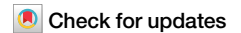


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How individual variation shapes ecological niches in two *Pipistrellus* bat species



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Niche partitioning is a crucial mechanism explaining species coexistence and biodiversity; however, the role of individual variation is less understood. As global changes reshuffle species communities, understanding coexistence mechanisms is vital. In this study, we use two co-occurring, morphologically similar bat species, Nathusius' pipistrelle (*Pipistrellus nathusii*) and the range-expanding Kuhl's pipistrelle (*P. kuhlii*), as models. We examine their niche partitioning across habitats and time, considering individual variations by analysing the spatio-temporal habitat selection of 58 radio-tracked individuals. For resource assessment, we use metabarcoding of guano samples. Our results show that individual variation in both species exceeded species-level differences. Nathusius' pipistrelle exhibits greater between-individual variation, while the range-expanding Kuhl's pipistrelle shows stronger within-individual variation, probably facilitating its expansion. This study emphasises the significance of individual variation in investigating animal niche partitioning. It suggests a contribution of within-individual variation in the range expansion of bat species, reshaping animal communities under global change.

The diversity of ecological communities can be maintained by niche partitioning¹. This process minimises competition between species through specialisation along niche axes such as habitat^{2,3}, time of activity^{4–6} and resource use^{2,3}. Traditionally, niche partitioning has been studied at the species or population level⁷. However, recent studies highlight significant behavioural variation at the individual level^{8–10}, demonstrating how individuals of a species can respond differently to environmental conditions, leading to variation between and within individuals.

Understanding how partitioning may operate across several niche axes while considering multiple levels (species, between and within individuals) is critical in the face of global change¹¹. For instance, due to climate change, warm-adapted species are expanding their ranges, while cold-adapted species are contracting theirs, leading to reshaped communities^{12,13}. The concept of niche partitioning can explain how these modified communities are maintained, which is essential for predicting the future impacts of global change on species diversity¹⁴. Existing research has examined how variation within and between individuals influences range expansion^{15–17}. For example, genetic variation has enhanced adaptive potential and facilitated range expansion in southern pygmy perch (*Nannoperca australis*) populations in response to climate change¹⁵, while colour variation has influenced

marsh harrier (*Circus aeruginosus*) colonisation of new breeding sites¹⁷. However, there is a lack of empirical studies exploring niche partitioning by considering individual variation and multiple niche axes within recently modified communities.

Bats are a particularly interesting group for studying niche partitioning in the context of global change. Given their high level of diversity, mechanisms such as niche partitioning along specific axes are likely essential for maintaining their diversity. There are numerous examples of range-expanding bat species and modified bat communities^{18–21}. This range expansion might be driven by their strong dependence on temperature and high mobility, allowing them to shift their geographic range rapidly²². Thus, by studying niche partitioning in bats, we can gain valuable insights into how animal communities will respond to global change.

To investigate niche partitioning in modified bat communities while considering behavioural variation across species, between and within individuals, we used two co-occurring bat species as models: the originally Mediterranean Kuhl's pipistrelle *Pipistrellus kuhlii* (Kuhl, 1817) and the more northerly Nathusius' pipistrelle *P. nathusii* (Keyserling and Blasius, 1839). In our study area in Central Europe, *P. kuhlii* first came in contact with *P. nathusii* approximately 20 years ago²³. Notably, both species are

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morphologically similar and share a similar echolocation behaviour, making known mechanisms of niche partitioning in bats, such as body size and calling behaviour, unlikely to be relevant^{24,25}. We simultaneously investigated niche partitioning along the axes of habitat, time, and resource use while accounting for the species, between and within individual levels. This comprehensive approach lets us understand how variation between and within species and across multiple niche axes may shape the recent co-occurrence patterns of recently modified animal communities.

Results

To understand the niche partitioning of *P. kuhlii* and *P. nathusii*, we captured 153 *P. kuhlii* (33 males, 120 females) and 135 *P. nathusii* (118 males, 17 females). Of these, we automatically tracked the movements of 49 *P. kuhlii* and 42 *P. nathusii*. After rigorous data filtering, we analysed movement data from 34 *P. kuhlii* (nine males, 25 females) and 24 *P. nathusii* (23 males, one female). The observed sex ratio for *P. nathusii* aligns with typical patterns reported for Central European populations²⁴. Tracking duration ranged from a minimum of one night to nine consecutive nights per bat (mean \pm SD: 2.9 ± 2.2 nights), with up to eight individuals tracked simultaneously (mean \pm SD: 1.9 ± 1.4 individuals).

Species-level niche partitioning

We located daytime roosts of bats in buildings on 333 occasions and in trees on 55 occasions. *Pipistrellus kuhlii* exclusively used buildings (234 occasions), while *P. nathusii* used buildings and trees (98 and 54 occasions, respectively). Analysis of nightly movement patterns revealed a slight preference for forests in *P. nathusii* compared to *P. kuhlii* (posterior mean \pm 95% credible interval = 0.66 ± 0.12 , 1.23). Conversely, *P. kuhlii* showed a stronger preference for arable land (posterior mean \pm 95% credible interval = -0.38 ± -0.62 , -0.16). For other land cover categories, we observed no significant differences in selection between species (Fig. 1). As expected, distance to daytime roosts significantly impacted bat habitat selection. In all land cover categories except forests and reed beds, bats exhibited lower selection ratios for habitats farther from their roosts. This aligns with well-established knowledge that bats typically forage near their roosts^{26,27}. Most forest patches and the large reed belt were far away from most daytime roosts, which probably resulted in the positive effect of distance to daytime roosts on the selection of these land cover categories.

The interaction term of habitat and time indicated weak temporal variation in habitat selection. Posterior estimates for the interaction effect were approximately ten times smaller than those for habitat selection alone (Fig. 1). In reed beds, vineyards, and arable land, these effects of time on habitat selection differed significantly among species. In those land cover categories, time had a significantly stronger negative impact on the selection ratios of *P. kuhlii* compared to *P. nathusii* (Fig. 1), meaning that *P. kuhlii* used those land cover categories earlier than *P. nathusii* (posterior mean \pm 95% credible interval = -0.018 ± -0.023 , -0.011 vs. -0.003 ± -0.007 , 0.001; -0.021 ± -0.028 , -0.014 vs. -0.003 ± -0.015 , 0.008; -0.023 ± -0.03 , -0.015 vs. -0.0005 ± -0.004 , 0.003; respectively).

The analysis of the dietary composition identified 124 genera, with Diptera being the most abundant insect order. The detected insects were quantified using two methods: weighted percentage of occurrence (wPOO) and relative read abundance (RRA). Given consistent results between these metrics for dietary differences between *P. kuhlii* and *P. nathusii*, only wPOO-based findings are presented here (see Supplementary Note 2 for RRA details). Permutational MANOVA revealed significant differences in the dietary composition between *P. kuhlii* and *P. nathusii* ($F = 1.74$, $df = 1$, $R^2 = 0.06$, $p = 0.006$, Fig. 1), although Pianka's niche overlap index indicated substantial overlap in the prey consumption ($O = 0.79$).

Variation between and within individuals

We assessed the variation between and within individual levels in spatio-temporal habitat selection. This was not possible for the dietary analysis, as repeated measurements would have been required to investigate individual variation in this parameter, and we collected only a single guano sample per

bat²⁸. Multivariate niche analysis revealed substantial variation between and within individuals for both *P. nathusii* and *P. kuhlii*, while accounting for species-level differences in spatial and temporal habitat selection. For *P. nathusii*, between-individual variation explained 44–75% (95% CI [26, 88]) of the variance captured by the model. This was up to twice as high as *P. kuhlii* (34–48% explained variance, 95% CI [21, 64]). These differences were significant in all land cover categories except for grassland and vineyards (Fig. 2). Interestingly, within-individual variation in habitat selection was higher in *P. kuhlii* (32–57% explained variance, 95% CI [23, 69]) than in *P. nathusii* (18–43% explained variance, 95% CI [9, 57]). Such species-specific differences were significant in salt lakes, reed beds, complex cultivation patterns, and arable land.

Discussion

Our results show that individual-level variation in spatio-temporal habitat selection exceeded species-level differences. While *P. nathusii* exhibited greater between-individual variation, *P. kuhlii* showed higher within-individual variation in habitat selection. We propose that the strong between-individual variation in *P. nathusii* may hinder species co-occurrence, whereas the pronounced within-individual variation of *P. kuhlii* is a potential mechanism facilitating its ongoing range expansion.

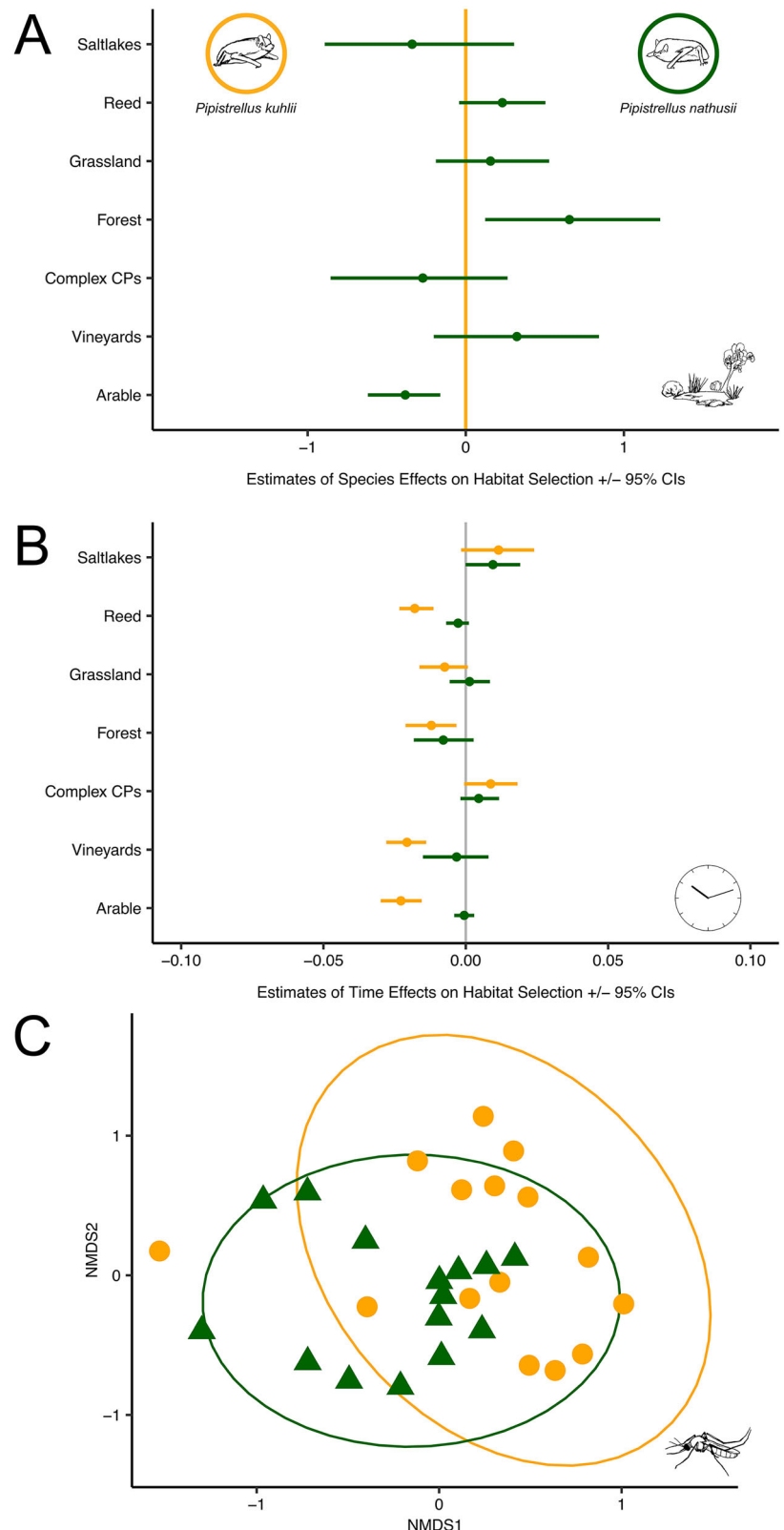
Genetic, environmental, and social factors have been proposed as primary drivers of pronounced individual variation^{29–31}. In our study system, both genetic and environmental influences on individual variation are unlikely. Although divergent genetic lineages exist for both species in Europe^{32–34}, our Central European study area is unlikely to be a contact zone for these lineages. Additionally, stable environmental conditions throughout the study period minimise the potential influence of environmental factors. Given that bats are social and use complex foraging strategies^{35,36}, we hypothesise that social dynamics are primarily responsible for individual differences. Both *P. nathusii* and *P. kuhlii* exhibit territorial behaviour during foraging, occasionally forming clusters in response to abundant prey^{36–38}. This territoriality may promote individual variation in foraging patterns among bats.

Interestingly, individual variation in foraging patterns differed between *P. nathusii* and *P. kuhlii*. Between-individual variation was stronger in *P. nathusii*, while within-individual variation was more pronounced in *P. kuhlii*. The stronger between-individual variation in *P. nathusii* is likely attributed to the predominance of males in our study area. Increased territoriality among males, particularly during the onset of the mating season in August, may contribute to between-individual effects in this species. This hypothesis aligns with comprehensive studies on the mating behaviour of *P. nathusii*, which demonstrate that males can occupy and actively defend mating territories^{39–41}. The high within-individual variation in *P. kuhlii*, accounting for over 50% of model variance in some land cover categories, is particularly striking. This variation may partially explain the rapid range expansion of *P. kuhlii*. Indeed, research has shown that species exhibiting high within-individual variation tend to adapt more to changing environmental conditions, as evidenced by studies on birds⁴², insects⁴³, and amphibians⁴⁴. Consequently, future investigations of expanding species should explicitly consider within-individual variation.

In addition to the individual variation, we also observed niche partitioning at the species level along the axes of habitat and resource use. *Pipistrellus nathusii* exhibited a stronger preference for forests than *P. kuhlii*, which favoured arable land. This species-level partitioning was also evident in our dietary niche analysis, revealing small but significant differences in diet composition. These findings align well with previous research, where *P. nathusii* showed similar habitat preferences in Germany and Poland^{45,46}, whereas *P. kuhlii* predominantly used agricultural areas in Israel⁴⁷. Notably, in these studies *P. nathusii* and *P. kuhlii* did not co-occur sympatrically.

Differences in habitat selection between bat species can be driven by habitat structure itself or dietary compositions within these habitats⁴⁸. Our dietary analysis, limited to the insect genus level, prevents a more detailed investigation of the habitat-prey relationship. Many insect genera contain multiple species with differing habitat preferences, and specific habitat

Fig. 1 | Niche partitioning of *Pipistrellus kuhlii* and *P. nathusii* across habitat, time and resource use. Orange colours indicate *P. kuhlii* ($n = 34$), and green colours indicate *P. nathusii* ($n = 24$). Points refer to posterior means and lines to 95% credible intervals (CIs). Panel A shows the selection of six different land cover categories by *P. nathusii* compared to *P. kuhlii* (vertical orange line). “Complex CPs” refers to the land cover category “Complex Cultivation Patterns”. CIs indicate significant differences in the selection of forests and arable land between *P. nathusii* and *P. kuhlii*. Panel B focuses on the interaction between time and habitat type of *P. kuhlii* and *P. nathusii*. Note that the x-axis in this panel has a finer scale (0.01 units) compared to the upper panel (0.1 units). *Pipistrellus kuhlii* selected reed beds, vineyards and arable land significantly earlier than *P. nathusii*. Panel C shows a non-metric multidimensional scaling (NMDS) ordination of insect genera detected in the guano of 15 *P. kuhlii* (orange points) and 15 *P. nathusii* (green triangles). The ellipses around each species represent the 95% confidence ellipses of the NMDS. The icons are hand-drawn and vectorised in Inkscape 1.2.

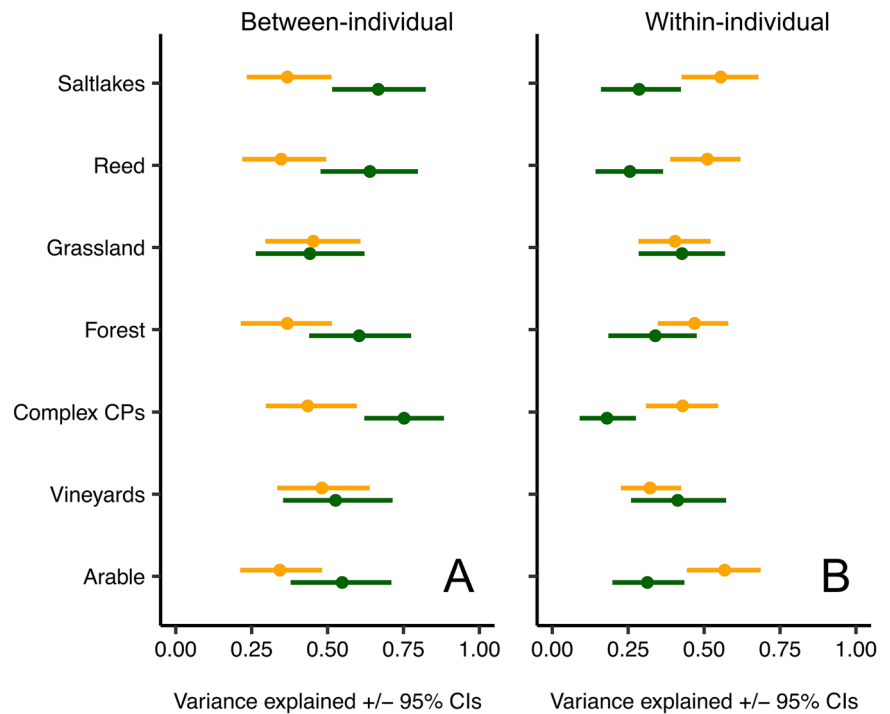


information is lacking for many insects⁴⁹. To determine whether habitat selection differences between bat species are driven by habitat structure or insect availability, we recommend a detailed assessment of prey availability across different habitats.

Temporal activity patterns also differed between *P. kuhlii* and *P. nathusii*. The latter showed consistent habitat selection throughout the

night, while *P. kuhlii* selected arable land, vineyards, and reed beds earlier at night. Although temporal habitat partitioning is documented in bats^{50,51} and other animals such as primates⁵² and felids⁵³, the need to nurse pups is likely a more plausible explanation for this behaviour than temporal habitat partitioning. Female bats, especially during lactation, are known to return frequently to their roosts at night⁵⁴. Moreover, previous studies on temporal

Fig. 2 | Variance of niche partitioning explained by individual variation in *P. kuhlii* (orange) and *P. nathusii* (green). The points show the mean proportions of variance in the niche models explained by differences between (A) and within (B) individuals for each species and land cover category. The lines indicate 95% credible intervals (CIs). “Complex CPs” refers to the land cover category “Complex Cultivation Patterns”. CIs indicate that between-individual variation was significantly stronger in *P. nathusii* across all land cover categories except grassland and vineyards. Conversely, within-individual variation was more pronounced in *P. kuhlii* in all land cover categories aside from grassland, forests and vineyards.



behaviour in bats have either focused on operational taxonomic units within acoustic frameworks that do not account for individual effects^{50,55}, or have examined situations where resources are limited⁵¹. Due to the high expected insect availability in our study system (grazing livestock, productive reed belt), resource limitation is unlikely to be a significant factor. Thus, we attribute the differences in temporal behaviour within our study to intrinsic factors, such as feeding pups, rather than to temporal niche partitioning. This interpretation is supported by the fact that temporal effects were an order of magnitude smaller than habitat effects.

Whether the strong individual variation promotes or impedes the coexistence of species is widely debated^{56–59}. While individual variation might allow some individuals to escape competition from a superior species, thereby facilitating coexistence, it can also reduce intraspecific competition relative to interspecific competition, thus potentially destabilising coexistence⁵⁹. In our study system, the nature of the co-occurrence of *P. nathusii* and *P. kuhlii* remains speculative. *Pipistrellus kuhlii* was first detected in the area in 2002²³, indicating a recent co-occurrence (approximately three *P. kuhlii* lifespans). However, historical records from the second half of the 20th century suggest that *P. nathusii* was the most common bat species in the region^{60,61}. Our field observations contrast with this, as we predominantly captured *P. kuhlii*, consistent with the findings of local bat experts²³. This may suggest that *P. kuhlii* is a successful competitor of *P. nathusii*. Similarly, *P. kuhlii* has been suggested to replace similar bat species in the Negev desert^{62,63}. While water scarcity in that ecosystem likely promotes competition, resource limitations are less apparent in our study area. However, this situation might change in the future due to the combined pressures of intensified agriculture, increasing water scarcity, rural sprawl, and a warming climate⁶⁴, coupled with the ongoing decline in insect populations^{65–67}. Thus, we anticipate increased competitive interactions between *P. kuhlii* and *P. nathusii* in the future.

While these potential future competitive interactions are plausible in our study area, they could differ in some parts of Europe. We observed differing sex ratios between *P. kuhlii* (predominantly females) and *P. nathusii* (predominantly males), a situation typical in many parts of Europe²⁴. Sexual segregation is frequently observed in bats and varies regionally^{68–71}. Given the sometimes observed influence of sex on bat behaviour^{68,72}, we encourage researchers to study niche partitioning while accounting for individual variation in other regions with different species compositions and sex ratios.

Our study system underlines the critical role of individual variation in understanding niche partitioning, contributing to a growing body of research investigating the stabilising mechanisms within animal communities^{8,9,73,74}. The strong within-individual variation in foraging behaviour exhibited by *P. kuhlii*, which has expanded its geographical range by approximately 394% in recent decades¹⁹, suggests that such variation may contribute to range expansion. Although we lack data on other potentially influential factors, such as temporal changes in resources or land use, our empirical findings support experimental results from studies on invasive plants⁷⁵ and slugs⁷⁶, which showed greater morphological and physiological within-individual variation than their non-invasive congeners. In light of the accelerating pace of climate and land cover change, within-individual variation may contribute to the reshaping of animal communities.

Methods

Our methodological workflow is presented in the Supplementary file (Supplementary Fig. 1).

Study area

We conducted our study in the Seewinkel region, located on the eastern shore of Lake Neusiedl in the east of Austria (47°44'N, 16°46'E). The climate is humid continental (Köppen classification), with an average annual temperature of 12 °C and annual precipitation of 458 mm (data averaged from 2018–2022, GeoSphere Austria). The terrain is flat with an elevation of 114 to 124 m a.s.l. The land cover is a mosaic of meadows, vineyards, temporary salt lakes and small forests, including parts of Europe's second-largest reed belt (Supplementary Fig. 2). Large parts of the region are protected under the Neusiedler See Seewinkel National Park. Land use primarily focuses on wine production and grazing, with cattle, horses, and water buffalo being the most common livestock. In the western part of the study area lies the small village of Illmitz, with a population of approximately 2300. In faunistic pilot surveys, we detected 18 bat species, including *P. nathusii* and *P. kuhlii*, which were the most abundant species.

Study species

Pipistrellus nathusii is a small bat with an average forearm length of 33.9 mm (SD = 0.89) and a body mass of 7.8 g (SD = 1.0) in our study area. Although females tend to be slightly larger and heavier, *P. nathusii* shows no

significant signs of sexual dimorphism. *Pipistrellus nathusii* is distributed across most of Europe, with females typically raising two pups in Northern Europe and hibernating in Central and Southern Europe^{77,78}. Shifts in hibernation and breeding areas have been observed throughout Europe^{79,80}. Similar to regions in southern Europe⁸¹, there is a strong male bias in Austrian *P. nathusii* during the summer⁸². Males exhibit various mating strategies, including establishing and defending territories during the mating season⁴¹ (August–October in our study area, own data).

Pipistrellus kuhlii is morphologically similar to *P. nathusii*, with an average forearm length of 34.7 mm (SD = 0.95) and a body mass of 7.2 g (SD = 0.9) in our study area. Like *P. nathusii*, *P. kuhlii* displays minimal sexual dimorphism, with females, on average, larger and heavier than males. Originally mainly distributed in the Mediterranean, it has expanded its range into Central and Eastern Europe over the last decades¹⁹. The mating season lasts approximately from August to October in our study area, with males displaying song flights as mating displays⁸³. As for *P. nathusii*, *P. kuhlii* typically raises two pups^{84,85}.

Pipistrellus kuhlii predominately forages solitarily or in small groups of 4–5 individuals but may aggregate to larger groups in areas of high prey availability^{36,37}. Although, to our knowledge, social foraging behaviour has not been studied in *P. nathusii*, similar behaviour might be expected given observations of such behaviour in other *Pipistrellus* species^{84,85}, and similar prey preferences to *P. kuhlii*. Specifically, *P. kuhlii* and *P. nathusii* are not specialised predators, but Diptera and Lepidoptera appear to be important prey^{86,87}.

Bat tagging

During June to August 2022 and 2023, we captured bats using hair nets and monofilament nets at 21 sites, including wooded and settlement areas. The nets were continuously monitored from sunset to midnight or midnight to dawn. We identified bats at the species level following the identification criteria outlined in Dietz and Kiefer⁸⁸. For every bat, we recorded the sex, reproductive status, and age (adults: ossified digits, subadults: visible growth plates near joints) and additionally measured forearm length and body mass.

We selected 91 adult individuals of *P. kuhlii* and *P. nathusii* for tagging, which showed no signs of physical constraints such as injuries and unusually high ectoparasite load (ticks, mites or bat flies). These criteria, defined as humane endpoints, were established a priori when applying for the Animal Experiment permit. Bats exhibiting such signs were released immediately. We shortened the dorsal hair of the bats between their shoulder blades and attached Very-High-Frequency (VHF)-Transmitters (LB-2x, Holohil Systems Ltd., Ontario, Canada) using surgical skin glue (Manfred Sauer GmbH, Lobbach, Germany). VHF transmitters weighed 0.27 g and 0.31 g, corresponding to 2.7–5.2% of the individual bat body mass (mean $3.9 \pm 0.5\%$, Supplementary Table S1). Tagged bats were kept in bags for five minutes to ensure complete hardening of the glue and released afterwards. In total, the identification and tagging procedure from capturing to release lasted for a maximum of 30 minutes.

Bat handling and tagging were conducted in accordance with Nature Conservation permit A4/NR.AB-10122-5-2022 (Federal State of Burgenland) and Animal Experiment permit 2022-0.137.202 (Austrian Ministry of Education, Science and Research). The latter was submitted with a protocol including the research question, key design features, and analysis plan.

Radio telemetry

Every day the transmitters were active, we located daytime bat roosts by “homing-in-on-the-animal”⁸⁹ with three-element Yagi antennas (Lotek UK Ltd, Wareham; Perdix Wildlife Supplies, Warwickshire, UK; ATM Inc., Isanti, USA) paired with radio receivers (Icom IC-R30, Icom GmbH, Bad Soden, Germany; Alinco DJ-X11, Alinco Incorporated, Osaka, Japan).

To track the nocturnal movement of the tagged bats, we used an automated VHF radio tracking system⁹⁰. We deployed a network of eight receiver stations in 2022 and ten in 2023, covering an area of approximately 85 km². Due to occasional material failures, single stations were not active

over the whole recording period. To ensure data quality, nights with fewer than seven functioning stations were excluded from the analysis. In brief (see Gottwald et al.⁹⁰ for more details), every receiver station consisted of four directional H-antennas (Pleco Solutions GmbH, Müllheim, Germany) mounted on an 8- to 12-metre aluminium pole. These antennas were connected to four RTL-SDR receivers (NooElec, Wheatfield, USA) and Raspberry Pi 3B+ computers (Raspberry Pi Ltd, Cambridge, UK). The receivers continuously logged signals within a predefined frequency range (250 kHz) and signal duration (0.01–0.03 s). Each signal was also assigned a timestamp. We set the receiver gain to 50 dB and the signal-to-noise ratio to 11 dB. Wi-Fi routers (TP-LINK M7000, TP-Link GmbH, Düsseldorf, Germany and RUT240, Teltonika Networks UAB, Kaunas, Lithuania) allowed us to synchronise the time stamps of the system with the internet and enabled remote access to the stations. This system configuration allowed us to track up to eight bats simultaneously. The system’s accuracy was validated using dummy transmitters and comparing manually located bats with estimated locations (Supplementary Note 1).

Processing of recorded signals

We applied a multi-stage filtering process to the recorded signals. The raw signals were filtered based on the known transmitter characteristics: transmitter frequency ± 2 kHz, a minimum signal duration of 20 ms and an inter-signal time interval of 1.1–1.4 s. Using those filtered signals, we estimated the direction of arrival for each signal at each station. This estimation was based on comparing signal strengths received by neighbouring antennas. We employed a cosine function to calculate the direction of arrival (i.e. the bearing of the signals). To further enhance data quality, we applied a Hampel filter on these bearings with a rolling window of 10 s and a median filter threshold of 0.5.

Following data filtering, we divided the data into individual bat-night combinations for further analysis. To estimate bat locations, we employed an azimuthal telemetry model that uses Markov chain Monte Carlo (MCMC) iterations⁹¹. These models incorporate the maximum detection distances of the stations, estimated during the accuracy tests, as prior information. We iterated the MCMC simulations 10,000 times, discarding the initial 2000 iterations as a burn-in period. Convergence of the MCMC algorithms was assessed using trace plots, and bat-night combinations with erroneous results based on these visual diagnostics were excluded from the analysis. To account for minor time synchronisation discrepancies observed between some stations, we allowed for a two-second variation of timestamps. The azimuthal telemetry model provides location estimates of bat individuals and the corresponding covariance matrices, allowing us to assess the associated uncertainty of location. To remove erroneous location estimates, we filtered them based on animal movement speed. Locations suggesting speeds exceeding 13 m s^{-1} (approximately the maximum flight speed of *P. nathusii*⁹²) were removed. To estimate the movement speed, we used the R package “ctmm”⁹³ because it allowed us to incorporate location uncertainty into the speed calculations. As a final filtering step, we excluded all points in the fourth quartile of location uncertainty (504–1199 m), as these points with low accuracy provide little information about the animals’ actual positions. Animals with insufficient residency time within the study area, resulting in model failure, were excluded. The remaining dataset consisted of 41 *P. kuhlii* and 38 *P. nathusii* individuals.

Activity classification

During summer, bats use roosts to rest from foraging and raise pups. To not confound roosts with foraging habitats, we excluded supposed roosting locations from the data. Based on the idea that moving transmitters have a higher variability of signal parameters than stationary transmitters⁹⁴, we calculated nine variables characterising signal variability and utilised a random forest algorithm to classify resting and moving episodes.

To train the random forest algorithm, we manually classified a dataset of 200,000 signals (100,000 stationary and 100,000 moving). This classification was based on our manual tracking data, visual observations of bat behaviour and knowledge of daytime roosting locations.

We then calculated the variability variables by segmenting the signals into five-minute chunks. Within each chunk, we used a sliding window of ten data points to calculate the maximum signal strength, mean signal strength, skewness, sum of squares, sum of squares of the mean for smoothed signals, variance and standard deviation of Hampel-smoothed signals, and the sum of squares of the Hampel-smoothed signals. Next, we randomly selected 70% to train the model and 30% to test its performance. We employed a forward feature selection approach using the “CAST” package⁹⁵ to identify the most relevant features, and then tuned the “mtry” parameter with the “caret” package⁹⁶. Finally, we evaluated the model’s accuracy on the test data using the ROC AUC score calculated with the “MLeval” package⁹⁷. After assessing the model’s performance, we used it to classify all recorded signals as stationary or moving. For subsequent analysis, we only considered the signals classified as moving.

Land cover data

To analyse the habitat selection of bats, we integrated land cover data from various sources. We used the CORINE land cover map⁹⁸ to obtain land cover classifications at a 100-m resolution raster format. We merged the uncommon categories “Discontinuous urban fabric” and “Sport and leisure facilities” into a single category named “Settlement” and “Complex cultivation patterns” and “Land principally occupied by agriculture with significant areas of natural vegetation” into “Complex Cultivation Patterns”. To differentiate between two important types of water bodies in the study, “freshwater lake” and “saltlake”, and to implement poorly represented forests, we also included vector data for standing water bodies from the Federal Ministry of Agriculture, Forestry, Regions and Water Management and forest data from the Federal Country Burgenland^{99,100}. Both vector datasets were converted to 100-m resolution rasters using the “terra” R-package¹⁰¹ to fit the resolution of CORINE. We implemented nine different land cover categories in the habitat analysis (Supplementary Table S2).

Temporal habitat analysis

We estimated the temporal space use patterns of bats throughout each night. We employed a method similar to that described in Byrne et al.⁶ to estimate time-explicit habitat preferences. Specifically, we calculated time-specific 50% utilisation distributions (UDs) for 30-min intervals. These UD were derived using dynamic Brownian Bridge Movement Models (dBBMMs) implemented in the “move” package¹⁰². Unlike our discrete location data collected at intervals of 2 s, dBBMMs represent movement as a continuous stochastic process over time. This allows us to account for the inherent temporal autocorrelation of the movement data¹⁰³. For the dBBMM calculations, we used a margin of three locations and a window size of 31 locations. To include location uncertainty in the models, we estimated the error associated with each location fix by calculating the square root of the eigenvalues of the covariance matrix associated with each location estimate. The sum of these square roots, divided by two, approximates the radius of the error ellipse, representing the potential uncertainty around the estimated location. When calculating the movement variance used by the dBBMMs, we excluded time lags exceeding one minute.

In the next step, we defined the proportion of each land cover category within a bat’s 50% UD area at 30-min intervals as used habitat and the proportion within the respective bat’s 95% UD as available area. While this time interval was chosen for convenience, similar results were obtained with 10-min and 1-h intervals (details in Supplementary Tables S3–S5). We calculated time-specific selection ratios *SR* for each bat. These ratios were calculated for each bat *i* by dividing the proportion of a specific land cover type *U* used within a 30-min interval *j* by the proportion of that land cover type within the available area *A* (Eq. (1)).

$$SR_{ij} = \frac{U_{ij}}{A_i} \quad (1)$$

Niche analysis

We investigated niches at the species, within- and between-individual levels in a multivariate Bayesian framework using the R package “MCMCglmm”¹⁰⁴. We analysed selection ratios for each 30-minute interval as response variables. We restricted the analysis to nights and individuals with known day roost locations (34 *P. kuhlii* and 24 *P. nathusii*), as habitats near roosts are crucial for bats^{26,54}. We also removed the night of tagging from the analysis. The “Settlement” land cover type was excluded due to its high correlation with “Reed” ($r = 0.62$) and assuming that settlement selection likely reflects roosting behaviour (most roosts were in settlements). Visual inspection of the location data revealed that individuals foraging on the lake frequently moved close to the reed, making these land cover types challenging to differentiate. As a result, the land cover type ‘Lake’ was excluded from subsequent analysis.

Fixed effects in the model included species, time in 30-minute intervals after sunset, and distance to roosts. Weather data were excluded from the model due to minimal variation in temperature (median: 20.1 °C, IQR: 18.3–21.9 °C), wind speed (median: 2 m·s^{−1}, IQR: 1.3–3.1 m·s^{−1}), and precipitation (median: 0 mm, IQR: 0–0.02 mm). Random effects included individual ID as random intercepts and slopes, with variance allowed to differ among species. Additionally, we implemented the recording night as a factor in the random structure to account for the annual and seasonal effects of movement patterns. We also modelled varying residual variance across species. Uninformative priors ($\nu = 1.002$) were chosen due to the lack of prior information on the movement behaviour of bats in our study area¹⁰⁴. In the MCMCglmm analysis, we employed a chain length of 30,000, a thinning interval of 10, and a burn-in period of 3000. The convergence of five independent chains was confirmed using Gelman diagnostics, ensuring all parameters had a potential scale reduction factor below 1.01, indicating convergence. To assess the relative contributions of between-individual variation (intercept of the ID) and within-individual variation (slope of the ID), we calculated the proportion of variance explained for each species following Houslay et al.¹⁰⁵. This was achieved by dividing the species-specific variance by the sum of all variance components within the random structure, which was also calculated for each species. All statistical analyses were conducted in R 4.3.1¹⁰⁶.

DNA extraction, library preparation and sequencing

We analysed the dietary patterns of *P. nathusii* and *P. kuhlii* separately from the spatiotemporal niche analysis due to incomplete guano sample collection from all tracked bats. The guano samples were collected from captured bats and immediately placed on dry ice. Subsequently, samples were stored at −20 °C for up to three months, followed by transfer to −80 °C storage until analysis.

Thirty samples (15 *P. nathusii* and 15 *P. kuhlii*) were prepared for DNA isolation by transferring them to PowerBead tubes, adding 800 µL lysis Buffer (Qiagen, Hilden, Germany), disrupting with a Vortex Adapter at maximum speed for 20 min, and incubation at 56 °C for 4 h. Then, samples were centrifuged for one minute at 20,000 × *g*, and the whole supernatant was transferred to a new tube. DNA isolation was done using a QIAamp PowerFecal Pro DNA Kit (Qiagen, Hilden, Germany), strictly following the manufacturer’s instructions. Two negative controls were included.

Enrichment PCRs and library preparation with double-end indexing for sequencing involved two rounds of PCR amplification using the arthropod-specific primers fwhF2 (5′-GGDACWGGWTGAACWGTW-TAYCCHCC-3′) and fwhR2 (5′-GTRATWGCHCCDGAAR-WACWGG-3′)¹⁰⁷, which target the cytochrome c oxidase subunit 1 gene and result in an amplicon size of 254 base pairs (bp). Firstly, the target locus was amplified using 10 µL reactions containing 5 µL of Multitplex Maternix Kit (Qiagen, Hilden, Germany), 2.5 µL of DNA, 10 µmol of each forward or reverse primer, and 1 µL nuclease-free water (Qiagen) using a Mastercycler® Nexus (Eppendorf, Hamburg, Germany). Cycling conditions were as follows: 15 min at 95 °C, 35 cycles of 30 s at 94 °C, 90 s at 50 °C, 60 s at 72 °C, and a final elongation at 72 °C for 10 min.

First-stage PCR amplicons were purified (SPRIselect Bead Protocol for Size Selection Beckman, Coulter) and used as second-step PCR amplicons using the Nextera Index Kit (Illumina, Inc., USA) to incorporate sample-specific identifier indices and sequencing adapters. Second-step PCRs contained 25 µL of 12.5 µL Multiplex Maternix Kit (Qiagen), 5 µL of the sample amplicon, 1 µL BSA, 5 µL of each of the two indices from the Nextera Index Kit, and 1.5 µL nuclease-free water using a Mastercycler® Nexus (Eppendorf, Hamburg, Germany). Cycling conditions were as follows: 15 min at 95 °C, 15 cycles of 30 s at 94 °C, 30 s at 55 °C, 60 s at 72 °C, and a final elongation at 72 °C for 10 min. Two negative and two positive controls were included for each batch of samples run.

PCR products were again purified, DNA yields were measured, and the equimolar pooled sets of 94 sample libraries, along with two PCR NTCs, were paired-end sequenced on an Illumina® MiSeq using the MiSeq Reagent Kit v3 (600-cycle; Illumina, Inc.) with an Illumina Miseq PE300 (min. 110,000 sequences/sample) using the V2 reaction kit (Illumina, San Diego, CA, USA) (performed by Sinsoma GmbH, Völs, Austria).

Sequence processing and analysis

Demultiplexing of the plate samples was performed using a specifically written bash script, and the quality of general data was checked with FastQC v0.11.8¹⁰⁸. Data trimming was done by removing the adapters and primer sequences using cutadapt v1.18¹⁰⁹, and merging of the forward and reverse sequences was done by using usearch-fastq_megepairs (settings: fastq_pctid 80% consensus at matching-position, fastq_maxdiffs eight wrong basepairs at matching-position). Ultimately, empty, unique and short (<100 bp) sequences and sequences without a partner were discarded using usearch¹¹⁰. Centroid clustering was done using usearch-cluster_smallmem with 0.99 id, and sequences were compared to the publicly available Nucleotide database provided by the NCBI using BLAST+ with maximum-target_seqs of 10¹¹¹.

The results of the blasting were processed using the R environment¹⁰⁶. For further clean-up, sequence IDs < 90, hits with information uncultured, synthetic construct, and environmental samples were discarded. Subsequently, fragments <150 bp and non-target hits (e.g. mammals and bacteria) were excluded. For taxon assignment, the following process was applied: 10 top blasting hits were evaluated, and clear species assignment was accepted if all ten hits were agreed upon. If not, the hit on the species level with the highest percentage ID was received. All unclear species-level assignments were shifted to genus or family level and manually checked. Finally, a plausibility check was done, checking results against the GBIF database and an internal database of species origin to evaluate whether the hits are plausible for the study area. This plausibility check indicated that the genus-level results were more reliable than the species-level results within our study area. Consequently, we focused our dietary pattern analysis at the genus level.

Statistical analysis of dietary patterns

We employed two standard metrics used in metabarcoding studies to quantify dietary composition in the guano samples: (i) weighted percent occurrence (wPOO) and (ii) relative read abundance (RRA)¹¹². To investigate dietary pattern differences between the bat species, we used the R package “vegan”¹¹³. Specifically, we calculated distance matrices for wPOO (Jaccard method) and RRA (Bray-Curtis method) and performed non-metric multidimensional scaling (NMDS)¹¹⁴. We assessed multivariate homogeneity of variance using the PERMDISP2 procedure implemented by the betadisper() function in the “vegan” package¹¹⁵. To test for significant differences in dietary patterns, we subsequently applied a permutation analysis of variance (perMANOVA) with 9999 permutations. Finally, to quantify dietary niche overlap between *P. kuhlii* and *P. nathusii*, we calculated Pianka’s index with 9999 bootstraps using the R package “spaa”¹¹⁶.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data required for the analysis can be found in the figshare database: <https://doi.org/10.6084/m9.figshare.27079759.v1117>¹¹⁷. The raw data sequences generated in this study can be downloaded from the NCBI Sequence Read Archive under the accession code PRJNA1234894¹¹⁸.

Code availability

The annotated code to analyse the data is provided in the figshare database: <https://doi.org/10.6084/m9.figshare.27079759.v1117>.

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Author contributions

M.M.: concept, fieldwork, analysis, writing; A.B.: concept, writing; E.K.: analysis, writing; I.H.: analysis; G.R.: concept, fieldwork; L.L.: analysis, writing; S.L.: fieldwork, analysis; M.S.: fieldwork, analysis; T.Z.: validity check of metabarcoding results, review, M.S.R.: supervision, review; all authors critically reviewed the manuscript and agree with the content.

Competing interests

The authors declare no competing interests.

Additional information

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