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ORIGINAL ARTICLE

Behavioral correlates of migration in bats – do migration strategies predict responses to a novel environment?

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Abstract

Migration is a life-history trait that shapes individual-by-environment interactions, affecting fitness. Currently, many species are changing their migration strategies, stressing the need to identify and better understand the behavioral correlates of migration. As a partial migrant, the noctule bat, *Nyctalus noctula*, allows for rare intra-specific investigations of the potential behavioral causes (or consequences) of variation in migration. Here, we combined in-situ behavioral assays with stable isotope analyses to investigate whether spatial and acoustic responses to a roost-like novel environment correlate with migration strategy (local or distant). Given a migrant's more frequent exposure to novel environments, we predicted migrants would enter a novel environment more quickly and show stronger spatial and acoustic exploration activity. However, individuals of local and distant origin did not differ in acoustic exploration (call activity per unit space), nor, contrasting to several bird studies, in spatial activity (number of chambers visited). Surprisingly, local individuals were more likely than migrants to enter the novel environment. Our findings suggest that small-scale exploration does not vary with migration, potentially because of similar selection pressures across migration strategies on small-scale exploration (e.g., exploration of roosts) as opposed to large-scale. Yet, our findings on the likelihood of entering a novel environment suggest that locals may be more risk-taking. Repeated measures would be necessary to determine if personality differences are underlying these responses. Our unique approach, combining behavioral assays with isotopic geolocation, gave us novel insight into an elusive taxon, highlighting the importance of studying behavioral correlates of migration across various taxa.

Significance Statement

The decision to migrate impacts both individual fitness and ecosystem connectivity, yet we know very little about the behavioral correlates of migration strategies. Studying such correlates is the first step to identifying the behavioral causes and consequences of migration. Here, we took advantage of a partially migratory species, the common noctule bat, and a unique measure of acoustic exploration, to test potential correlations between migration strategy and small-scale emergence and exploration. We found local individuals more likely to enter a novel environment than migrants and that migration strategy did not predict acoustic exploration. This is the first study examining novel environment responses and migration in bats and reveals contrasting behavioral correlates of migration compared to other taxa. Our research, therefore, highlights the importance of including more non-model species in the study of the causes and consequences of animal migration.

Keywords Animal migration · Bats · Behavioral assay · Echolocation · Exploration behavior · Stable isotope analysis

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Introduction

Whether animals decide to migrate affects ecosystem functioning and has consequences on the individual (e.g., physiological), population (e.g., demography), and species level (e.g., covarying life-history traits) (Cresswell et al. 2011; Hobson et al. 2019). It is, therefore, crucial to better understand variation in migratory behavior.

Populations of partial migratory species can offer important insights into the behavioral correlates of migration. Partial migratory populations are composed of individuals that remain local throughout the year and individuals that migrate over long distances. Partial migration is ubiquitous in various taxa, including insects (Menz et al. 2019), amphibians (Grayson et al. 2011), fish (Espinoza et al. 2016), birds (Arnekleiv et al. 2022), and mammals (Purdon et al. 2018). Individuals of partially migratory populations respond with different migration strategies to the same environmental cues. It can, therefore, be expected that individuals of such species show corresponding variation in behavioral responses to challenges in other contexts as well. Such behavioral correlates may indicate underlying behavioral syndromes as drivers of migration strategies (e.g., Found and St. Clair 2016). Indeed, roaches (*Rutilus rutilus*) with a shorter latency to emerge into a novel environment were more likely to migrate from a lake (Chapman et al. 2011), and migrating blue tits (*Cyanistes caeruleus*) showed a shorter latency to approach a novel object than residents (Nilsson et al. 2010). Yet, as far as we are aware, no study investigated if long-distance migrants and locals of the same species and population differ in how they explore, i.e., examine and investigate, a novel environment, a behavior which is likely crucial for detecting novel resources in unfamiliar and changing habitats. Interestingly, echolocating bats, although understudied in this context, would allow detailed quantitative investigation, not only of how individuals move but also how they sample environmental information during exploration.

Despite their species richness and pivotal role in ecosystem functioning (Kunz and Fenton 2005; Ghanem and Voigt 2012), little is known about migration in bats (Popa-Lisseanu and Voigt 2009). However, novel tools have now become available to study their migration strategies. Using non-invasive isotopic geolocation (Popa-Lisseanu et al. 2012), we can estimate the breeding origins of European bats. Isotopic geolocation uses naturally occurring differences in stable isotope ratios, for example, stable hydrogen isotope ratios in precipitation water (δ^2H_P), which are governed by global-scale hydrologic processes. The isotopic differences in precipitation are seasonally and spatially predictable by latitude and elevation and allow the reconstruction of so-called isotopic landscapes, i.e., isoscapes, which assign an isotopic signature to specific locations (Hobson 1999, 2008; Bowen et al. 2005; Courtiol et al. 2018). This regionally specific isotopic signature is incorporated into consumer tissue via diet and drinking water. Analyzing stable hydrogen isotope ratio of keratinous material (δ^2H_K; e.g., fur), which is metabolically inert, provides a direct reflection of the location of fur growth and thereby allows for the tracking of animal movements (Hobson and Wassenaar 1996; Popa-Lisseanu et al. 2012; Sullivan et al. 2012; Baerwald et al. 2014; Voigt et al. 2015; Hobson 2018). By analyzing stable hydrogen isotopes in bat fur, Lehnert et al. (2018) confirmed high variability in the migratory behavior of common noctule bats (*Nyctalus noctula*) across Europe. Additionally, they observed a high degree of consistency in migratory behavior within individuals.

To investigate whether migration strategy and exploratory behavior correlate, we estimated the migration strategies and quantified the emergence and subsequent exploration behavior for wild female noctule bats. We took advantage of a well-monitored colony in Brandenburg, Northeastern Germany, where the population comprises local, year-round present individuals and individuals on migration using this area as a stopover or wintering site. We combined isotopic geolocation, based on hydrogen, with an in situ maze-like novel environment assay. This novel environment assay was recently established to quantify exploratory behavior in another tree-dwelling bat species, the Nathusius' bat (*Pipistrellus nathusii)*, and revealed individually consistent differences in spatial activity and 'acoustic exploration', i.e., the level of environmental cue sampling per unit space (Schabacker et al. 2021). Given that migrants frequently encounter different and novel habitats, we predicted long-distance migrants to emerge quicker into a novel environment and to exhibit more exploratory behaviors (i.e., increased spatial and acoustic exploration activity) in the test arena than local noctule bats of the same population.

Methods

Study species

Noctule bats are distributed throughout Europe. They are insectivorous and typically roost in tree holes or crevices or anthropogenic structures like attics or bat boxes. Common noctules migrate in early autumn and spring (Sluiter et al. 1966; Hutterer et al. 2005). Albeit much of noctule bat migration is still cryptic, banding efforts revealed that the general migration pattern unfolds along a Northeastern–Southwestern axis (Steffens et al. 2004; Hutterer et al. 2005; Lehnert et al. 2018; Lindecke et al. 2022), and some individuals were shown to cover more than 1600 km between breeding and hibernating sites (Dietz et al. 2009). Copulation occurs while bats migrate through different habitats. This ensures the mixing of spatially segregated populations and increases genetic diversity (Petit and Mayer 2000). Pups are born in early summer (June/July).

General study approach

Between April 11th and 25th, and October 3rd and 28th of 2019, we sampled a total of 89 adult females from a wild colony of Noctule bats near the village of Prieros, Brandenburg, Germany (52°13’24"N, 13°45’16"E). We collected adult female bats in the early evening (April) or late afternoon (October) from roost boxes located 4–5 m above the ground. To minimize disturbance in the population, we prioritized roost boxes based on the presence of previously tested bats (identified by passive integrated transponders (PIT) tags, see Supplementary Information) or based on group size (as assessed from outside the box). Following removal from roost boxes, we determined sex, body mass (digital pocket scale, 0.01-gram scale, and spring balance, 0.1-gram scale, +/- 0.1 g), and forearm length (analog vernier dial caliper, 0.1 mm scale). We excluded juveniles (when clearly distinguishable based on morphological characteristics (Brunet-Rossinni and Wilkinson 2009; Kravchenko et al. 2020)) and males from further study due to evidence of female-biased migration in this species (Lehnert et al. 2018).

Female bats (mean ± standard deviation: weight: 29.3 ± 4.1 g, forearm length: 54.2 ± 1.2 mm) were kept together in roosting groups in a dark environment (darkened plastic boxes, approximately 30 × 20 × 15 cm) until they were subjected to the behavioral assay (two hours later, on average). The boxes were equipped with cloth and heat packs to stimulate normothermia. Subsequently, we removed females from these boxes and conducted the behavioral assays primarily after sunset (or briefly before ($N = 4$; 35 to 9 min before sunset)), a time during which noctule bats are naturally active. Assays took place in a tent within 200 m of the place of capture, providing a standardized environment to ensure minimal external influences. Ambient temperatures were comparable between the months, with a mean of 10.9 ºC (range: 5.6–17.6 °C) in April and 10.4 °C (range: 6.0–18.0 °C) in October. After the behavioral assay, we took a dorsal fur sample from just above the uropatagium for isotopic geolocation (Voigt et al. 2015). The samples were stored dry at ambient temperature until further analysis. Observers were blind to the migratory strategy of the subjects since the stable isotope results were only known after the quantification of the behavioral responses.

Stable isotope analyses

Similar to other migratory bats, common noctule bats molt in summer before autumn migration (Ilyin 1990; Kravchenko et al. 2020). Accordingly, collected fur samples indicate the location where an individual spent the previous summer (2018 for April samples and 2019 for October samples). Fur samples of juveniles represent the location where they were born. Since Lehnert et al. (2018) provided evidence for high individual repeatability of noctule bat migration strategies, we here assume that bats did not change their migration strategy between 2018 and 2019.

All stable hydrogen isotopes from bat fur samples were analyzed at the stable isotope lab at the Leibniz Institute for Zoo and Wildlife Research (Berlin, Germany). To prepare the samples for analysis, we cleaned off all external contaminants and oils with a chloroform:methanol (2:1) solution. The samples were placed in the cleaning solution for 24 h on a shaking platform (Phoenix GmbH). The fur samples were then dried for ten days in a drying oven (Heraeus Function Line, ThermoFischer Scientific, Bremen, Germany) at 50 °C.

We analyzed samples in sequence with keratin reference materials with known stable isotope ratios for the non-exchangeable portion of hydrogen. We used four in-house standards: sheep wool from Sweden (-167.9 ± 1‰), sheep wool from Spain (-108.3 ± 1‰), goat wool from Tanzania, Africa (-66.3 ± 0.9‰), and USGS42 standard (-74 ± 0.5‰) from Tibetan human hair. A detailed description of the preparation of the standards is reported in Popa-Lisseanu et al. (2012). We weighed samples and standards using a microbalance (Sartorius ME5, Göttingen, Germany) to 0.274 ± 0.01 mg and placed them into 3.3 mm × 5 mm silver-foil capsules (IVA Analysetechnik e.K. Meerbusch, Germany). We folded capsules into small packages and stored them in a 96-well microtiter plate. After preparation of the plate, we left it in a drying oven at 50 °C for 24 h to remove extra moisture. Subsequently, we transferred samples and standards into the carrousel of a Zero Blank autosampler (Costech Analytical Technologies Inc., Italy) of the high-temperature elemental analyzer (HTO Elementaranalysator HEKAtech GmbH, Wegberg, Germany). The samples were flushed for one hour with chemically pure helium (Linde, Leuna, Germany) as a carrier gas at a flow rate of 100 ml/min, eliminating remaining moisture and thus suppressing the influx of ambient H_2O. The foil packages were then pyrolyzed in the element analyzer at 1450 °C. The gas chromatograph separates H_2, N_2, and CO at 80 °C and introduces the resolving H_2 through the Conflo III interface (ThermoFischer Scientific, Bremen, Germany) into the isotope ratio mass spectrometer (Delta V Advantage IRMS, ThermoFischer Scientific, Bremen, Germany). We used only those samples for further analysis where the amplitude peak of the δ^2H sample did not exceed 6500 mV. This is based on repeated measures of in-house keratin standards better than 3‰ (which is equivalent to one standard deviation). Consequently, we had to exclude seven samples. The robustness of this single isotope approach was confirmed using a triple isotope approach on a subset of the data (See Supplementary Information).

Behavioral assay and analysis

Prior to the behavioral assay in the experimental arena, we confirmed a bat's normothermia by measuring skin temperature with a thermocouple (Peakmeter, PM6501; Thermocouple, Sensor SSP-1-150, Peakmeter, Shenzhen, China, +/- 2.2 °C). Skin temperature (> 30 °C) is a non-invasive measurement that accurately reflects rectal temperature (Barclay et al. 1996). The experimental arena in which the bats were subsequently placed mimicked a potential novel roost, and we thus regarded its exploration as relevant for a tree-dwelling bat species. The maze-like arena (Fig. 1 and 40 × 40 × 5 cm) consisted of nine separate chambers connected through small gates (3 × 2.5 cm) on the upper half of the walls. A rubber non-slip mat overlaid the floor to provide a good texture for crawling, a behavior intuitive to tree-dwelling bats. A layer of insect screen overlaid the entire maze, preventing a bat's escape and offering another climbing opportunity. The entrance to the maze was an opaque start tube (10 × 3 cm) attached to the maze but blocked by a small wooden dowel, which was removed at the start of an assay. The entire maze was placed horizontally – to stimulate natural exploration behavior in all directions – in a larger box (70 × 45 × 8 cm) with a transparent lid. We monitored the bat's movement from an aerial perspective by mounting a night vision camera (Sony Digital Camcorder, DCR-SR72E, Sony, Tokyo, Japan) on a tripod equipped with a horizontal arm positioned 1.5 m above the maze. Light was provided by an infra-red flashlight (T38, Evolva Future Technology, Shenzhen, China), shining at an angle from a fixed position. We captured vocalizations through a directional USG Electret Ultrasound microphone (polar pattern 180°, Avisoft Bioacoustics/Knowles FG, Berlin, Germany) connected to an ultrasound recorder (UltraSoundGate 116Hb, Avisoft Bioacoustics, Berlin, Germany), which was placed within the larger box pointing to the center of the maze.

At the start of an assay, we placed the bat in the opaque start tube (10 × 3 cm), while vertical and horizontal barriers in the form of a small wooden dowel still obstructed the exit. After an acclimatization period of 20 s, we removed the barrier and gave a maximum of three minutes for the bat to emerge from the start tube. We recorded the bats' emergence times, i.e., the time it took for an individual to emerge completely from the start tube: (1) latency to head emergence (s), (2) latency to full body emergence (s), and (3) duration of emergence (s) (i.e., the difference between (1) and (2)). If a bat did not emerge within three minutes, we terminated the test since forcing it into the maze would likely lead to a different type of behavioral response than what we were interested in. After a successful emergence, bats were allowed to explore the maze for two minutes, and we recorded an individual's exploratory behavior as (4) the number of unique chambers discovered, (5) the total number of chambers visited, and (6) the number of times a bat poked its head in an adjacent chamber. These response measures are congruent with those reported in Schabacker et al. (2021) and were later quantified in detail using the open-source event logging software BORIS (Friard and Gamba 2016; version 7.9.1). After each test, we removed potential

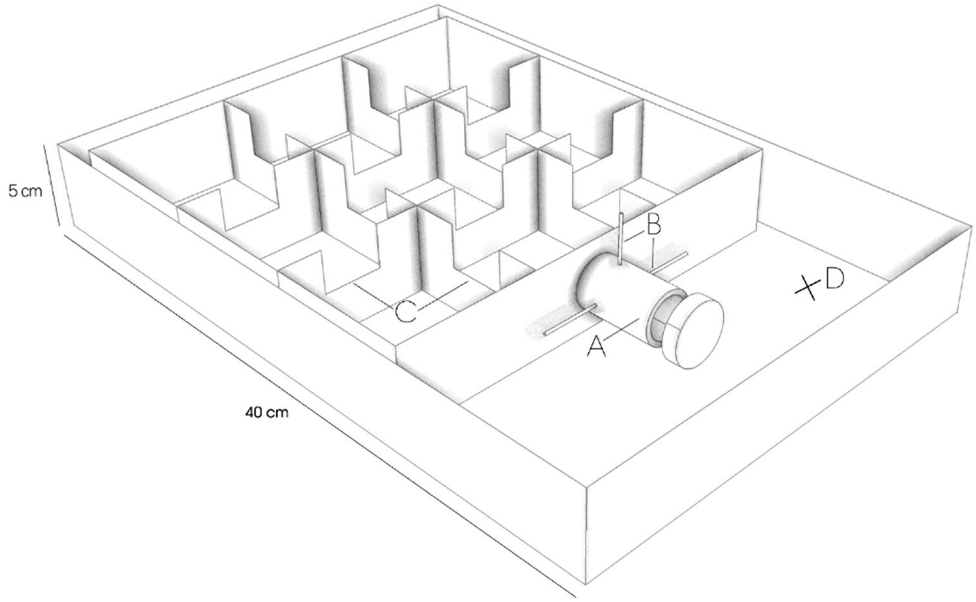

Fig. 1 Schematic drawing of the maze used during behavioral assay. (**A**) Opaque start tube (10 × 3 cm) where bats were placed at the start of each assay. (**B**) Wooden dowel obstructing the entrance to the maze (only the vertical dowel was used for common noctules). (**C**) Gates connecting single rooms. (**D**) Position of the microphone. ©Rebecca Scheibke

olfactory cues by sterilizing the maze with a mild, unscented detergent. Halfway through the night, we rotated the setup to control for potential orientation biases. There was no significant correlation between the likelihood to emerge and the orientation of the setup ($P > 0.30$). Afterward, bats were released on the same night and within 100 m of the original capture location.

Audio analysis

We recorded echolocation activity during the exploration of the novel environment and assessed the number of echolocation calls in Avisoft SASLab Pro (Avisoft Bioacoustics, Version 5.2). Preceding the analysis, we converted the sampling frequency from 250 kHz to 150 kHz. Spectrogram computation was accomplished via Fast Fourier Transformation 256, parameters set to Hamming window (bandwidth 1270 Hz, resolution 977 Hz) and volume normalized to 75%. Vocal start and stop commands given by the observer allowed the synchronization of video and audio recordings. We identified distinct echolocation calls via Avisoft's call detection and template-based spectrogram comparison feature, which we verified and corrected via visual inspection. This enabled us to count (7) the total number of echolocation calls after full-body emergence. We quantified (8) 'acoustic exploration' as a response measure, representing acoustic sampling of the environment using echolocation while accounting for spatial activity (number of chambers visited). Following Schabacker et al. (2021), this was calculated as the residuals of (7) the total number of echolocation calls emitted over (5) the total number of chambers visited during the assay. These residuals represent the variance that is not explained by the fitted regression line (see Results and Supplementary Information). Lastly, we quantified the number of emitted air puffs (see Supplementary Information).

Statistical analysis

All analyses were conducted using the statistical software R, version 4.2.1 (R Core Team 2022).

Isotopic geographic assignments

To delineate the origin of captured noctule bats in Brandenburg, we performed isotopic geolocation based on the R package "*IsoriX*" and tightly followed the workflow described in Courtiol et al. (2018). Briefly, the workflow is divided into three main components: generation of the isoscape, fitting the calibration model, and geographically assigning unknown samples to the most probable place of origin. We built the isoscape based on hydrogen isotope ratios in precipitation water (δ^2H_P) obtained from the Global Network of Isotopes in Precipitation (GNIP) database, which is a publicly available database of global isotope data. We fitted a geostatistical mixed model to predict the spatial distribution of δ^2H_P roughly covering Europe (longitude range: -30° East to 60° West, latitude range: 30 North° to 70° North; Supplementary Fig. S1). Subsequently, we used the transfer function provided by Lehnert et al. (2018) to relate δ^2H_f values as a linear function to δ^2H_P values. This transfer function uses a combination of δ^2H values of local, non-migrating insectivorous bat species and those of noctule bats sampled during their non-migratory period across Central and Eastern Europe (Voigt et al. 2014; Lehnert et al. 2018; Voigt and Lehnert 2018). We opted for this multispecies-informed transfer function rather than a single-species function, as only a relatively small sample size-informed transfer function would have been available for noctule bats, which might not cover the full range of variation in the δ^2H tissue values. The multispecies function, however, results in a lower spatial resolution but generally ensures a more comprehensive and reliable assignment (Voigt and Lehnert 2018). By applying this function, we were able to directly map the assignment samples onto the isoscape. We used the *isofind* function to test the probability of a sample originating from the candidate location Prieros, Brandenburg, Germany, under the null hypothesis that the unknown location of origin is identical to the candidate location. For assignments where the P-value fell below $\alpha = 0.05$, we rejected the null hypothesis and concluded a migratory status for the respective individual. Finally, assignments were visualized highlighting areas with the most probable place of origin (Fig. 2).

Emergence, spatial activity, and acoustic exploration behavior

Following Schabacker et al. (2021), we focused on three relevant and independent response measures: full body emergence (yes/no), the total number of chambers visited, and acoustic exploration.

To test if the response to a novel environment varies with migration strategy, three (generalized) linear models were constructed, with body emergence (yes/no, binomial), the total number of chambers visited (Poisson), or acoustic exploration (normal) as the dependent variable and migration strategy (local/migrant) as the independent variable of interest. Control variables included the season the sample was taken (April or October) and the body condition of the subject as weight (g) divided by forearm length (mm). We conducted backward stepwise model selection, always keeping the independent variable of interest (i.e., migration strategy) in the model. Control variables with $P \geq 0.1$ were removed from the model. Qualitative conclusions regarding

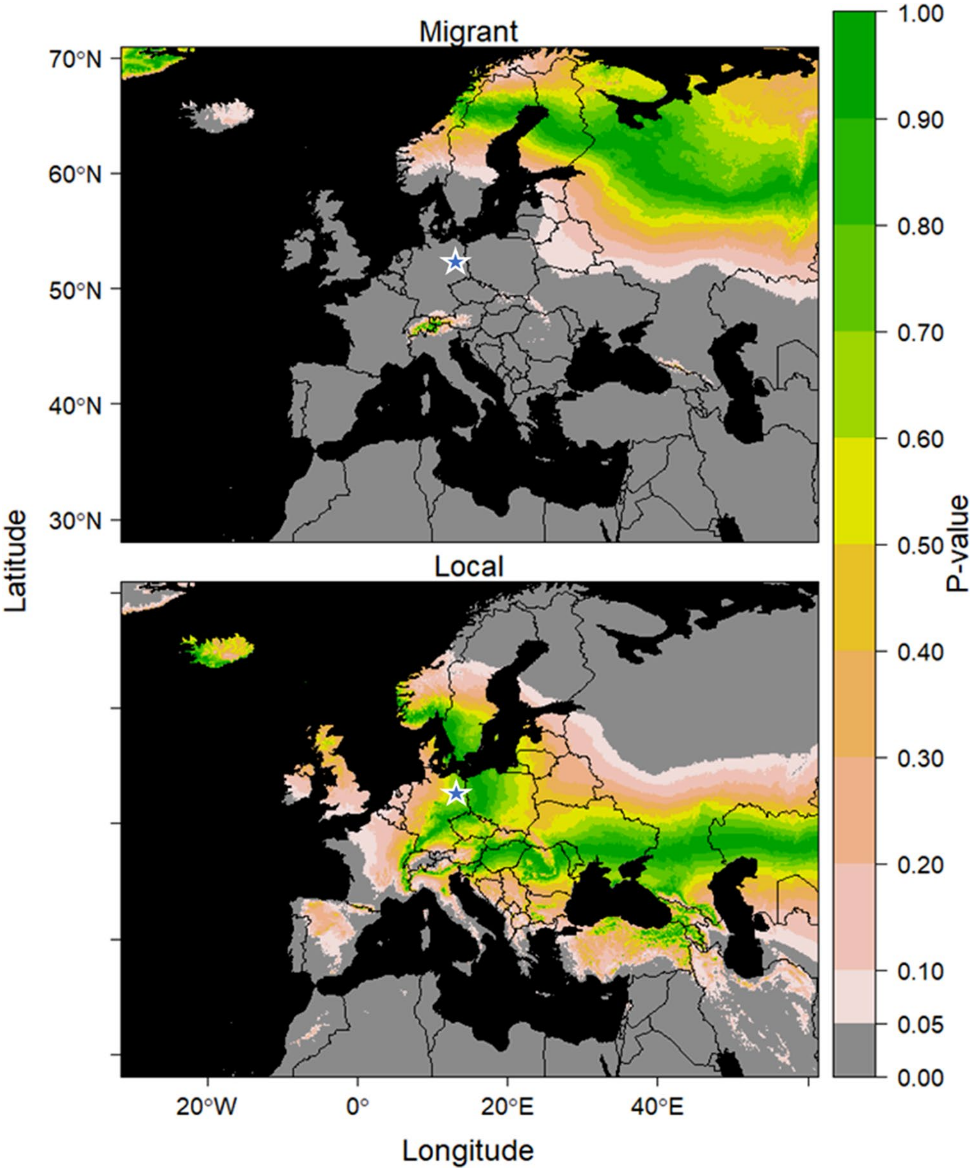

Fig. 2 Geographic probability distribution of the most probable place of origin of an assigned migrant (upper panel) and an assigned local bat (lower panel). The color scale indicates the level of certainty of correct assignment (expressed as P-value). Bats for which a local status could be excluded using an α = 5% threshold were assigned a migrant status. Bats for which a local origin could not be excluded were assigned a local status, i.e., originating from the sampling location Prieros, Brandenburg, Germany (~40 km Southeast of Berlin, indicated on the maps by the blue star). Isoclines (regions of similar δ^2H_P values) follow latitude closely and thus resolve animal movements from East to West poorly. However, there is substantial evidence for migration happening along an axis from Northeast to Southwest, making it unlikely that bats carrying the ”local” isotopic fingerprint are actually migrants stemming from more Eastern regions on the same latitude (e.g., as suggested in the lower panel)

the effect of migration did not differ between the starting and final models. Model assumptions were verified using the packages ‘dHARMA’ (Hartig and Hartig 2017) and ‘performance’ (Lüdecke et al. 2021), using the functions: check_collinearity(), simulateResiduals() and plot(). Due to detected underdispersion in the Poisson model, we also conducted a generalized Poisson regression using the ‘VGAM’ package, but this did not lead to qualitatively different conclusions. The data and code underlying the analyses can be accessed through the Open Science Framework (Snijders and Schabacker 2022).

Our initial intention was to also investigate individual repeatability. However, due to the low number of repeated assays (See Supplementary Information), we decided to focus our analysis on the behavioral responses during the first assay only. Moreover, for several assays, the migration strategy could not be reliably determined, and not all bats emerged into the arena, resulting in different sample sizes per analysis (Table 1).

Table 1 Sample size overview

Analysis category	*N*	Migrants/Locals
Total assays	98	-
Total unique bats assayed	89	-
Total unique stable hydrogen isotope samples	82	49/33
Total unique bats that emerged into the arena	45	-
Total unique bats with a stable hydrogen isotope sample that emerged into the arena	41	19/22

Results

Based on the stable hydrogen isotope analyses, 60% of the bats were classified as long-distance migrants (Supplementary Table S1, Supplementary Fig. S2) and migrants were as likely to be previously handled (banded) as local conspecifics (Fisher Exact Test: OR (95% CI) = 0.57 (0.20–1.54), $N = 89$, $P = 0.26$). Only 51% of the bats emerged into the novel environment arena, and these were most likely to be locals ($P = 0.01$, Supplementary Table S2, Fig. 3a).

Individuals that emerged into the novel environment varied considerably in their behavioral exploration responses (Supplementary Fig. S3a-e), e.g., the total number of chambers visited ranged from four to 28, and the number of calls emitted after emergence ranged from 474 to 1443. As expected, the number of calls was strongly correlated to the total number of chambers visited (both variables square root transformed; $r = 0.42$, $N = 45$, $P = 0.004$, Supplementary Fig. S4a). Despite this strong correlation, there was substantial variation in how thoroughly bats acoustically explored the novel environment (Supplementary Fig. S4b). The variation in exploration responses was, however, not driven by migration strategy since migrants did not show higher spatial exploration activity (the number of chambers visited, $P = 0.70$, Supplementary Tables S3, S4, Fig. 3b) nor stronger acoustic exploration than locals in the novel environment ($P = 0.37$, Supplementary Table S5, Fig. 3c). Lastly, there were no notable correlations between any of the quantified behavioral responses (i.e., emergence latency, number of chambers visited, acoustic exploration, number of air puffs and number of head pokes into adjacent chambers; Supplementary Table S6).

Discussion

Little is known about the behavioral correlates of migration in partial migrants and, specifically, whether migratory individuals may be characterized by more exploratory responses to a novel environment. Here, we conducted one of the first novel environment tests in a partially migratory population. In contrast to our expectations, we found that local individuals were more likely to emerge into the novel environment than long-distance migrants, which may be explained by local bats being more risk-taking. Furthermore, we found no correlation between spatial exploration activity, acoustic exploration (i.e., environmental cue sampling), and migration strategy, suggesting that explorative behavior is equally important for migratory and local noctule bats.

Local individuals are more likely to enter the novel environment

We observed a correlation between emergence behavior and migration strategy, but in the opposite direction than expected. As migrants are more often confronted with novel environments, we expected migrants to be more likely to emerge into the novel environment. Yet the long-distance migrants were less likely to emerge than the local individuals. This also appears to contrast with related movement ecology studies in other taxa. For example, roaches (*Rutilus rutilus*) that emerged quicker from a refuge migrated more often from a lake (Chapman et al. 2011). In bank voles (*Myodes glareolus*), individuals with shorter latencies to emerge and investigate an unknown area occupied larger home ranges (Schirmer et al. 2019). Lastly, in two warbler

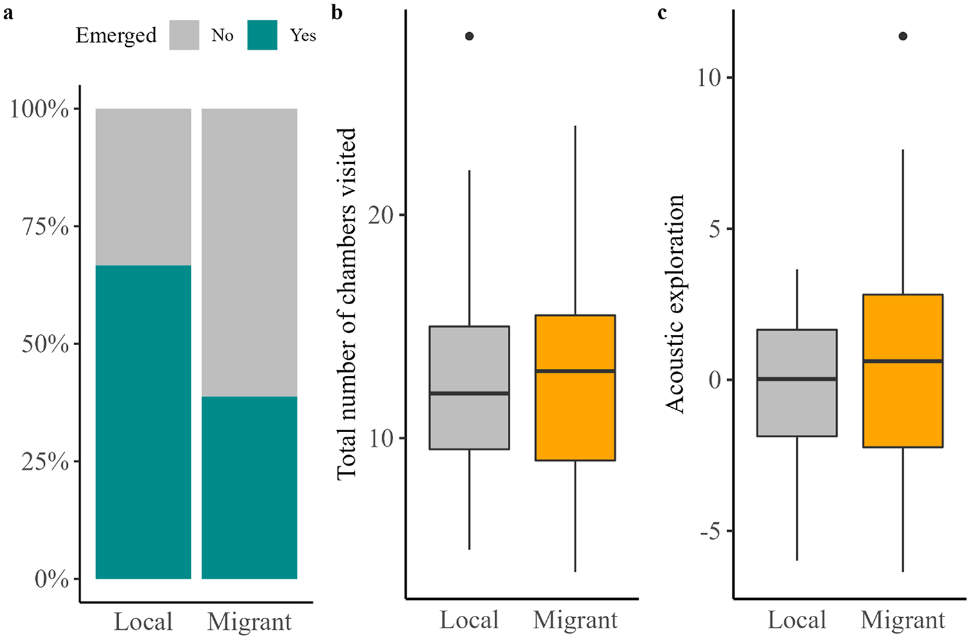

Fig. 3 Noctule bats' behavioral responses to the novel environment assay as a function of their migration strategy. Local individuals were (**a**) more likely to emerge into the novel environment (maze) ($N_{total} = 82$), yet local individuals and long-distance migrants did not differ in (**b**) their spatial exploration activity (total number of chambers visited) or (**c**) their acoustic exploration (residuals of the number of echolocation calls emitted over the number of chambers visited) ($N_{total} = 41$). Box plots in panels (**b**) and (**c**) depict the median as the central line and interquartile range with whiskers of 1.5 interquartile distances

species (*Sylvia* sp.), more individuals from the migratory species entered a novel environment than individuals from the closely related local species, and they did so more quickly (Mettke-Hofmann and Greenberg 2005; Mettke-Hofmann et al. 2009).

Fast emergence into a novel environment from a secure place may be interpreted as a form of risk-taking (Carter et al. 2013). As local individuals spend extended periods in the same location, they likely have more complete information about their current local environment simply because they had more opportunities to sample (Dall et al. 2015). These individuals could then be expected to be very well informed about predation risks throughout the year and thus might behave more confidently, i.e., risk-prone (Error management theory: Johnson et al. 2013; Feyten et al. 2019). In contrast, migrants might benefit from behaving warily and vigilantly because they do not have extended knowledge about predation danger in their current environment (Dangerous niche hypothesis: Greenberg and Mettke-Hoffmann 2001; Mettke-Hofmann et al. 2013). A more risk-averse behavior in migrants could thus compensate for the increased risks associated with migration behavior, especially in prey species (Found and St. Clair 2016). It is important to note that local bats were not more likely to emerge because they were more habituated to human handling since local bats were not more likely to be previously banded (and thus handled) than long-distance migrants.

No difference in spatial activity and acoustic exploration between intra-specific migration strategies

Bats actively manipulate the level of echolocation pulses they emit and thus individually control incoming information from the environment. We expected migrants to be characterized by more acoustic exploration as they could benefit more from continuously updating their information when moving through novel environments. However, despite substantial variation in spatial exploration activity and acoustic exploration, we found that neither of these measures varied with migration strategy. Our results thus suggest that spatial activity and environmental cue sampling are equally used by locals and migrants, possibly because spatial and acoustic exploration is crucial also outside the migration context, such as during foraging and orientation inside the roost (Kunz 1982; Schnitzler et al. 2003). In our assays, we let bats choose whether they entered the novel environment since forcing non-emerging bats into the novel environment would likely result in fear-related behavioral responses rather than exploration. We, however, acknowledge that with only 50% of the bats emerging, it is possible that the migrants that did emerge were not representative of the general level of acoustic exploration and spatial exploration activity exhibited by migrants.

Unfortunately, due to a low recapture rate, we were not able to collect enough repeated measures to test the individual repeatability of the behavioral responses. We can thus not conclude whether the variation in the recorded behavioral responses is indicative of personality. We do see some interesting parallels with Nathusius' bats, for which we previously demonstrated repeatability of the same behavioral responses (Schabacker et al. 2021). Similar to noctule bats, these migratory Nathusius' bats showed substantial levels of variation in spatial and acoustic traits and a strong correlation between spatial exploration activity and echolocation activity. In contrast, acoustic exploration in noctule bats did not vary with other exploratory behaviors, such as the number of head pokes into adjacent chambers, as we found in Nathusius' bats. We hope to instigate future research focusing on the repeated examination of novel environment responses, and especially acoustic exploration, in echolocating bats to gain further insight into the behavioural syndromes that may underly the observed behavioral variation. This could be achieved by housing bats temporarily (e.g., 24 h) on-site, rather than depending on recapture, and conducting repeated tests the following night, prior to release.

Potential implications for the conservation of migrants

Animal migration is under pressure, and a better understanding of the underlying mechanism that may make migrants more vulnerable to changing environments would allow for more targeted conservation plans (Wilcove and Wikelski 2008). We found long-distance migrants to be less eager to enter a novel environment, meaning that migratory bats may be more affected by novelty-associated stress. Exposure to novelty increases effects associated with physiological stress (Pfister 1979), yet not all individuals are affected equally. Studies with free-ranging sparrows showed that when confronted with novelty, inquisitive birds exhibited the lowest stress response, measured as stress-induced corticosterone (Lendvai et al. 2011). This has important implications since energy attributed to stress responses will not be available for other energetically demanding activities, such as migration. Given the rapidly changing world, especially for migratory bats, which are continuously confronted with anthropogenically changed roosts and stopover sites (Voigt and Kingston 2016), future research should investigate if migrants and locals indeed differ in their endocrinological stress responses towards novelty. Furthermore, we did not find evidence that migrants and locals differ in their ability to detect changes in the environment. So, migrants should not have more difficulty locating suitable novel roosting spots or avoiding fatal collisions with novel anthropogenic objects (e.g., wind turbines: Voigt et al. 2012; Lehnert et al. 2014) than locals. This is relevant since noctule bats are a common victim of wind turbines (Lehnert et al. 2014).

Conclusion

Our unique approach, combining behavioral assays with isotopic geolocation in an elusive and vulnerable taxon, gave us novel insight into the behavioral correlates of migration. In contrast to our hypotheses, we found no relationship between spatial or acoustic exploration activity and migration strategy and found local individuals more likely to enter an unfamiliar environment than long-distance migrants. This does not allign with related movement ecology studies in other taxa. Revealing such species-specific relationships will be essential for a better and more comprehensive understanding of the potential behavioral causes and consequences of migration.

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Data availability The datasets and code generated and analyzed during the current study are available through the Open Science Framework (OSF): https://doi.org/10.17605/OSF.IO/KXTJ5. A key to the variables in the OSF is available on the final pages of the Supplementary Information and the OSF Wiki page.

Declarations

Ethics approval The use of animals adheres to the guidelines of the Animal Behavior Society/Association for the Study of Animal Behaviour. All fieldwork and associated procedures were conducted in agreement with the authorities and in accordance with German law under a German animal welfare permit (number 2347-25-2018) and conservation permit (number LFU-N1-4743/128 + 25#314731/2018).

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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