf et al. 2007; von Merten 2011).

Here, we ask whether similar links can be found between life history and learning ability. Does the ability to learn associations reflect the slow-fast life-history continuum? To what extent can life-history traits explain the variation in learning and flexibility between species?

We hypothesize that animals with fast life-history traits rely more heavily on simple, stereotyped behaviors such as fixed decision-making rules. Slow-lived animals with long lifespans may invest more heavily in future resource availability and thus reap long-term benefits of associative learning and memory (e.g., return to productive prey patches, recognize profitable prey season after season). We examined this hypothesis by comparing the foraging strategies of two species that are similar in size and diet, but lie on opposite ends of the mammalian life-history spectrum: bats and shrews.

Generally, body size is an excellent predictor of life-history strategy: the larger an organism, the more slowly it lives and the longer its lifespan (Millar and Hickling 1991). Bats are a notable exception. For small-bodied mammals, bats have extraordinarily long lifespans (over 30 years in some species (Barclay and Harder 2003), with a record of 41 years in a free-living Brandt's bat (Podlutzky et al. 2005)). They also have a low reproductive rate (Barclay and Harder 2003). Shrews are similar to bats in body size, but in contrast they have high metabolic rates and produce many offspring within a short time period (Churchfield 1990). Further, they have much shorter lifespans: Depending on the species, shrews live only 1 year (most shrews of the genus *Sorex*, like our study species) or up to 3 or 4 years (only a few of the larger-sized species; Churchfield 1990).

We investigated whether learning abilities and life-history strategies are associated by comparing learning rates in a standardized foraging task in the Natterer's bat, *Myotis nattereri*, and the common shrew, *Sorex araneus*. These species are sympatric over large areas of Europe. They have similar body weights (approximately 8–10 g, own data) and similar brain sizes (*S. araneus*: 205–216 mg (Fons et al. 1984); *M. nattereri*: mean 220 mg (Baron et al. 1996)). Both feed mainly on insects and other small invertebrates, which they locate in cluttered forest habitats (Churchfield

1990; Siemers and Swift 2006). Despite their similarities, the life histories of the two species differ strongly. *S. araneus* live little more than a year and typically produce two or three litters with an average of six pups per litter within this year (Churchfield 1990). They have an extraordinarily high resting metabolic rate of 6.1–8.3 ml O₂/[g·h] (Kleiber 1961; Taylor 1998) and must feed every 2–3 h to avoid starvation (Churchfield 1990).

In contrast, for small-bodied mammals, bats have extraordinarily long lifespans. It is difficult to measure, but mean longevity in bats ranges from 9 to 23 years (Barclay and Harder 2003) with several records of over 30 years in free-living individuals [*Rhinolophus ferrumequinum* (Corbet and Harris 1991); *Plecotus auritus* (Lehmann et al. 1992); *M. lucifugus* (Davis and Hitchcock 1995); *M. brandtii* (Podlutzky et al. 2005)]. For *M. nattereri*, we do not have data for all life-history parameters; when data are missing, we give the name and data of other, similar-sized bats of the same genus. *M. nattereri* can live more than 20 years in the wild (Dietz et al. 2009). *M. nattereri* give birth to a single pup per year (Swift 2001). They search for food in one to two bouts per night (Siemers et al. 1999) and do not forage during the day (Smith and Racey 2005). The metabolic rate of *M. nattereri* has not been measured, but we expect it is approximately 2.4 ml O₂/[g·h], the resting metabolic rate of *M. lucifugus*, a similar-sized bat in the same genus (Speakman and Thomas 2003). This metabolic rate lies within the normal range for a mammal of this size (Kleiber 1961). Considering their disparate life-history traits, we have chosen the Common shrew and the Natterer's bat as representatives of extreme ends of the slow-fast life-history continuum.

In addition to differences in life history, bats and shrews differ socially and ecologically. Many bat species, including Natterer's bats, are social (Kerth 2008), while shrew species of the genus *Sorex* are solitary (Rychlik 1998). Sociality has been connected with cognitive abilities in a variety of taxa (Pérez-Barbería et al. 2007). In addition, as volant mammals, bats experience considerably less predation (Pomeroy 1990) and cover larger areas while foraging, thus likely encountering more complex and variable habitats than ground-dwelling shrews. We will examine the possible influences of these differences on learning and life history in detail in the discussion.

We compared the learning abilities of bats and shrews by measuring their ability to locate a food reward in a four-arm crawling maze. Although bats typically fly to locate prey, most bats, including Natterer's, crawl and even run well (Riskin et al. 2006); some bat species use terrestrial locomotion in foraging (vampire bats: Schutt and Simmons 2006; Altenbach 1979; New Zealand short-tailed bats: Jones et al. 2003). In the discussion, we examine the implications of using a crawling maze for a species

that naturally forages in flight. We concealed a reward at the end of one of the arms of the maze; this arm was clearly marked with stimuli from four sensory modalities. The animals could find the reward in one of three ways: random search, algorithmic search, or associative learning. We defined algorithmic searches as movement patterns following a fixed decision-making rule, for example, always turning clockwise or always turning counterclockwise. We predicted that short-lived, fast life-history strategy shrews would solve the task using primarily random or algorithmic searches, whereas the long-lived, slow life-history strategy bats would learn to associate the stimuli with the food reward. Furthermore, we expected that memory for a successful foraging strategy would be stronger in bats than in shrews.

Methods

Study species

We tested 9 common shrews, *S. araneus*, and 9 Natterer's bats, *M. nattereri*. All shrews were caught in the area surrounding the Max Planck Institute for Ornithology in Seewiesen, Germany, between June and October 2009 (license issued by "Regierung von Oberbayern": 55.1-8642-8-2007). Seven bats were caught at Brunnen Mayer, Germany, in September 2008 (license issued by "Untere Landschaftsbehörde, Kreis Coesfeld": 70 2-0085/0) and kept at the Max Planck Institute for Ornithology in Seewiesen, Germany. Two bats were caught at the Zitadelle in Berlin, Germany, in 2003 (license issued by "Senatsverwaltung für Stadtentwicklung des Landes Berlin": OA-AS/G/605) and kept at the University of Tübingen, Germany.

Shrews were housed individually in terraria in a climate-controlled room (16–18°C, 60–70% humidity). The terraria were furnished with soil and moss as litter; hay was provided as bedding material. On days when experiments were not conducted, shrews were fed with 3 g mealworms and 4 g minced beef heart daily. Water was available ad libitum. (For feeding scheme on experimental days, see Experimental design section below.)

The Seewiesen bats were housed together in an aviary, the Tübingen bats in a flight tent, both in climate-controlled rooms (20–21°C, 65–75% humidity). On days when experiments were not conducted, bats were offered mealworms and water ad libitum. (For feeding scheme on experimental days, see Experimental design section below.)

Bats and shrews were kept on an inverted light-dark schedule (9 pm light on, 9 am light off). The majority of experiments were conducted in Seewiesen. The two Tübingen bats were tested in Tübingen under similar conditions.

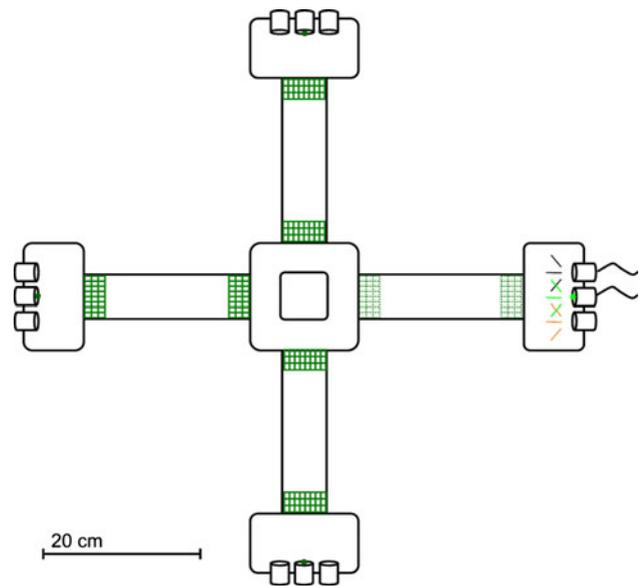


Fig. 1 The maze with start, acclimatization, and end boxes connected by tubes. The rewarded end box (here on the right) was marked by acoustic, visual, and olfactory stimuli presented from separate cylindrical containers; dummy containers were positioned in the other three end boxes. The inner surface of the arm leading to the rewarded box was lined with a small strip of plastic mesh to serve as a tactile or echo stimulus; the other arms were lined with a small strip of plastic mesh on their outer surfaces

Experimental setup

All experiments were conducted inside a separate climate-controlled room (18–20°C, 60–70% humidity), dimly illuminated with a 25-W red light bulb. The experimental setup consisted of a four-arm maze constructed from modified transparent polypropylene storage containers (EMSA GmbH, Germany; Fig. 1) surrounded by a wooden barrier (100 × 100 cm, height 47 cm) to minimize external cues. The central part of the maze consisted of a start box (16.5 × 16.5 × 13 cm) containing an additional acclimatization box (8 × 8 × 5.5 cm) to hold the animal until the trial began. The acclimatization box was lifted remotely with a pulley to initiate the trial. From each of the four sides of the start box, a transparent tube (length 20 cm, inner diameter 4.5 cm, GM GmbH, Germany) led to an end box (13.5 × 10 × 9 cm). One of these end boxes contained four stimuli and two mealworms as a food reward. For each trial, the rewarded end box was determined using a random number generator; trials were pseudo-randomized such that the same end box was never rewarded twice in succession.

Sensory stimuli

The stimuli in the end box with the mealworms included sound, a colored light, an odor, and tactile/echolocation

cues. We offered stimuli from four sensory modalities to minimize the effect of species' differences in perception. All four stimuli were presented simultaneously for the duration of each trial.

For the acoustic cue, we synthesized a 10-ms frequency sweep from 22 to 2 kHz (sampling rate 48 kHz; Audition, Adobe Systems, USA). A portion of this stimulus is audible to both the bats (Siemers and Schnitzler 2000) and shrews (Konstantinov and Movchan 1985). We broadcast this stimulus as a wav-file at the rate of one sweep per second repeatedly for the duration of each trial using an MP3-Player (SA 1100 512 MB, Philips, Netherlands).

We used a single green LED for the visual cue. Green light can be perceived by both bats (Dietrich and Dodt 1970) and shrews (Sigmund 1985).

For the olfactory cue, we used an essential oil of vanilla (Primavera Life GmbH, Germany) presented on a piece of cotton wool. It has been demonstrated that both bats (Kolb 1961) and shrews (Churchfield 1980) can use olfaction during foraging.

Acoustic, visual, and olfactory cues were each presented from small cylindrical containers positioned at the rear wall of the rewarded end box (Fig. 1). To prevent the animals from using the presence of the cylindrical containers per se as indicators of the food reward, we presented similar containers without the sensory stimuli at the rear wall of the other three end boxes.

For tactile cues, we lined the first and last 1.5 cm of the inner wall of the tube leading to the rewarded end box with plastic mesh (4-mm² holes). Shrews have an acute sense of touch (Anjum et al. 2006); Natterer's bats likely also use tactile information (Czech et al. 2008). In addition, Natterer's bats show high echolocation performance (Siemers and Schnitzler 2004); as such, the mesh likely served as an echolocation cue to them as well. Evidence suggests that shrews can use call reverberations to glean information about habitat type (Siemers et al. 2009), so it is possible that the mesh also served as an echo cue to them. The first and last 1.5 cm of the remaining three tubes were lined with plastic mesh on the outside, so that the four tubes would appear visually similar.

Experimental design

Before beginning our experiments, we allowed the animals to explore the maze to acclimate to the novel setting. In acclimatization trials, we placed mealworms at the end of every arm and offered no sensory stimuli marking the rewards. Initially, animals would try to escape or would not move at all from the start box, but after initial experience with the maze all animals responded by locating and consuming the mealworms. An animal was considered ready to

begin experiments when it began to explore as soon as the acclimatization box was lifted.

At the beginning of each trial, we placed the animal in the acclimatization box in the center of the maze for 30s. The box was transparent and porous, allowing the animals to perceive sensory cues from the reward box. At the end of the acclimatization period, we began the trial by lifting the acclimatization box and releasing the animal into the start box. A trial ended when the animal had either found and consumed the food reward or after 15 min had elapsed. We allowed 15–30 min to pass from the start of one trial to the start of the next. We conducted 10 trials per day in two 5-trial blocks, one in the morning and one in the afternoon.

We conducted trials when the animals were motivated to feed. To induce moderate levels of hunger in both species, bats and shrews were fed modified versions of their natural feeding regime. In nature, shrews of the genus *Sorex* feed every 2–3 h day and night (Churchfield 1990). On the days shrews were used in the experiments, they were fed 2 h before the experiments began; they obtained all other food during the experiments. Natterer's bats do not forage during the daytime (Smith and Racey 2005). On the days they were tested, they obtained all food during the experiments. Following testing each day, both bats and shrews were fed to satiation. All animals fed readily in the maze, indicating that these feeding regimes were sufficient for motivating both species to forage.

All our study animals acquired a consistent foraging strategy within 1 to 3 days, a period we termed the initial testing phase. An animal was judged to have acquired a consistent strategy when it used the same strategy to find the food reward in 7 of 10 consecutive trials. Animals that investigated the arms systematically in a clockwise or counterclockwise sequence were said to exhibit "algorithmic search". Those that chose the arm with food directly from the start box, without investigating other arms first, were said to exhibit "cue-directed search". Trials in which an animal used neither algorithmic nor cue-directed search were classified as "random search". Once the acquisition criterion was reached, we conducted a single trial without a food reward. All animals persisted with their strategy in the absence of the food reward, indicating that they were not locating the reward on the basis of cues emanating from the reward per se.

The initial testing phase was followed by a one-week and a one-month retention test, 7 and 28 days after reaching the criterion, respectively. Each retention test lasted 1 day with a maximum of 10 trials. Due to the differences in experimental exposure after the initial trials, two bats and one shrew could not be used in the retention trials. In all phases, we only scored trials in which the animal found and consumed the food reward.

Analysis

All experiments were recorded on miniDV tapes with a camera mounted directly above the maze (recorder: DCR-TRV 80E, Sony, Japan; camera: WAT-902H2 Ultimate with 1.4/3.5 mm objective, Watec, Japan). Tapes were used to verify notes taken by the experimenter seated next to the maze.

We assessed foraging efficiency by calculating a simplified path length, the distance an animal covered from the onset of the experiment until it discovered the food. We assigned a value of 2 each time an animal moved less than halfway down an arm, and a value of 4 each time an animal moved more than halfway down an arm. We calculated species means on the first ten trials of the initial testing phase and on the ten one-week and the ten one-month retention trials. We compared the change in the path length score over time within species and the difference in the path length score between species.

We evaluated the differences in the animals' responses to the maze by comparing the number of trials the two species required to establish their first strategy and which strategy this was. We then evaluated whether animals retained their original strategy over time, acquired a new one, or reverted to random search.

We measured the ability to associate the sensory stimuli with a food reward by comparing the number of bats and shrews that learned to use a strictly cue-directed search strategy.

All statistics were calculated using SPSS 16.0 (IBM, USA), except for the Fisher's exact test on associative learning, which was calculated using Systat 12.02 (Systat Software, Inc., USA). As our data were not normally distributed (Kolmogorov-Smirnov test, $p < 0.05$), we used non-parametric tests. When necessary, we corrected the p values of post hoc tests applying the Dunn-Šidák correction for multiple testing, using the formula $p' = 1 - (1 - p)^k$, where p' is the corrected p value and k is the number of tests used.

Results

Both bats and shrews showed a reduction in the path length over time (Fig. 2; Friedman ANOVA; bats: $\chi^2(2) = 5.852$, $p = 0.051$; shrews: $\chi^2(2) = 7.000$, $p = 0.030$). Most animals showed a reduction in the path length within the initial testing phase. However, we could not directly test this effect because some individuals demonstrated a consistent strategy in fewer than 10 trials (as described above, we stopped the initial phase once the animal had acquired a consistent foraging strategy). We thus compared the reduction in path length from up to the first 10 trials of the initial testing phase to the one-week and the one-month retention phase.

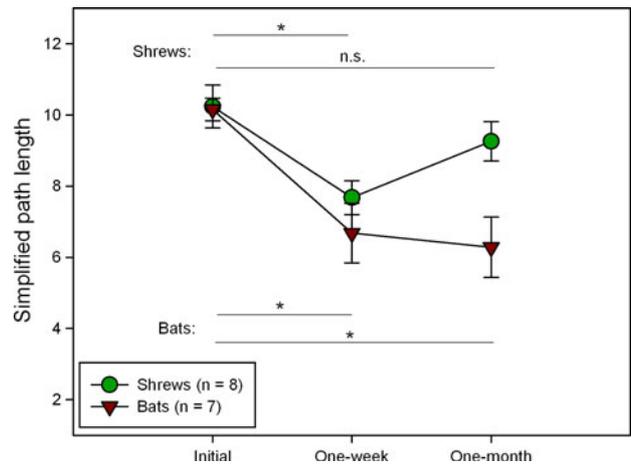


Fig. 2 Simplified path length (mean \pm SEM) required for bats and shrews to find the reward in the three stages of the experiment. For statistical details see text

Both bats and shrews showed a significant reduction in path length from the beginning of the initial testing to the one-week retention (Fig. 2; post hoc Wilcoxon signed-rank test, p values corrected after Dunn-Šidák; initial testing versus one-week retention: bats: $T = 1.0$, $p' = 0.046$; shrews: $T = 1.0$, $p' = 0.016$). For bats but not shrews, this reduction continued through the one-month retention (initial testing vs. one-month retention: bats: $T = 1.0$, $p' = 0.046$; shrews: $T = 14.0$, $p' = 0.641$). There were no significant differences between bats and shrews for initial testing phase and one-week retention trial path lengths (Fig. 2; Mann-Whitney test, p values corrected for multiple testing using Dunn-Šidák; initial testing: $U = 27.0$, $p' = 1.000$; one-week retention: $U = 22.5$, $p' = 0.909$). In the one-month retention trials, however, path lengths of the bats were significantly shorter than those of the shrews (Fig. 2; $U = 7.5$, $p' = 0.044$).

On average, bats and shrews showed no difference in the number of trials needed to acquire their first consistent strategy (Fig. 3; Wilcoxon rank-sum test; $W_s = 67$, $p = 0.107$). All individuals acquired a strategy during the initial testing phase (Table 1).

The majority of bats (6 of 9) and shrews (6 of 9) first used a combination of algorithmic and cue-directed search to find the reward. The majority of shrews retained this mixed strategy in both the one-week (8 of 8) and one-month (7 of 8) retention tests. The only shrew that learned to use a strictly cue-directed search strategy in the initial testing phase switched back to algorithmic search in the retention phase trials. Most bats, in contrast, used algorithmic search as an interim strategy and then switched to cue-directed search. Those bats that had learned to use cue-directed search in the initial testing phase (2 of 9) retained this strategy in both the one-week and the one-month retention. Bats that had not acquired cue-directed search in the

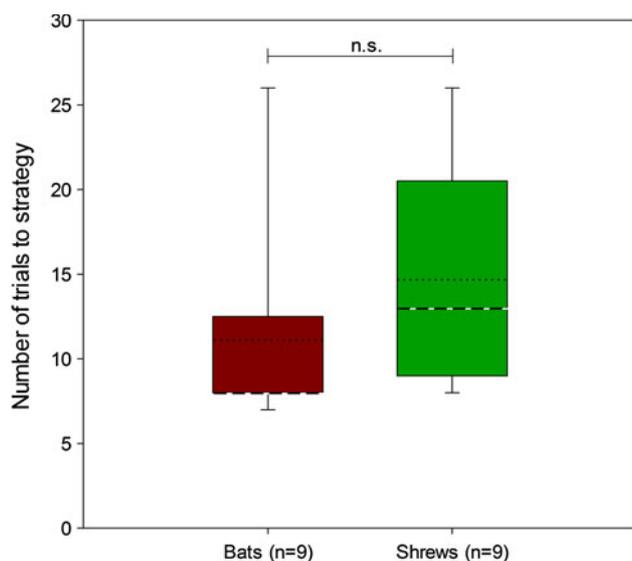


Fig. 3 Number of trials required for bats and shrews to acquire their first consistent strategy in the four-arm maze. Boxes show 25–75% range of data, whiskers 10–90% range of data. Median is shown as dashed line, mean as dotted line. For statistical details see text

Table 1 Number of trials required for each individual to acquire its first consistent foraging strategy (either algorithmic or cue-directed search) and the number of trials necessary to acquire a cue-directed search

Shrews	Trials to a consistent strategy	Trials to associative learning	Bats	Trials to a consistent strategy	Trials to associative learning
1	8	n/a	1	8	17
2	9	–	2	8	26
3	22	22	3	8	n/a
4	9	–	4	8	18
5	11	–	5	8	n/a
6	26	–	6	12	–
7	15	–	7	7	–
8	19	–	8	13	13
9	13	–	9	26	26

Individuals that never learned the association between the food reward and the sensory stimuli are identified by a dash (–). Individuals assigned “n/a” could not be included in the final analysis because of the inconsistencies in the testing protocol

initial testing phase increased their cue-directed performance and decreased their algorithmic search strategy over both the one-week (cue-directed search in 4 of 7) and one-month (5 of 7) retention tests.

Bats and shrews used the same proportion of random search trials: initial testing phase: mean (\pm SEM) proportion of random trials used by bats = 0.12 ± 0.04 ; mean(shrews) = 0.16 ± 0.03 ; Mann-Whitney test: $U = 19.0$, $p = 0.303$; one-week retention: mean(bats) = 0.07 ± 0.03 ; mean(shrews) =

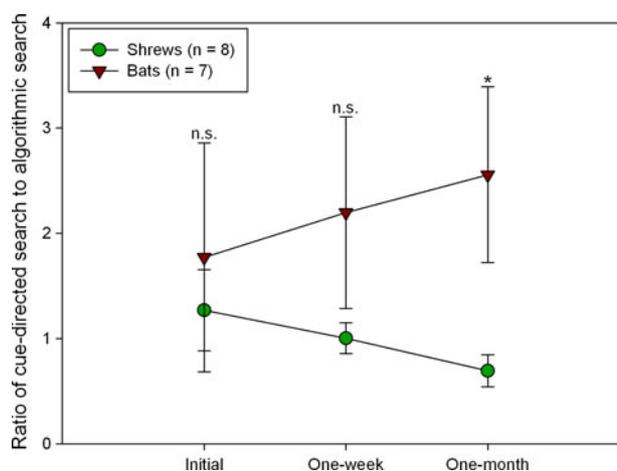


Fig. 4 Ratio (mean \pm SEM) of cue-directed to algorithmic search at the three stages of the experiment. For statistical details see text

0.05 ± 0.03 ; $U = 24.5$, $p = 0.8378$; one-month retention: mean (bats) = 0.06 ± 0.03 ; mean(shrews) = 0.15 ± 0.04 ; $U = 14.5$, $p = 0.159$. Thus, we omitted random searches from further analysis and calculated a ratio of the number of trials exhibiting cue-directed search to the number of trials exhibiting algorithmic search. Scores above 1 indicate more cue-directed than algorithmic search; scores below 1 indicate more algorithmic than cue-directed search. Shrews scored near 1 in all three testing periods (Fig. 4), reflecting a consistent mixture of algorithmic and cue-directed search. The bats scored above 1 on all three test periods (Fig. 4), indicating more cue-directed than algorithmic search. Their use of cue-directed search increased over time, even during the retention periods. The higher cue-directed performance of bats compared with shrews was not significant in the initial testing phase nor in the one-week retention tests (Fig. 4; initial testing phase: $U = 22.5$, $p = 0.556$; one-week retention: $U = 25.0$, $p = 0.756$); but it was significantly higher in the one-month retention tests ($U = 7.5$, $p = 0.015$).

As an overall result, both bats and shrews were able to use both strategies, algorithmic and cue-directed search (Table 1). However, significantly more bats than shrews learned to use strictly cue-directed search (Fig. 5, Fisher’s exact test (two-tailed): $p = 0.04$).

Discussion

Our study supports the hypothesis that life-history traits can predict learning propensity. Fast-lived shrews improved their foraging efficiency by switching from random to algorithmic search to find prey in a standardized maze. Similar-sized but slow-lived bats also shifted from random to algorithmic search, but subsequently switched to associative learning, thus further increasing their foraging

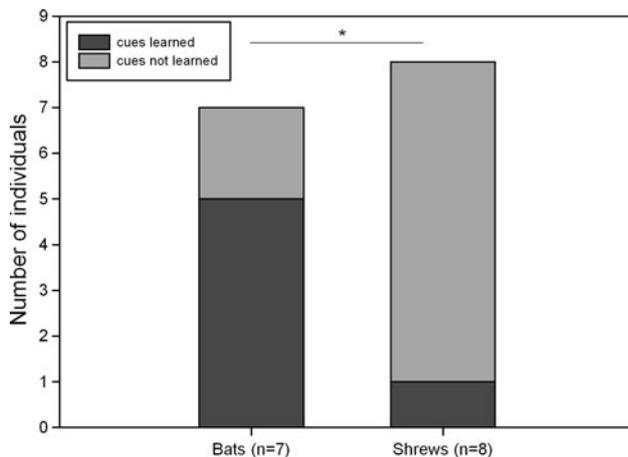


Fig. 5 Number of individuals that learned to associate the cues with the food reward, either during initial phase or during one of the retention phases. For statistical details see text

efficiency. In addition, bats showed increased retention ability compared with shrews. To our knowledge, this is the first evidence linking life-history strategies with associative learning and memory.

Other studies have found similar high rates of associative learning and memory in bats. Siemers (2001) showed that Natterer's bats, the species used in this study, can learn to associate a novel object with a profitable prey patch. He suggests that because the direct detection of prey by echolocation is often hindered by vegetation clutter, these bats must rely on indirect cues such as habitat structure to signal prey abundance. Page and Ryan (2005) found that fringe-lipped bats quickly learn novel associations between frog calls and prey quality. Ratcliffe and ter Hofstede (2005) show that fruit bats can readily associate novel chemical cues with prey. Flower bats can associate echo, scent, and visual cues with nectar rewards in cue-directed search (Carter et al. 2010; Thiele and Winter 2005; von Helversen and von Helversen 1999, 2003; Winter et al. 2005). Horseshoe bats can learn to discern the profitability of prey by means of different artificial echo cues (Koselj et al. 2011). In addition, there is evidence that bats can retain learned behavior for long periods and over hibernation (Ruczynski and Siemers 2010).

In contrast, few studies document learning and memory in shrews. Those that have investigated learning show that shrews forage better when they use algorithmic search (Pierce 1987) and spatial learning (Köhler 1993; Punzo and Chavez 2003). To our knowledge, ours is the first study to investigate cue-directed, associative learning and memory in shrews.

One drawback of our study is that while shrews were tested in their natural foraging mode (walking/crawling), bats were not (flight). One way to overcome this difficulty

is to use a different arena for each species, one that allows for flight for the bat, crawling for the shrews. Using different arenas invites its own potential problems, however. Differences in the performance could be attributed to the differences in arena type, difference in spatial scale, etc. While each approach has its drawbacks, our strategy was to keep as much constant in our testing paradigms as we could, to allow for better comparison of the two species. Many bat species are adept at maneuvering on the ground (Riskin et al. 2006), and we were careful when designing our maze to ensure that both Natterer's bats and common shrews could move through the maze easily and would readily find and consume mealworm prey. However, it is possible that bats did not perform as well as in the crawling maze as they would have in a more natural setting. While testing animals in artificial conditions is not ideal, we argue that, if anything, our results underestimate the differences in learning we find between the species for the following reason: Of the two strategies, algorithmic search and associative learning, likely the more sophisticated is associative learning. According to "constraints of learning" theory, animals perform to the best of their cognitive abilities in the natural conditions that call for them (Shettleworth 1972). The fact that we found bats outperforming shrews even when the situation was less natural for the bats speaks to the bats' cognitive abilities. We would expect that, given a task closer to what they experience in nature (one that requires flight rather than crawling), we would see yet better cognitive performance in the bats. In effect, because of the foreignness of the task for the bats, we feel that our current test is a conservative measure of bat foraging cognitive ability.

Ideally, to study the effect of life-history traits on learning and memory, we must conduct comparative studies on species that differ only in their life-history traits. We chose *M. nattereri* and *S. araneus* because they represent opposite extremes on the life-history continuum while sharing many key traits such as diet, habitat characteristics, body size and brain size. In addition to life-history strategy, however, other factors differ between bats and shrews. Two of the most important are sociality and flight.

Most bat species for which we have data are social. This is well known for the European *Myotis*, including our study species, *M. nattereri* (Kerth 2008). *M. nattereri* typically lives in stable colonies of 20–50 individuals (Dietz et al. 2009). In contrast, shrews of the genus *Sorex* are generally solitary (Rychlik 1998). In a wide range of taxa, social species show higher learning performance on foraging and spatial learning than solitary ones (Costanzo et al. 2009; Dukas and Real 1991). In carnivores, ungulates, primates, and some insectivores, sociality has been associated with higher cognitive abilities and a larger brain (Pérez-Barbería and Gordon 2005; Dunbar 1992; Dunbar and Bever 1998). In bats, there is a positive relationship between social group

size and neocortex size (Barton and Dunbar 1997). However, despite being social, bats have a comparatively simple cortex structure (Baron et al. 1996) and do not have enlarged brains compared with similar-sized mammals, including shrews (Fons et al. 1984). Thus, the higher level of sociality of bats does not seem to be reflected in their brain size. Whether their sociality has an influence on their learning cannot be answered with our study.

A second and perhaps more fundamental distinction between bats and shrews is flight. The ability to fly has several major consequences for the ecology and life history of bats. Flight allows bats to be highly mobile and forage over much broader spatial scales than ground-dwelling shrews. Thus, the forest habitat in which both study species forage likely appears patchier and more complex to bats than to shrews. Bats may benefit from learning and remembering cues associated with profitable prey patches in their large and complex three-dimensional foraging environment. Shrews, restricted to the less complex two dimensions of the ground, may have better foraging success using systematic search. There is evidence that mobile species and species confronted with more complex habitats are better learners than sedentary species or species foraging in less complex environments (Micheli 1997; Potting et al. 1997; Haupt et al. 2010). Our results are consistent with these findings.

The evolution of flight had a second crucial consequence on the ecology of bats: the ability to fly is associated with a decrease in predation (Holmes and Austad 1994; Pomeroy 1990). Flight may both expose bats to fewer types of predators and allow them to escape better (Barclay and Harder 2003; Fenton et al. 1994; Driessens and Siemers 2010). Nocturnality further shelters bats from predation (Speakman 1995). While quantifying bat predation events is extremely difficult, Speakman (1991) uses known parameters and indeed estimates very low predation risk for nocturnally foraging bats. While both bats and shrews are active at night, the high metabolic rates of shrews necessitate foraging during the day as well (Churchfield 1990); for this reason as well as their lack of flight, shrews likely experience increased predation compared with bats.

Animals suffering from high predation pressure may be forced to be more cautious and invest more into anti-predator behavior than into learning. In within-species experiments in fish, it has been shown that populations facing lower predation pressure exhibit higher learning ability than populations under high predation pressure (Brown 2005; Brydges et al. 2008). Our results are consistent with these studies.

A decrease in predation pressure, one consequence of the ability to fly, in turn has consequences on the life history of bats. By facing lower predation pressures, volant mammals have a higher adult survival rate than ground-dwelling mammals of the same size (Holmes and Austad

1994; Austad and Fischer 1991; Pomeroy 1990). Species with longer life expectancies can afford to reproduce later in life and invest more into growth (Harvey and Zammuto 1985), thus exhibiting typical slow life-history traits. In contrast, animals like shrews with riskier life styles (i.e., animals with a high “hazard factor” (Edney and Gill 1968)) are under selection to reproduce quickly and die early. It is possible that long-lived bats benefit from learning and retaining information about their environment that improves not only current but future foraging success. Thus, we argue that it may not be flight itself, nor the resulting higher mobility, that has selected for improved learning abilities in bats compared with shrews, but rather the implications of flight on life-history strategies. As outlined above, the ability to fly, lower predation pressure, increased longevity, and slow life history are all tightly associated. We suggest that this suite of evolutionarily interlinked characters fostered increased learning in bats.

Our data demonstrate that slow-paced bats have stronger associative learning and better memory retention than their fast-paced counterparts, shrews. We suggest that these differences in learning ability relate to the different life-history strategies of our two study species. Our conclusions are based on data from two species from the extreme ends of the slow-fast life-history continuum. To further test the effect of life-history traits on learning, memory, and search strategy, it will be necessary to investigate multiple species across a continuum of life-history strategies, from slow to fast.

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