



# Local site fidelity and long-distance migration: twelve years of Nathusius' pipistrelle ecology in the UK

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## Abstract

Migratory bats remain poorly understood despite their ecological importance and increasing exposure to anthropogenic threats. We present twelve years of monitoring of *Pipistrellus nathusii* at Bedfont Lakes, the first bat box site in the UK to document use by this species. Using recapture data from box checks and trapping, alongside automated telemetry, we investigated box occupancy, roost fidelity, social structure and migratory movements. Box occupancy was highly dynamic, varying by sex and season, with a clear autumn peak coinciding with migratory aggregations and mating activity. Occupancy was significantly influenced by box orientation and design, while microclimatic effects were limited. Roosting area fidelity was high, with several males recaptured across years, suggesting the coexistence of resident strategies alongside wide-ranging migrants. Social organisation ranged from solitary males to mixed-sex groups, reflecting seasonal variation in group composition consistent with seasonal harem formation. Network analysis revealed a sparse, highly clustered structure with no deviation from random associations. Long-distance ring recoveries, including a female recorded 2,018 km away in Russia, and Motus detections across Europe confirmed transboundary migration. These findings highlight the value of long-term, multi-method monitoring in revealing complex movement strategies in *P. nathusii*. The long-distance movements documented here also emphasise the transboundary nature of bat conservation, as migratory individuals may encounter multiple anthropogenic pressures, including wind-energy infrastructure, across different countries and jurisdictions. Effective conservation of migratory bats therefore requires international coordination and a better understanding of how local sites contribute to broader migratory networks.

**Keywords** Artificial roost · Banding · Bat box monitoring · Migratory bats · Telemetry · Motus Wildlife Tracking

## Introduction

Understanding the ecology of migratory animals remains a major challenge, especially for species that are difficult to detect in the wild or whose routes and seasonal behaviours

are poorly documented. Migratory animals are hard to study due to the broad scale of their movements, the unpredictability of their seasonal locations, and the logistical difficulty of tracking individuals over long distances (Bowlin et al. 2010). These challenges are particularly pronounced for species that travel thousands of kilometres across national borders, prompting international agreements such as the Convention on Migratory Species to promote cooperation in their monitoring and conservation (Trouwborst 2012). Gathering long-term data is difficult but essential for understanding their ecology and designing effective conservation strategies (Fleming and Eby 2003; Hutterer et al. 2005; Marques et al. 2014).

Among flying vertebrates, bats are unique as the only mammals capable of powered flight, with several species undertaking seasonal long-distance migrations (Fleming and Eby 2003). However, compared to their avian counterparts, the migratory ecology of bats is still poorly

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understood. Their nocturnal behaviour and generally small body sizes limit opportunities for direct observation and make them incompatible with most solar-powered tracking technologies (O'Mara et al. 2014). Meanwhile, they face increasing threats from habitat loss, climate change, and wind turbines (Voigt et al. 2015; Frick et al. 2017; Festa et al. 2023; Kerth and Wolf 2025). These pressures highlight the urgent need to improve monitoring and advance our understanding of bat movements, habitat use, and ecological needs throughout their annual cycle. In this context, site-based, long-term studies are especially valuable, as they provide critical insights into how local behaviours can be connected to broader migratory patterns.

Europe is home to at least 16 migratory bat species, four of them long-distance migrants (Hutterer et al. 2005). Among these, the Nathusius' pipistrelle (*Pipistrellus nathusii*) stands out with documented movements exceeding 2,000 km between breeding areas in northeastern Europe and wintering sites in western and southern Europe (Hutterer et al. 2005; Alcalde et al. 2021; Russ 2022). It occupies a broad Palearctic distribution from the Iberian Peninsula and British Isles, to western Russia and Asia Minor (Hackländer and Zachos 2020; Russ 2022). In autumn, females have been observed to migrate southwest to mate with territorial males before both sexes move to hibernation sites (Roer 1960; Bastian 1988; Brosset 1990; Lina 1990; Russ 2022). Yet the inland routes and specific sea crossings remain poorly resolved, an important gap given increasing threats from offshore and onshore wind farms along potential migratory corridors.

*Pipistrellus nathusii* was long considered a vagrant in the UK, with the first individual documented in 1940 and only sporadic sightings in subsequent decades (Hermann 1992; Russ 2022). In the past two decades, however, focused monitoring efforts have shown that UK populations include both residents and migrants (Russ et al. 2001; Bat Conservation Trust 2010; Russ 2022). Acoustic monitoring and the Bat Conservation Trust's National Nathusius' Pipistrelle Project (NNPP) have greatly expanded knowledge of the species, highlighting strong habitat associations with large waterbodies and river catchments (Russ et al. 2001; Lundy and Montgomery 2010), and documenting long-distance movements between the UK and several European countries, including Russia, Latvia, and Poland (Kruszynski et al. 2021; Kruszynski 2022; Lagerveld et al. 2023, 2024). The UK appears to function primarily as a wintering area, with only occasional breeding roosts reported (Russ 2022; Bat Conservation Trust 2023). Yet, many aspects of the species' ecology remain poorly understood in the UK, including seasonality, roosting ecology and site fidelity.

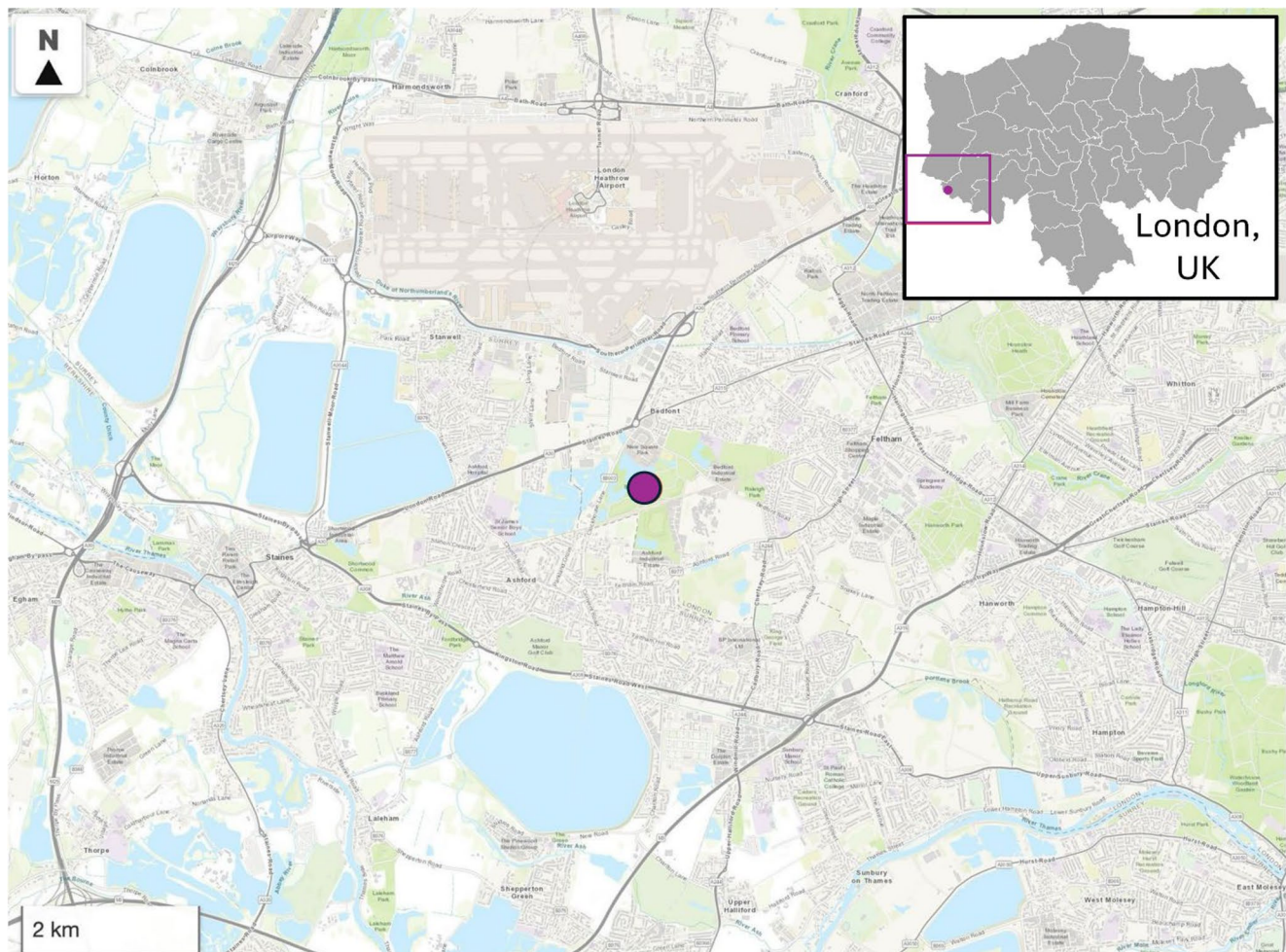
Long-term monitoring of artificial roosts such as bat boxes can provide valuable insights into the ecology of *P. nathusii*, including seasonal roost use, phenology, site fidelity, social associations, and movement (Flaquer et al. 2005; Ciechanowski and Jarzembowski 2009; Baranauskas 2009). When combined with individual marking and telemetry, repeated monitoring at a single site can also connect local patterns of roost use with movements occurring at much broader spatial scales.

Bedfont Lakes Country Park, on the edge of Greater London, provides a unique opportunity to examine these aspects of *P. nathusii* ecology through a long-term dataset integrating complementary monitoring approaches. It was the first UK site where *P. nathusii* were recorded using bat boxes, and has subsequently been monitored using box checks, trapping, ringing, and, more recently, automated telemetry. Here, we use twelve years of monitoring to investigate roosting ecology, seasonal patterns of box use, site fidelity, and individual associations, and examine movements beyond the local area through recapture and telemetry data. By integrating these approaches, we assess how sustained monitoring at a single site can provide insights into the ecology of a wide-ranging migratory bat and inform its conservation.

## Methods

### Study site

This study was conducted at Bedfont Lakes Country Park in Hounslow, London, UK (51°26'33"N, 000°26'43"W). This country park is a reclaimed gravel pit and landfill site that was established in 1995, and covers 72.5 hectares with extensive lakes, wetlands, woodland and wildflower meadows. It includes a private nature reserve in the park's northern sector, bounded by Clockhouse Lane, North Lake, South Lake, and adjacent reedbeds. The site has a temperate climate, characterised by mild temperatures and moderate rainfall, with seasonal flooding and winter goat grazing contributing to structural heterogeneity. Vegetation inside the reserve consists of wet woodland dominated by crack willow (*Salix fragilis*), oak (*Quercus* spp.), holly (*Ilex aquifolium*), and elder (*Sambucus nigra*), and diverse ground vegetation. The park lies less than 5 km from several rivers, including the River Thames, River Colne, Wraysbury River, Longford River, and River Crane, as well as a network of large reservoirs that supply water to London (Fig. 1). These features are particularly relevant given the association of *P. nathusii* with rivers and other waterbodies as movement corridors and feeding habitats (Russ 2022). The site was designated as Site of Importance for Nature Conservation (of Metropolitan Importance) in 2007.



**Fig. 1** Location of Bedfont Lakes Country Park in Hounslow, London, UK. The site (purple point) lies within a landscape of rivers and reservoirs, including the nearby River Thames, River Colne, Wraysbury River, Longford River, and River Crane

Bat boxes were first installed at Bedfont in 1996, placed ~2–3 m above ground in a range of microhabitats, including woodland interiors, edges, and glades.

### Bat box monitoring, trapping and ringing

An annual Natural England survey licence was first issued in 2012 to research *P. nathusii* via bat box checks, trapping and ringing. Between 2012 and 2024, we monitored bat use of 49 boxes, of a mixture of model types including Schwegler woodcrete models (Schwegler Vogelund Naturschutzprodukte, Germany), a Harlech woodstone box, and wooden slot design boxes. For each bat box, we recorded the coordinates, box design and placement orientation (Table S1). To further understand the microclimatic characteristics that make bat boxes suitable for *P. nathusii*, we installed iButton® dataloggers in 16 of the 49 bat boxes, selected to ensure representation of the different box types and orientations

present at the site. Dataloggers recorded temperature and relative humidity at 90-minute intervals for a full year.

Each year, we checked boxes from spring to autumn, although the timing and frequency of checks varied among years depending on personnel availability and other logistical constraints. Monitoring generally occurred between March or April and October, with reduced sampling during the breeding periods to minimise disturbance to sensitive colonies. Checks were less frequent in March, primarily due to delays in obtaining annual monitoring permits, and in June, when historically low or absent occupancy resulted in checks being omitted in some years. No surveys were done in 2020 due to the COVID-19 pandemic. From 2021 onward, we implemented disinfection protocols to enhance biosecurity, in accordance with IUCN guidelines (Shapiro et al. 2024). All bats found during box checks were identified to species following Dietz and Kiefer (2016), and all *P. nathusii* individuals were ringed using 2.9 mm rings

manufactured by the Zoological Society of London and distributed by the Bat Conservation Trust. Ringing was done following best practice guidelines (EUROBATS 2003), and for every recapture, ring condition was carefully assessed, and rings were cleaned or replaced as necessary. For each individual, we recorded sex, age, reproductive status, forearm length, 5th digit length and weight.

To increase capture and ringing efforts and to enable the deployment of Motus transmitters, we conducted two to four targeted trapping sessions annually during spring and autumn migration periods between 2013 and 2024 (excluding 2020–2021 due to COVID-19 restrictions). To capture bats, we used a combination of 3-bank and 2-bank harp traps (TrapR and Austbat), ground mist nets, and on occasion a triple-high mist net system (Bat Conservation and Management, Inc.). Traps were spaced at least 100 m apart, placed mostly adjacent to the lakes in areas with surrounding vegetation cover. We used acoustic lures (AT100, Binary Acoustic Technology and Apodemus Batlure) placed 1–1.5 m above ground alongside the traps to broadcast *P. nathusii* advertisement calls on a continuous 2-second loop, to increase capture effectiveness (Hill et al. 2014). Traps were opened at sunset and checked every 15 min for at least two hours, extending surveys under favourable conditions. Individual processing and biometric data recording were the same as for individuals found in the bat boxes.

### Motus telemetry

After a decade of monitoring the local *P. nathusii* population, we expanded our research to investigate migration patterns via automated telemetry. We joined the Motus Wildlife Tracking System (Taylor et al. 2017) by installing a receiver station on the visitor centre at Bedfont Lakes (51°26'29"N, 000°27'09"W) in 2023. We tagged ten *P. nathusii* with Lotek VHF NanoTags (NTQB2-1; 0.28 g in weight) in April 2023 and an additional two in April 2024. Tagged bats had a mean body mass of 7.8 g (range: 6.9–8.8 g). Adult females were prioritised for tagging, given existing evidence that they undertake longer migratory journeys than males (Petersons 2004), and to address gaps in current UK migration datasets. We captured individuals for tagging either from bat boxes or through trapping efforts as explained above. We affixed the tags, programmed with a 7.1-second burst interval, using Torbot medical adhesive, adhering to established guidelines from EUROBATS (2003). After attachment, we held bats in cloth bags placed over warmers to allow the adhesive to set. Bats caught via trapping were released at the site of capture, while those retrieved from boxes were held until after sunset and released. We confirmed successful post-release flight using handheld Lotek SRX receivers and thermal cameras

(Pulsar Helion 2 XP50 Pro). Tags offered a tracking duration of approximately 40 days.

### Data analyses

All data management, analyses and mapping were done in R (R Core Team 2025). To examine overall numbers, we summarised annual counts of newly ringed individuals and recaptures. Using unique ring IDs, we reconstructed recapture histories to determine recording span (days between first and last capture), number and type of recapture events, and inter-recapture intervals, with descriptive statistics summarised by sex. We plotted individual timelines to illustrate long-term site fidelity and long-distance recoveries, and spatial use of bat boxes was visualised using sex-specific kernel density heatmaps.

Using bat box occupancy data, we assessed roost fidelity at two spatial scales: individual boxes and clusters of nearby boxes ("roosting areas"). We defined roosting areas based on spatial proximity, their placement within distinct clearings or on trees along adjacent sections of trails, and long-term patterns of interchange observed during the 12-year monitoring period. Groupings reflected clusters of neighbouring boxes among which bats were repeatedly observed moving. The assignment of each box to a roosting area is provided in Table S1, and their spatial extent is shown in Fig. S1. This approach reflects bat roosting behaviour, where individuals switch among nearby roosts while maintaining fidelity to a general area (Lewis 1995), therefore, focusing only on box-level analyses may underestimate biologically meaningful fidelity. Fidelity analyses were restricted to individuals with  $\geq 3$  recaptures. Fidelity was scored according to whether an individual returned to the same box or roosting area as in its previous capture (1 = same, 0 = different), and aggregated to obtain individual numbers of returns and transitions. Overall fidelity was estimated using generalised linear models with a binomial error distribution and logit link. Individual variation was tested by comparing a model including individual identity with the intercept-only model using a likelihood ratio test.

To assess how box characteristics influenced box use, we modelled the number of *P. nathusii* per Box  $\times$  Date combination using a negative binomial generalised linear model with a log link in *glmmTMB* (Brooks et al. 2017; McGillicuddy et al. 2025). Year was centred, scaled, and included as a quadratic term. Because boxes occupied by other bat species were unavailable to the focal species, we restricted inference to boxes that were available for use by *P. nathusii* during each check. Box type and orientation were included as fixed effects. To improve model stability and account for the low number of observations within some orientation categories, predictors were simplified: orientations were

grouped as north-facing boxes (N, NNE, NE, and NW), south-facing boxes (S, SE, SSW, and SW), east- and west-facing boxes. Box types were grouped as 2 F-DFP, 1FD, and “other” for rarer box types. A random intercept for Box ID was evaluated but not retained due to singular fits. Model diagnostics were assessed using *DHARMA* (Hartig 2024), marginal means using *emmeans* (Lenth 2025), and pseudo- $R^2$  statistics using *performance* (Lüdtke et al. 2021). As a sensitivity analysis, we also fitted an analogous binomial generalised linear mixed-effects model using presence/absence as the response variable instead of total bat count.

To evaluate microclimate effects, we fitted another model restricted to boxes with dataloggers. Daily temperature and humidity records (mean, min, max, range) were summarised and reduced using principal components analysis (PCA) to two box-level axes (PC1 and PC2) representing combined temperature–humidity gradients, which were included as fixed effects.

To examine seasonal box use, we modelled *P. nathusii* presence during individual box checks using a binomial generalised linear mixed-effects model. Because the timing of box checks varied among years, particularly in summer, month was included as a fixed effect, with box ID and year included as random intercepts. Only months in which monitoring occurred were included in the analyses. Post-hoc pairwise comparisons used *emmeans* (Lenth 2025), with Tukey adjustment for multiple comparisons. Estimated marginal means were used to derive predicted probabilities of box use, with pairwise differences expressed as odds ratios with 95% confidence intervals.

To assess seasonal shifts in sex composition, we fitted a binomial generalised linear mixed-effects model using *glmmTMB*. Analyses were conditional on a box being used by *P. nathusii* and were restricted to spring and autumn. Separate models compared male-only versus female-only boxes and mixed-sex versus female-only boxes. In each model, season was included as a fixed effect (reference: autumn), with year and box ID as random intercepts. Summer was excluded because monitoring effort varied among years and monthly analyses revealed substantial differences in box use between July and August. Model coefficients therefore represent differences in the log-odds ratios of male-only and mixed-sex occupancy relative to female-only occupancy. Wald z-tests and two-tailed p-values were used to evaluate differences.

To quantify associations among individuals, we constructed social networks at the roosting area level, using individuals with sufficient repeated observations to estimate associations reliably (Farine and Whitehead 2015). Associations were defined as individuals co-occurring within the same roosting area during a sampling event. We built a group-by-individual (GBI) matrix and calculated association strengths using the Simple Ratio Index (SRI) in *asnipe*

(Farine 2013). Networks were analysed in *igraph* (Csardi and Nepusz 2006), deriving node-level metrics including degree (number of associates per individual), strength (sum of association weights, reflecting overall connectivity), eigenvector centrality (influence within the network based on connections to well-connected individuals); and network-level metrics including modularity (the extent to which the network is structured into distinct communities) and clustering coefficient (the tendency of an individual's associates to also associate with each other).

To test whether network structure differed from random expectations, we ran 1,000 pre-network permutations using the trial-swap algorithm in *asnipe*, constrained by sampling day and roosting area. Observed metrics were compared to null distributions using two-tailed tests. Networks were visualised using *ggraph* (Pedersen 2022) and *tidygraph* (Pedersen 2023), with node size scaled by degree and nodes coloured by community. Weak edges (SRI < 0.05) were removed for visualisation clarity.

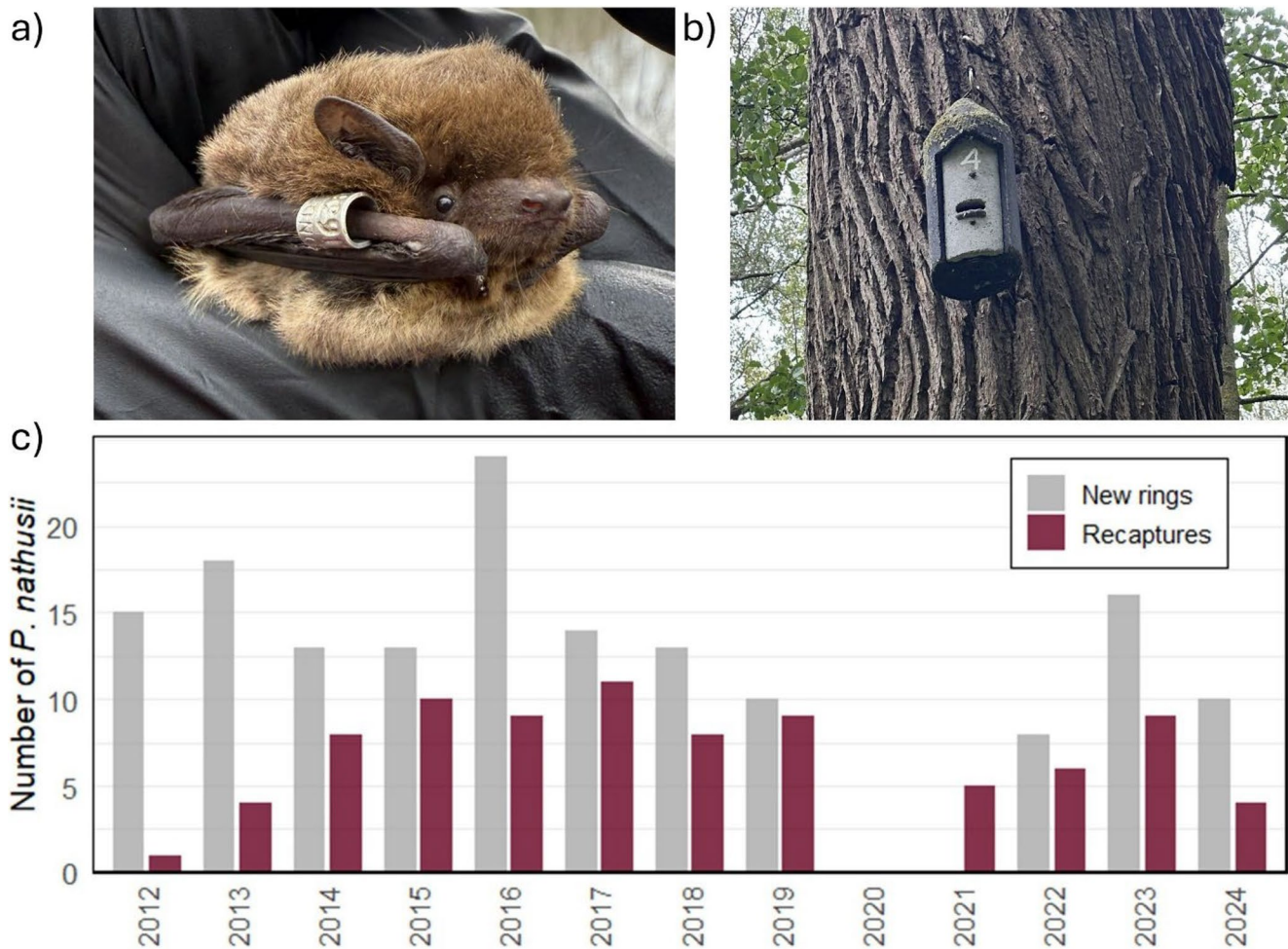
## Results

Between 2012 and 2024, we conducted 90 box checks and 19 trapping sessions at Bedfont Lakes. We ringed 155 *Nathusius*' pipistrelles (69 males and 86 females). Annual numbers of newly ringed bats ranged from 8 to 24 and annual recaptures from 1 to 11, excluding the COVID-restricted years (Fig. 2).

### Ringed bat recaptures

Between 2012 and 2024, 35 males (71.4%) and 14 females (28.6%) ringed at Bedfont were recaptured at least once (timeline in Fig. 3). Notably, female H5223, ringed on 16 October 2016 in a group of seven, was recovered 4.8 years later in Molgino, Russia on 30 July 2021 (Briggs and Briggs 2022), 2,018 km from Bedfont, setting a UK migration distance record. On three occasions, males that were ringed at other UK sites (J6507 at East Molesley, Surrey; J6163 at Long Pit, Dungeness; and, J13265 at Stockers Lake, Hertfordshire/Greater London) were recaptured at Bedfont. The longest recording span amongst these was the Dungeness male, recaptured 6.9 years later.

Several bats showed long-term site fidelity: male J6364 has been followed for 6.1 years (26 Aug 2018–29 Sep 2024), with 21 total recaptures. Males J6134 (30 May 2017–17 Apr 2022) and J6368 (26 Aug 2018–16 Apr 2023) span ~4.7 and ~4.6 years, respectively (Fig. 3). Among females, H1271 (23 Sep 2013–17 Apr 2016; ~2.6 years) and H1266 (3 May 2013–5 Apr 2015; ~1.9 years) are the longest-spanning recaptures so far. Mean intervals between recaptures were



**Fig. 2** Field photographs and summary data from Bedfont Lakes. (a) Male *Pipistrellus nathusii* ringed on the right forearm. (b) Schwegler woodcrete bat box at the study site. (c) Annual counts of *P. nathusii* from 2012–2024, showing the number of newly ringed animals and

recaptures. Data reflect combined totals from monthly bat box surveys and trapping sessions, excluding 2020 when no surveys were conducted due to COVID-19 restrictions

241.3 days for males (range 6–2536) and 433.3 days for females (range 7–1748).

### Box roost occupancy and fidelity

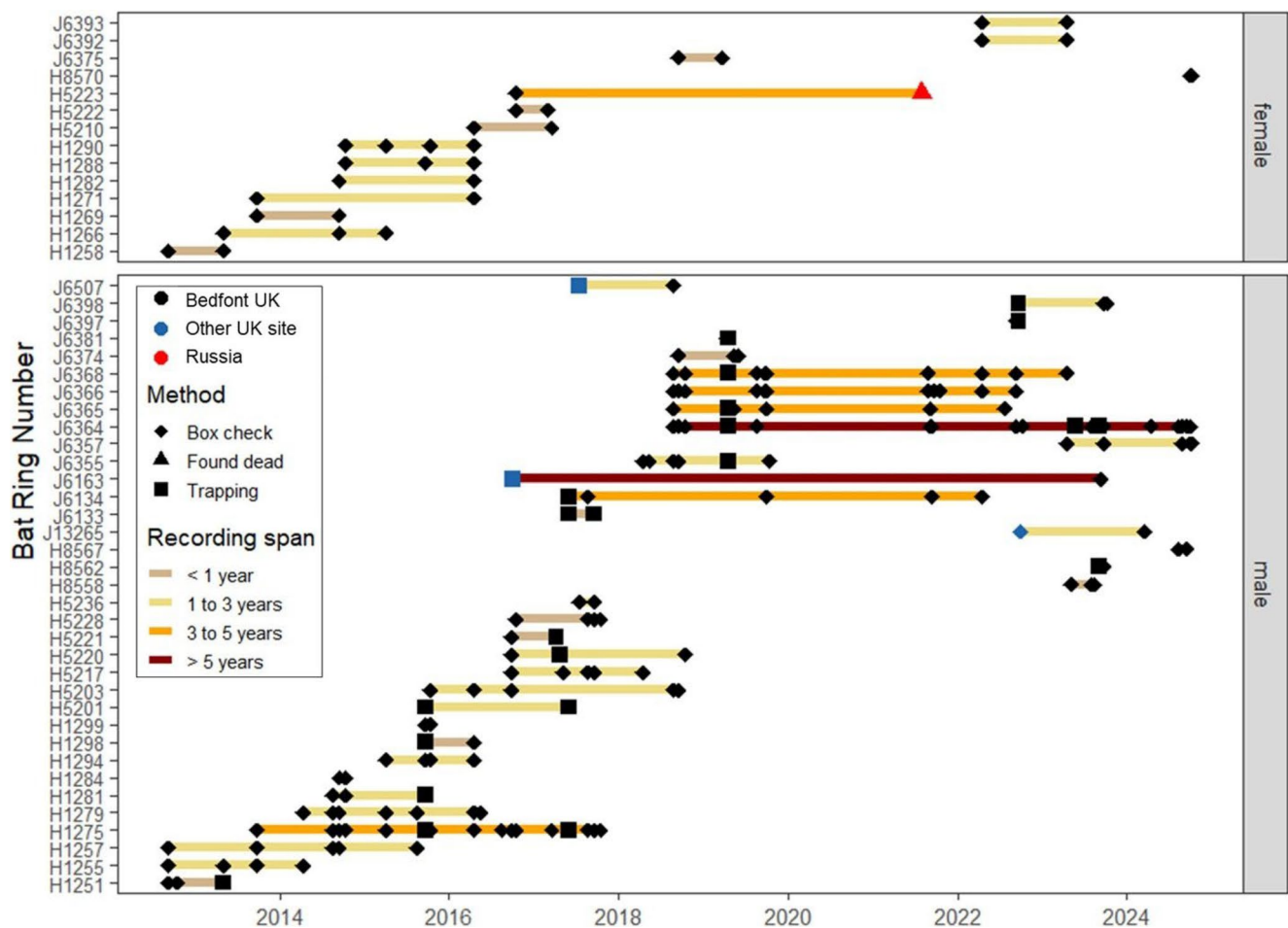
*Pipistrellus nathusii* were detected in every box model except the 2 M, 1B, 2FN and Harlech woodstone bat boxes. Box use was uneven, and most captures were in 2 F-DFP boxes, the most common model on site (Table S1). Box checks revealed diverse social group compositions, with solitary males most frequently encountered, but also mixed-sex groups of varying size and composition (Table 1).

Many individual *P. nathusii* showed high fidelity to certain roosting areas (Fig. 4a), which are detailed in Table S1. Across the 21 individuals with  $\geq 3$  roost records, the probability of returning to the same area between consecutive checks averaged 76.0% (95% CI: 66.8–83.2%), with some approaching 100%. However, in most cases, the underlying

box use showed switching among nearby boxes even when remaining in the same area. Variation in roosting area fidelity among individuals was significant ( $\chi^2 = 42.76$ ,  $df=20$ ,  $p=0.002$ ). In contrast, fidelity to individual bat boxes was lower and more variable (mean=21.2%, 95% CI: 14.4–30.0%), with estimates ranging from 0% to 75%, and no evidence that individuals differed more than expected by chance ( $\chi^2 = 23.11$ ,  $df=20$ ,  $p=0.284$ ). Spatially, females used fewer boxes in high-density clusters (Fig. 4b), whereas male box use was more dispersed and of lower density (Fig. 4c).

### Determinants of bat box occupancy

Box occupancy varied across years and was influenced by box orientation and type (Table S2). West-facing boxes supported significantly higher counts than north-facing boxes ( $\beta = 1.082 \pm 0.367$ ,  $z = 2.95$ ,  $p = 0.003$ ; IRR  $\approx 2.95$ ), whereas



**Fig. 3** Timeline of recapture histories for *Nathusius' pipistrelle* (*Pipistrellus nathusii*) recorded at Bedfont Lakes Country Park, 2012–2024. Each row on the y-axis is a unique individual, arranged by sex (females above, males below). Points mark encounter events, point

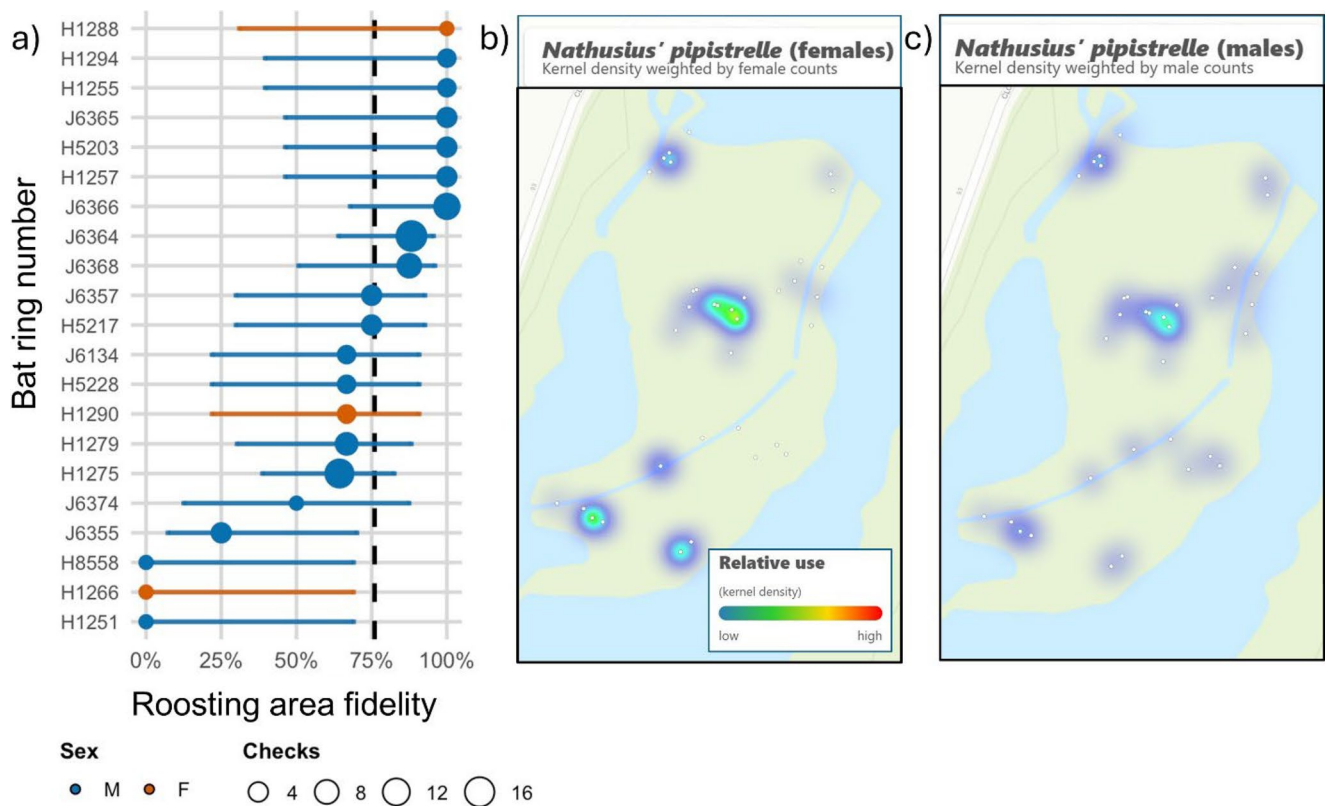
shape indicates the method of recording, and point colour indicates the location. Coloured line segments indicate that individual's total recording span

**Table 1** Summary of observed group compositions of *Pipistrellus nathusii* by sex and number of individuals in bat boxes

| Group Composition       | Occurrences |
|-------------------------|-------------|
| Single Male             | 106         |
| Single Female           | 4           |
| Two males               | 1           |
| Two females             | 3           |
| One male, one female    | 29          |
| One male, two females   | 8           |
| One male, three females | 5           |
| One male, four females  | 2           |
| One male, five females  | 2           |
| Two males, five females | 1           |
| Three males, one female | 1           |
| Four males, one female  | 1           |

east- and south-facing boxes did not differ significantly from north-facing boxes (east:  $\beta=0.406\pm0.304$ ,  $z=1.34$ ,  $p=0.181$ ;  $IRR\approx1.50$ ; south:  $\beta=0.092\pm0.218$ ,  $z=0.42$ ,  $p=0.674$ ;  $IRR\approx1.10$ ). Pairwise comparisons similarly

showed higher counts in west-facing boxes compared to north- and south-facing boxes, while no other contrasts were significant. Relative to 2 F-DFP boxes, 1FD boxes supported higher bat counts ( $\beta=0.844\pm0.370$ ,  $z=2.28$ ,  $p=0.023$ ;  $IRR\approx2.33$ ) whereas other box types (grouped) supported fewer bats ( $\beta=-2.769\pm0.473$ ,  $z=-5.85$ ,  $p<0.001$ ;  $IRR\approx0.06$ ). The contrast between 2 F-DFP and 1FD was weaker in the pairwise comparisons, but both 2 F-DFP and 1FD supported significantly higher counts than the pooled “other” category. Results from the model using presence/absence as the response variable were concordant with the count model (Table S3). Occupancy was higher in west-facing than north-facing boxes ( $\beta=1.000\pm0.500$  SE,  $z=2.00$ ,  $p=0.045$ ), while boxes in the “other” category had lower occupancy than 2 F-DFP boxes ( $\beta=-2.413\pm0.496$  SE,  $z=-4.86$ ,  $p<0.001$ ). Occupancy did not differ significantly between 1FD and 2 F-DFP boxes ( $\beta=0.874\pm0.496$  SE,  $z=1.76$ ,  $p=0.078$ ). The subset model that included datalogger data showed that neither microclimate PC1 nor PC2 was



**Fig. 4** Roost fidelity and spatial use of *Nathusius' pipistrelle* (*Pipistrellus nathusii*) at Bedfont Lakes, 2012–2024. **(a)** Individual roosting area fidelity: points show the estimated fidelity (probability of returning to the same area) with 95% confidence intervals. The dashed line marks the overall population mean, and point size reflects the number of

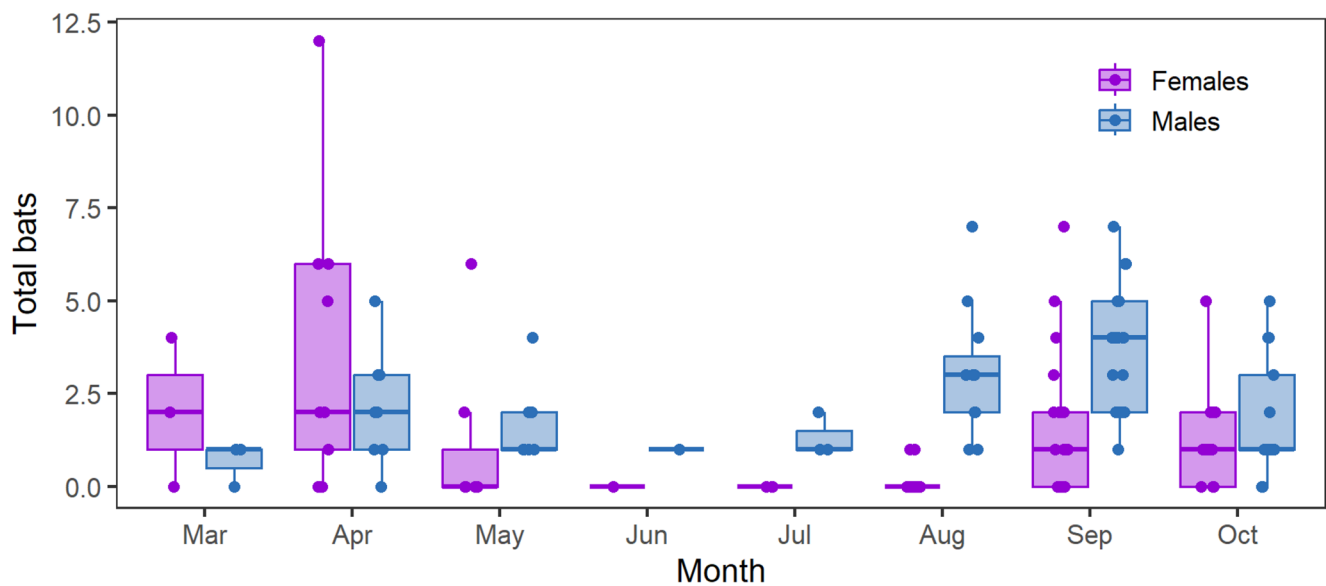
records per bat. Only bats with  $\geq 3$  checks are included. **(b–c)** Kernel-density heatmaps of relative box and area use based on the number of *P. nathusii* recorded per box: **(b)** females only, **(c)** males only. Warmer colours indicate higher relative use; white circles mark box locations

associated with bat abundance (PC1:  $\beta=0.048$ ,  $p=0.684$ ; PC2:  $\beta=0.278$ ,  $p=0.154$ ; Table S4).

### Seasonal patterns in bat box occupancy

Records of bat box occupancy at Bedfont Lakes varied strongly across the active season (Fig. 5). In March, records of *P. nathusii* were rare, with just eight individuals recorded over the study period (6 females, 2 males). More individuals were recorded during April checks, (53 individuals; 34 female, 19 males), compared with May (20 individuals; 8 females, 12 males). Records of *P. nathusii* were typically low or absent in June and July, and boxes were therefore not checked during these months in all years. In late summer and autumn, records were higher, with 36 individuals recorded in August (2 females, 34 males), and the highest number of records occurring in September (94 records; 30 females, 64 males). In October 40 individuals were recorded (16 females, 24 males). Group size also differed among months, with the largest aggregations (up to 6–7 bats) observed during checks in April, September, and October, whereas smaller clusters were more typical in May and August.

Because timing of box checks varied among years, particularly during the summer, temporal variation in box use was analysed by month rather than by pooling observations into broad seasons. Relative to March, occupancy probability was significantly higher in April ( $\beta=1.027 \pm 0.510$  SE,  $z=2.01$ ,  $p=0.044$ ), August ( $\beta=1.451 \pm 0.498$  SE,  $z=2.91$ ,  $p=0.004$ ), and September ( $\beta=1.845 \pm 0.486$  SE,  $z=3.80$ ,  $p<0.001$ ). Occupancy did not differ significantly from March in May, June, July, or October (Table S5). Sex composition shifted markedly between spring and autumn (Table S6). Relative to autumn, the probability of male-only occupancy was significantly lower in spring ( $\beta=-3.310 \pm 1.130$  SE,  $z=-2.94$ ,  $p=0.003$ ), corresponding to 27.3-fold higher odds of male-only versus female-only box use in autumn than in spring. Similarly, the odds of mixed-sex occupancy rather than female-only box use were significantly lower in spring ( $\beta=-2.620 \pm 1.150$  SE,  $z=-2.28$ ,  $p=0.023$ ), corresponding to 13.7-fold higher odds of mixed-sex versus female-only box use in autumn. These results indicate a pronounced seasonal shift in roost composition, with female-only groups occurring more frequently in spring, whereas male-only and mixed-sex boxes predominated in autumn.



**Fig. 5** Monthly counts of female and male *Pipistrellus nathusii* recorded during bat box checks at Bedfont Lakes Country Park between 2012 and 2024, covering the active season from March to October

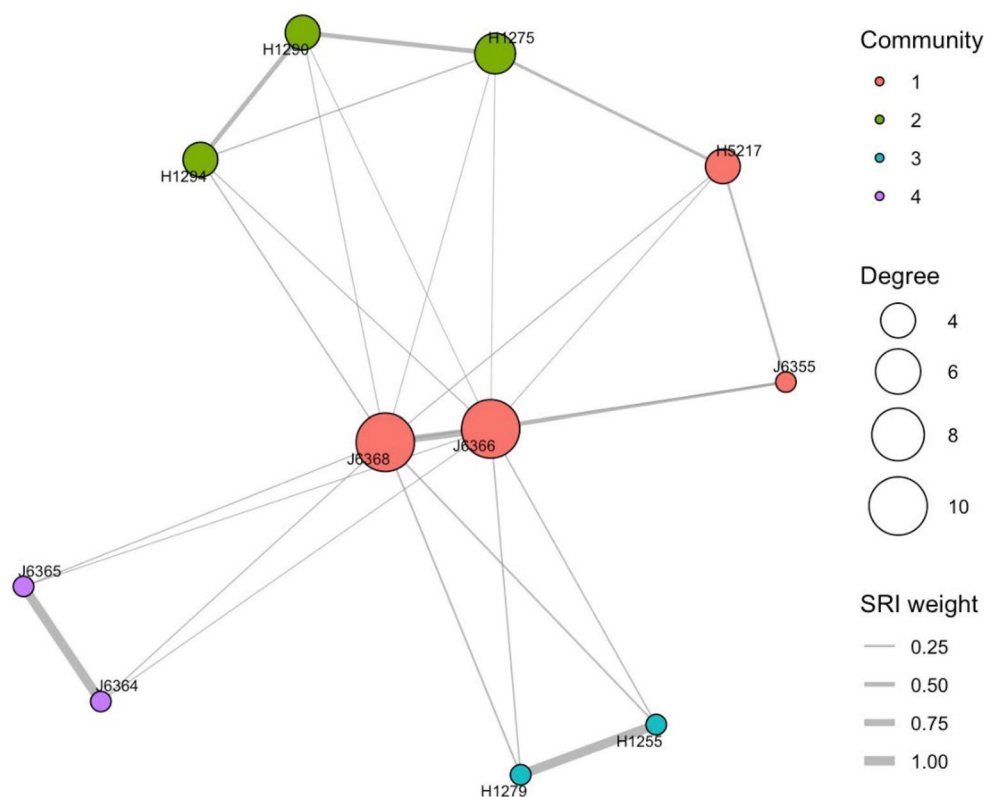
### Social network structure at the area level

The network of individuals with  $\geq 4$  observations included 11 bats across 16 observation events. Association strengths were generally low (mean SRI=0.133, median=0), with 26 non-zero edges, indicating a sparse network characterised by many weak associations (Table S7). Despite this, the network showed high clustering (average clustering

coefficient=0.85), indicating that individuals tended to associate within localised groups. Although modularity was moderate (0.39), suggesting some degree of community structure, it did not differ from random expectations ( $p=0.10$ ).

Community detection identified multiple clusters, including one more connected central group and smaller peripheral groups (Fig. 6). Network structure was centred

**Fig. 6** Social network of bats at the area level based on co-occurrence within roosting areas. Nodes represent individual bats and edges represent association strength (SRI) which reflects proportion of co-occurrences relative to the number of observations. Edge width is proportional to association strength, node size reflects degree, defined as the number of individuals a given bat is associated with, and node colour indicates community membership. Only edges with  $SRI \geq 0.05$  are shown for visualisation clarity



on two individuals (J6366 and J6368), which had the highest degree (10 connections each), strength, and eigenvector centrality, indicating a key role in network connectivity. Most other individuals had lower degree (3–5 connections) and strength and formed more peripheral nodes within smaller clusters.

Permutation tests indicated that degree and strength did not differ from random expectations (most  $p \approx 1$ ), which likely reflects limited variation in the null distributions, driven by the relatively small number of multi-individual observation events and the overall sparsity of the dataset. In contrast, eigenvector centrality was higher than expected for several individuals (e.g. H1275, H1279, H1294, H5217, and J6355;  $p < 0.05$ ), suggesting that some bats occupied more central positions within the network than expected by chance. Overall, these results suggest that the observed network structure is largely driven by spatial and temporal overlap, with limited evidence for strong preferential associations, although some individuals may play disproportionately central roles.

## Migration patterns

Motus radio telemetry data provided clear evidence of extensive migratory movements by *P. nathusii* tagged in the UK (Fig. 7). In 2023, of the ten bats tagged (nine females, one male), six remained local to Bedfont Lakes, while four undertook long-distance movements (Table S8). One female (J6392, tag 94) was tracked across six Motus stations over three weeks, eventually reaching Germany. Another (H8555, tag 95) was last recorded on the Suffolk coast, with no subsequent detections on the continent.

Both females tagged in 2024 were detected outside of Bedfont (Fig. 7; Table S8). H8560 (tag 186) was detected at Sylt on the German/Danish border on 5 June 2024, despite no intermediate detections along the UK coastline. H8559 (tag 185) was recorded at the Sandwich Bay Motus station on 10 May 2024 (Fig. 7). Overall, half of the tagged bats (all females) demonstrated migratory movements across or toward continental Europe within weeks of release.



**Fig. 7** Migration routes of Nathusius' pipistrelle (*Pipistrellus nathusii*) tagged at Bedfont Lakes, UK, and subsequently detected by the Motus Wildlife Tracking System. Each line connects the capture site

at Bedfont Lakes to subsequent detection stations across Europe, with colours distinguishing individual bats and their Ring numbers shown in the legend

## Discussion

This long-term study provides a detailed account of the roosting ecology, seasonal dynamics, and migratory behaviour of *P. nathusii* at a UK bat box site. Twelve years of monitoring show that Bedfont Lakes is used by both migratory individuals and by bats that maintain prolonged associations with the site, adding individual-level evidence to previous studies documenting resident and migratory components of the UK population (Russ et al. 2001; Russ 2022). Repeated recaptures demonstrate prolonged associations with the site, while recoveries outside the UK, including a movement of over 2,000 km to Russia, confirm connections with wider European populations. Together, these findings highlight how sustained, site-based monitoring can reveal patterns of site fidelity and migration that would be difficult to detect through shorter-term studies.

Bat box use at Bedfont Lakes was highly dynamic within and between years, potentially reflecting a combination of local population changes, weather conditions, immigration from surrounding regions, or broader migratory movements. Such variability is consistent with the flexible life history of migratory bats, whose local abundance is influenced not only by habitat suitability, but also by large-scale movement dynamics (Fleming and Eby 2003). Box check data should nevertheless be interpreted cautiously because they provide only snapshot detections (Jonker et al. 2025), and cannot detect individuals using alternative roosts such as in tree cavities. Repeated detections of the same marked individuals across multiple years, however, demonstrate genuine sustained association with the site.

Recapture histories revealed marked variation in site persistence. Most *P. nathusii* were detected only briefly, but several males were repeatedly recaptured over multiple years, including one recorded 21 times over more than six years. Although females comprised slightly more newly ringed individuals (86 females versus 69 males), males accounted for 71.4% of subsequent recaptures and were generally encountered at shorter intervals. This is consistent with known sex-specific differences in movement, with females undertaking extensive seasonal migrations, whereas males remain relatively sedentary during the mating period and show fidelity to mating roosts or areas (Petersons 2004; Jahelková and Horáček 2011; Alcalde et al. 2021; Vasenkov et al. 2022). This interpretation is also consistent with our telemetry results, in which all detected long-distance movements involved females, whereas the single tagged male remained local. Bedfont may therefore be used by both transient migrants and more site-associated individuals, as reported elsewhere in Europe (Ciechanowski and Jarzembowski 2009; Lagerveld et al. 2024). However, because recapture probability was not explicitly modelled,

the greater frequency of male recaptures should be interpreted as consistent with sex-specific differences in site use rather than direct evidence of greater male site fidelity.

Fidelity to individual boxes was low, consistent with widespread roost-switching behaviour in temperate bats (Lewis 1995; Kerth and Reckardt 2003), which is thought to reduce predation risk, parasite load, and competition while allowing individuals to track microclimatic conditions and ephemeral resources. In contrast, fidelity to broader roosting areas was substantially higher, with individuals consistently returning to the same roosting area despite switching among individual boxes. This suggests that *P. nathusii* use spatially cohesive roost networks rather than maintaining strong fidelity to individual roosts (Kerth and König 1999; Willis and Brigham 2004). Significant individual variation in roosting-area fidelity may reflect differences in sex, condition, or behavioural strategy, including the establishment and defence of mating territories or repeated use of particular areas by males (Hutterer et al. 2005; Russ 2022). Thus, while *P. nathusii* exhibits low fidelity to individual roosts, it maintains stronger attachment to localised roosting areas, and certainly to the overall site.

Box characteristics also influenced use. West-facing boxes supported higher counts than north-facing boxes, potentially because greater afternoon sun exposure provides more favourable thermal conditions (Fontaine et al. 2021; Willemsens et al. 2025). Although temperature and humidity inside the boxes were not significant predictors of occupancy, this result should be interpreted cautiously given the small, non-random subset of boxes monitored for microclimate, which may not capture the full range of conditions across the box network. Box design also influenced occupancy, with 1FD models supporting the highest counts, while 2 F-DFP boxes also supported higher numbers than the pooled “other” category. However, uneven representation of box types limits inference, and further work with balanced designs is needed to disentangle structural preferences from sampling effects.

Social organisation varied from solitary males - the most frequent aggregation type - to mixed-sex groups and occasional all-female groups. Male-only use was particularly prevalent during late summer and early autumn, consistent with male territoriality and seasonal harem formation (Baranauskas 2009; Lagerveld et al. 2024). Mixed-sex groups, often consisting of a single male and multiple females, suggest that boxes may function as mating roosts. This interpretation is supported by the pronounced seasonal pattern in box use, which increased in late summer and peaked in September, coinciding with autumn migration and mating activity. In contrast, occasional female-only groups in spring may represent females using the site temporally during migration before moving to maternity areas

elsewhere. These patterns are consistent with known sex-specific migratory and reproductive strategies described for *P. nathusii* (Flaquer et al. 2005; Alcalde et al. 2021), and with a mating system in which males may defend roosts or associated territories and attract multiple females (Jahelková and Horáček 2011).

Social networks were sparse, with generally weak associations among individuals. Although clustering was high, modularity did not exceed random expectations, and degree, strength, and overall network structure showed little evidence of non-random social organisation. Some individuals had higher-than-expected centrality, but overall the results suggest that associations primarily reflect spatial and temporal overlap within shared roosting areas rather than active social structuring (Farine 2013, 2017). This is consistent with the fluid social organisation and frequent roost switching observed in many temperate bats (Kerth and Reckardt 2003; Willis and Brigham 2004).

Movement data extended these local patterns to much broader spatial scales. The recovery of a Bedfont-ringed female *P. nathusii* in Molgino, Russia - over 2,000 km from its original capture site - represents one of the longest documented bat movements in Europe and confirms transcontinental connectivity between UK sites and north-eastern European breeding grounds (Russ 2022). Additional recaptures of males originally ringed at other UK locations demonstrate interchange within national populations. Automated telemetry additionally detected cross-sea movements of tagged females towards continental Europe, providing information on the timing and direction of movements that ringing alone cannot resolve. Given the small number of tagged individuals, however, these observations should be considered indicative rather than representative of population-level movement patterns, and further tracking across individuals and years is needed to determine the generality of the movements observed here. Unpublished stable isotope data from Bedfont have also suggested variation in likely geographic origins of individuals using the site, with some showing isotopic signatures consistent with local or regional origins and others with more distant origin in northern or eastern Europe (BSG Ecology 2014). Although these data should be interpreted cautiously, they provide complementary context for local and long-distance movements documented here through ringing and telemetry. Stable isotope approaches have similarly been used to investigate geographic origins and migratory pathways of *P. nathusii* elsewhere in Europe (Kruszynski et al. 2021).

This study demonstrates the value of integrating multiple long-term approaches - ringing, box monitoring, and telemetry - to uncover complex ecological strategies in a migratory bat. Each method carries inherent limitations: Box checks sample only intermittently and may underestimate

true occupancy, Motus detections depend on receiver coverage and tag retention and ethical constraints limit recapture intensity due to the need to balance data collection with disturbance. Despite these constraints, the longitudinal nature of the dataset enabled the detection of rare but ecologically significant processes, including site fidelity, seasonality dynamics, and long-distance movements. Such insights are unlikely to emerge from short-term studies and highlight the need to maintain long-term monitoring frameworks.

An important limitation is that these data derive from a single site, and patterns observed at Bedfont Lakes should not be assumed to represent *P. nathusii* populations elsewhere in the UK or across its range. Bedfont represents a highly managed, urban fringe wetland with an established network of artificial roosts, and characteristics of this setting may influence patterns of occupancy, site fidelity, sex ratios, seasonal use, and social interactions. Comparative long-term data from other sites across the species' range are needed to determine the extent to which the patterns observed at Bedfont Lakes are general features of *P. nathusii* ecology. Nevertheless, the 12-year dataset provides temporal resolution rarely available for this species, while ring recoveries and automated telemetry extend inference beyond the study site and demonstrate that at least some individuals using Bedfont Lakes are connected to populations and migratory movements operating over much broader geographic scales.

From a conservation perspective, these findings highlight the importance of sustained monitoring for migratory bats. *Pipistrellus nathusii* may encounter multiple anthropogenic pressures as individuals move across habitats, countries, and jurisdictions, including habitat loss and risks associated with wind-energy development (Voigt et al. 2015; Lagerveld et al. 2023, 2024). Protecting important habitats such as wetland complexes, riparian zones, and reservoir systems therefore needs to be considered alongside maintaining ecological connectivity and coordinating conservation across national borders. Long-term roost monitoring contributes demographic and behavioural information that is difficult to obtain through other methods, including survival, dispersal, and individual life histories derived from recaptures (Ruegger 2016).

The full value of such schemes is stronger in combination with larger research efforts. As demonstrated here, combining bat box and roosting area monitoring with ringing and automated telemetry provides a more complete understanding of bat ecology and migratory behaviour. Expanding the Motus network both at inland sites and along the southern and eastern coasts of the UK would substantially improve detection of onward movements, help distinguish resident from migratory individuals, and better delineate key migratory gateways. Such collaborative infrastructures are essential for capturing movements that extend beyond national

borders and identifying periods of heightened vulnerability, such as spring and autumn migration peaks. The UK's participation in international frameworks such as EUROBATS and the Agreement on the Conservation of Populations of European Bats (UNEP/EUROBATS) is strengthened by long-term datasets like those from Bedfont Lakes, which provide the empirical foundation to inform transboundary conservation policy. Coordinated monitoring along the species' flyway will be critical for developing evidence-based strategies for migration-safe infrastructure, and the protection of key stopover habitats.

In conclusion, twelve years of integrated monitoring show that *P. nathusii* using Bedfont Lakes in the UK cannot be characterised as purely transient or resident, but instead exhibits a complex interplay of seasonal settlement, mating aggregation, and long-distance migration. The coexistence of resident males, transient females, and mixed roosting groups highlights the multifaceted role that artificial roost networks such as Bedfont Lakes can play within wider migratory systems. Continued investment in long-term monitoring, international collaboration, and technological integration will be essential to advance conservation of this species across its flyways. In the context of expanding wind energy and accelerating environmental change, understanding the movement ecology of migratory bats is not only a research priority but a conservation imperative.

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**Author contributions** Patty Briggs: Conceptualisation, Methodology, Investigation, Resources, Data curation, Writing – Original draft, Funding acquisition, Project administration; Brian Briggs: Conceptualisation, Investigation, Resources, Writing – Review and editing;

Huma Pearce: Methodology, Investigation, Resources, Data curation, Writing – Review and editing; Maria Sagot: Methodology, Formal analysis, Investigation, Visualisation, Writing – Original draft; Cecilia Montauban: Conceptualisation, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – Original draft, Visualisation, Supervision.

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**Data availability** Data available upon request to the corresponding author.

## Declarations

**Ethics statement** All bat species are protected in the UK, and all fieldwork was conducted under licences issued by Natural England (2025-84552-CL19/20-BAT & 2023-66463-SCI-SCI *Nathusius* Project). Bat capture, handling, ringing, and tagging procedures followed established best-practice guidelines of the Bat Conservation Trust and EUROBATS. From 2021 onwards, enhanced biosecurity procedures were implemented in accordance with IUCN SSC Bat Specialist Group field hygiene guidelines.

**Competing interests** The authors declare no competing interests.

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