



# Foraging fidelity and individual specialisation in a temperate bat *Myotis nattereri*

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## Abstract

This study explores whether Natterer's bats exhibit fidelity to their foraging sites and individual specialisation in their use of habitat types. The research tracked 34 individual bats in two different landscapes, with some bats tracked twice over varying time intervals. The study found that Natterer's bats show consistency in their fidelity to foraging sites across different landscapes and intervals between observations. The bats repeatedly exploited specific foraging areas, and some showed individual specialisation in their habitat use. The study also found considerable variation in individual behaviour. The research suggests that a single full night of radio-tracking data can serve as a useful proxy for longer periods and contribute to more robust descriptions of resource requirements by Natterer's bats in their breeding seasons. This study emphasises the importance of maximising the number of individuals from which movement data is obtained to inform conservation and management of temperate bats, whilst ensuring that the data represent a meaningful measure of behaviour. The results also suggest that protecting a mosaic of habitats rather than a single habitat may be important for Natterer's bats, given their individual specialisation in habitat use.

**Keywords** Habitat use · Natterer's bat · Territoriality · Site fidelity · Summer colony

## Introduction

Bats in the UK face many anthropogenic threats including habitat loss and mortality caused by wind turbines (Arnett et al. 2016; Baerwald et al. 2008; Cryan and Barclay 2009; Horn et al. 2008; Rydell et al. 2010; Zimmerling and Francis 2016) or roads (Altringham and Kerth 2016; Berthinussen and Altringham 2012; Kitzes and Merenlender 2014; Lesiński 2008). Threats can also affect their roosts, reduce or degrade available foraging habitat or interfere with the connectivity between habitats (Mickleburgh et al. 2002). The long history of bat population decline coupled with the wide diversity of threats to bats has led to their current protection under national legislation in the UK, primarily the conservation of habitats and species regulations 2019 (UK Government 2019).

Favourable Conservation Status (FCS), an underpinning principle of the Conservation of Habitats and Species Regulations 2019, requires information on the natural range and use of space of a species in order to protect them (UK Government 2019). Only then can an assessment of the size and viability of a population be made, as well as an assessment of the requirements of the resources the species needs to remain viable (Hillen et al. 2009). However, determining habitat types required for effective conservation of bats can be difficult due to their ability to fly long distances. For example, in summer, bat roosts and foraging sites can be kilometres apart allowing individuals to access a wide range of habitats across extensive landscapes (Rainho and Palmeirim 2011). This can make it difficult for field workers to maintain observations of their habitat use.

Since the conservation of roost sites is important for the maintenance of bat populations, e.g. (Kapfer et al. 2008), roost provision or the mitigation of roost loss is already common in the management of bat populations. In addition to this, many species use a network of roosts which increases the resilience to the loss of a few roosts (August et al. 2014; Johnson et al. 2012; Rhodes et al. 2006; Silvis et al. 2015). Conversely, bats appear loyal to their foraging sites despite

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roost loss (Dawo et al. 2013; Silvis et al. 2015). Hence, the conservation of foraging sites may be even more important than that of roost sites in the conservation of bats, although this is rarely considered. This is of some concern, especially as determining priorities for FCS requires a robust understanding of bats use of space.

It is not clear why some bats appear loyal to their foraging sites/exhibit foraging site fidelity (Hillen et al. 2010; Kapfer et al. 2008), nor if this behaviour is specific to temperate forest bats or if it is a more general behaviour found in other bat species. Egert-Berg et al. (2018), showed that bats exploiting spatially predictable food sources repeatedly returned to specific productive sites. Male *Noctule* bats *Nyctalus noctula* have also shown repeated use of the same foraging strategy (foraging trajectories and areas) (Roeleke et al. 2016). In addition, Kerth et al. (2001) suggest that foraging site knowledge could be a crucial resource which has been suggested to increase hunting efficiency (Kapfer et al. 2008). Other possible reasons why bats exhibit foraging site fidelity include saving energy; foraging animals are expected to make choices in order to minimise energy expenditure whilst maximising energy intake (Arthur et al. 2015). For example, a previously used beneficial habitat may have a higher probability of providing sufficient resources than an unexplored new habitat (Call et al. 2008). An additional suggestion is that site fidelity may be an evolutionary safety strategy to avoid resource depletion and to lead to reliable available food sources for every colony member throughout the season or years (Dawo et al. 2013).

Recently, the idea of bats exhibiting foraging site fidelity has been extended, to suggest that it may be a result of the territorial defence of feeding areas through the use of social calls (Gadziola et al. 2012; Götze et al. 2020; Guo et al. 2019; Luo et al. 2017). Territorial defence of feeding areas is thought to minimise feeding competition (Wrangham 1979), maximise feeding efficiency through familiarity with the distribution of food resources (Hillen et al. 2009; Pusey et al. 1997), or directly impact reproductive success (Thompson et al. 2007). Foraging site fidelity or territoriality could therefore have significant impacts on conservation and management objectives when used in combination with tools and measures to describe bats use of space. Studies to support bat conservation may therefore need to shift from general descriptions of species habitat preferences and the assumptions that as long as these habitats are accessible FCS can be maintained, to considering other aspects of behaviour, such as foraging site fidelity or individual specialisation (Araújo et al. 2011).

Bats, like many other mammals, may have individual habitat preferences (Araújo et al. 2011; Cryan et al. 2012) and this may be influenced by their social status. For example, dominant females may have preferential access to the best resources (Honer et al. 2010), inheritance of

foraging sites (Mackie and Racey 2007) or resources (Dawo et al. 2013) may occur, or individuals might exhibit territoriality or personality traits (Patrick and Weimerskirch 2014) which affects their access to foraging areas. Sexual segregation may also occur where females exclude males from the more profitable habitats (Angell et al. 2013). Alternatively, foraging variation may occur due to individual specialisation, such that individuals differ significantly in their prey or habitat utilisation, independent of class effects (Bolnick et al. 2002).

Individual specialisation has important evolutionary (Bolnick et al. 2002), ecological and management implications as it implies that interactions between individuals and their environment are not uniform across a landscape (Thiemann et al. 2011). If bats do exhibit individual specialisation in their habitat choice, then there might not be a preferred habitat per species as often asserted by the literature, e.g. (Arlettaz 1999; Catto et al. 1996; Robinson and Stebbings 1997; Russo et al. 2002), but instead a mosaic of habitats may be critical to their conservation. Therefore, the influence individual expressions of behaviour may have on our understanding of species requirements should be accounted for in measures of resource use and be considered in conservation planning and management.

Here the aims were to produce robust descriptions of individual bats' foraging sites and descriptions of the habitats they use, to explore the fidelity individual bats show in their foraging behaviours (repeated use of foraging site, distance travelled) and to determine whether Natterer's bats in this study show individual specialisation in their use of foraging habitats.

## Materials and methods

### Study sites

Natterer's bats (*Myotis nattereri*) were caught from two different summer communities, a roost in a church at Low Catton, East Yorkshire, UK (53.98° N, 0.93° W: altitude 15 m) in 2003 (May–August), and from woodlands on the Wallington Estate, Northumberland, UK (55.15° N, 1.96° W: altitude 160–200 m) between 2013 and 2015 (May–September). Low Catton is a very small rural village in a mixed agricultural landscape typical of lowland England, consisting of mainly arable land with some pasture and small scattered parcels of woodland. Wallington Estate is a patchwork of parkland, lakes, and woodland, within a mixed pastoral landscape, including arable and woodland parcels as well as open moorland, typical of an upland agricultural landscape in England.

## Bat capture and radio tracking

Bats were caught on an approximately weekly schedule at roosts using a static hand net or harp trap (on an extendable pole). The frequent roost switching behaviour of the bats at Wallington also required their capture from free flight, using mist nets or harp traps and an acoustic lure. As most of the bats were caught from roosts, predominantly female bats were caught and tracked due to temperate bat maternity roosting behaviours during the summer.

The capture, handling and marking of bats were carried out under annual licence from Natural England (e.g. 2014–6454-SCI-SCI) and all work was approved following ethical review. Captured bats were described noting sex, age (adult/juvenile), reproductive condition (pregnant, lactating, post lactating and non-reproductive; by palpation of the abdomen and identification of hairless nipples on females), forearm length (0.1 mm), weight (to 0.1 g), and any existing mark. Unmarked bats were marked with a unique ring (2.9 mm alloy; BCT, England). Bats were selected for tracking based on their age; when adults were caught, they were selected over juveniles. Selected bats were fitted with radio transmitters (Pip AG317; Biotrack, Dorset, England) attached to the skin between the scapulae using a hypoallergenic dermal adhesive. A small patch of fur was trimmed at the point of attachment to ensure reliable adhesion. A maximum of two bats were marked with transmitters in one tracking session to ensure that a complete and continuous night of data could be collected from all deployed tags within their short battery life (7–10 days).

Individual bats were usually radio-tracked by single workers using the close approach method (White and Garrott 1990) and a Telonics TR-4 receiver (Telonics, Arizona, USA) attached to three-element flexible Yagi antenna or vehicle mounted omni-directional antennae (Kenward 2001). Bats were tracked to and from roosts (i.e. emergence until return), with their locations recorded at 10-min intervals. An ‘observation’ throughout his manuscript will refer to an individual bats’ recorded location. Ten-minute intervals were selected for observations to prevent temporal correlation between consecutive fixes whilst still observing regular movement patterns (Kenward 2001).

Due to the difficulty in obtaining triangulations from fast flying animals (Mackie and Racey 2007) especially across undulating terrain (e.g. Wallington), approximate locations of bats were inferred using the null points, signal strength, and variation in signal amplitude with workers trained to estimate transmitter distance into broad distance categories using practice tags at a range of distances. An estimate of the space within which the bat was known to be moving (a polygon) was marked on a detailed map. Rather than estimate a point considered to be the location of a bat in time with some measure of spatial error,

our approach described a wider area within which the bat was known to be. The shape and size of each observation also capture the unique context of the observer’s location relative to the bat as well as elements of the landscape which might add information by modifying the signal (e.g. attenuators such as dense woodland). By constantly moving, analysis can combine unique observations of a bat exploiting even a small patch to identify precisely where the bat is spending time.

The more traditional approach of description using triangulated points, which uses only a bearing (prone to considerable error), was impractical and costly, requiring at least two workers to co-ordinate effort (constant communication to ensure agreement on approximate location of bat, as well as ensuring a sufficient separation of bearings) for little apparent gain in precision.

Tracking was undertaken in two phases. In phase one, priority was given to simply maintaining contact with the bat and capturing its general foraging strategy (i.e. commuting routes, approximate location of its favoured foraging patches and a loose schedule of behaviour). Trackers commonly stayed closer to access routes and vehicles to ensure a rapid response to unexpected bat movement, though this often resulted in more uncertain estimates of location. In the second phase, trackers planned to optimise the quality of data by anticipating bat behaviour and committing themselves to closer approaches on foot where this was possible. However, the intention was always to ensure continual contact with the bat throughout its period of activity (at 10-min intervals). Data was only collected from tracking in the second phase of work for every bat, and bats were followed repeatedly until a single complete night of data was acquired. Phase one tracking often took 2–3 nights (e.g. to establish tracking strategies for bats travelling long distances quickly or those traversing difficult to cross barriers in the landscape such as rivers) and at least one additional night of effort to secure a complete, continuous, and uninterrupted night of foraging data. Different workers were used to establish general foraging strategies (phase one tracking), especially where a number of bats were tagged simultaneously. However, the same worker (SM at Wallington, JA at Low Catton) undertook all data collection during phase two to ensure a consistency in the inference and the confidence of its observation. Nights of tracking data with continuous gaps of more than 20 min were excluded from the analysis. All roost positions were recorded using a handheld GPS device. Observations were digitised using ArcGIS (v.10.2; ESRI) with subsequent analysis carried out in R (v. 2.1) (Team 2013). Some bats were retracked at varying intervals, with data presented here including the deliberate retracking of bats over subsequent days (using the same radio transmitter), or at greater intervals where they were incidentally recaptured, either within a summer season or between years.

Foraging cores representing areas of high use were described for each complete bat-night. Observations were transformed into point clouds by placing a single spatially randomised point into each polygonal observation. For each single night of data, areas of high use were then identified using a non-parametric clustering approach, *clusthr* function in *adehabitatHR* (Calenge 2006): 95% inclusion. The randomisation method was repeated five times and the resulting polygonal clusters were then intersected to find the areas common to all iterations (*gIntersection* function in *rgeos*) (Supplementary Fig. 1). These clusters, hereafter foraging cores, are the statistical unit in all subsequent analyses and represent the product of a complete night of foraging by a single bat and are discrete patches (often > 1 per night) that include the centres of high-density use presumed to be the area most exploited by that bat on that night.

## Data analysis

### Exploring habitat use

The habitats most used by bats were identified by pairwise quantitative comparisons of proportions of habitat types within foraging cores, undertaken using compositional analysis using the *compans* function in the *adehabitatHR* package (Calenge 2006). The area of habitat types in each bat's foraging core was compared to that in the 'available foraging area', defined here by combining all observations for each community (Low Catton or Wallington) and creating a community minimum convex polygon (MCP). Categorical descriptions of habitat types were taken from LCM2007 (Morton 2011) land cover map (Table 1). The proportional use of different habitat categories within each community MCP was then compared.

To quantify individual specialisation of habitat use, Roughgarden's index (1972) was used which compares within-individual components of niche width (WIC) to the total niche width exhibited by a population (TNW). Calculations of WIC and TNW were carried out using the R package *RinSp* using the 'PSicalc' function (Zaccarelli et al. 2013). For each individual, the proportional similarity

index ( $PS_i$ ) was calculated following Fodrie et al. (2015).  $PS_i$  was based on habitat deviations of an individual's habitat use, in its foraging core, relative to the mean habitat use of all other tracked bats in the available foraging area. A  $PS_i$  value approaching 1 represents a more generalist habitat use, whereas approaching 0 would indicate a more specialised use of habitat. The mean  $PS_i$  among individuals was used to determine the average amount of specialisation in habitat use across all bats in this study and individuals were deemed to be specialists if their  $PS_i$  value was below the mean communities'  $PS_i$  value. Monte Carlo permutations were run with 999 replicates to assess whether observed WIC/TNW and  $PS_i$  values differed significantly from a random distribution of values subsampled from the population.

### Foraging fidelity

The potential of a single complete night of radio-tracking data to act as a proxy for a more prolonged description of an individual's foraging space use was explored. Pairwise comparisons were carried out for each bat either within the calendar year or between years by comparing the foraging cores used between nights and calculating the proportion of overlap, using the *gIntersection* function in the *rgeos* package (Bivand et al. 2018). This was then compared to the proportion of overlap the foraging cores had with every other bat foraging core from that community to describe the similarity of foraging space use across differing intervals. Multiple-response permutation procedure analyses were conducted, function *MRPP*, in the *vegan* package (Oksanen et al. 2013), using the Euclidian distance metric and 1000 iterations with individual proportion overlap as the response variable.

To explore whether the foraging strategy used to produce individual foraging space use measured at varying intervals was repeatable, foraging distance (hereafter Distance, from roost to the most heavily used core) was compared to foraging schedule (hereafter Speed, period from emergence to arrival at the most heavily used foraging core) across all the data. Observations of the same bat were compared to observations of different bats with

**Table 1** Habitat types and relevant LCM2007 land class types

Habitat name	LCM2007 BHSUB class
Arable	Arable
Deciduous woodland	Broadleaf, mixed and yew woodland
Coniferous woodland	Coniferous woodland
Unmanaged grassland	Semi-natural grassland; calcareous grassland; rough low productivity grassland
Managed grassland	Improved grassland; neutral grassland; acid grassland
Other habitats	Bog; built-up areas; dwarf shrub heath; fen marsh and swamp; freshwater; inland rock; littoral sediment; montane habitats; salt water; supra-littoral rock; supra-littoral sediment

1000 permutations, using the `rpt` function in package `rptR` (Stoffel et al. 2017), with individual distance and foraging schedules as the response variables. Similarities between bats in their patterns of foraging space use were explored using a linear model (`lm`), with Distance as the response variable and Speed and Site (Wallington/Low Catton) as the predictors.

## Results

Thirty-four individual bats, 17 from Wallington and 17 from Low Catton, were tracked for at least one full night (Table 2). Six bats were tracked over multiple years and 24 bats were tracked twice during the same year (Table 3). This produced 29 foraging cores (nights of data) available for pairwise comparisons of foraging site fidelity at Wallington and 32 nights at Low Catton. This resulted in a mean foraging period of 319.8 min (per bat per night; range 159.6–409.8). Tracking usually represented most, if not all, of the period of dark at 55° N in summer (Table 4).

In terms of movement dynamics, the relationship between the distance of the roost of departure and the most used foraging core, and the speed travelled between them, was of interest as it represented independent choices (Fig. 1). Some bats choose to travel long distances and some bats choose to travel quickly, but there was not a consistent relationship between the two ( $R^2 = 0.217$ ,  $F_{(3,30)} = 4.062$ ,  $p = 0.95$ ).

### Foraging site fidelity

At both Wallington (Figs. 2 and 4) and Low Catton (Fig. 3), a greater degree of foraging core overlap was observed for the same bats tracked repeatedly within the same year ( $0.92 \pm 0.06$ , range 0.57–0.9) than between different bats ( $0.62 \pm 0.02$ , range 0.25–0.99) and this difference was significant, post hoc Tukey tests  $p < 0.01$ . Similarly, at Low Catton the means for the comparison of foraging cores for same bat was  $0.92 \pm 0.02$ , range 0.66–1 whilst the mean between different bats was  $0.29 \pm 0.01$ , range 0–1 (Figs. 3 and 5).

There was also a higher degree of spatial overlap for the same bats tracked repeatedly between years than for different bats at Wallington (Figs. 4 and 5). This too was significant (post hoc Tukey tests  $p = 0.02$ ); same bat mean  $0.80 \pm 0.03$ , range 0.63–0.96; different bats' mean  $0.61 \pm 0.01$ , range 0.24–0.97. Individual bats tracked repeatedly also showed significantly more consistency in their foraging behaviour (distance to most used foraging core and time taken to travel to most used foraging core) at both sites than pairwise comparisons with other individuals (Table 5).

### Individual specialisation and habitat use

Bats did not select the habitats exploited in their foraging cores at random. At both Wallington and Low Catton, the selection of preferred habitats was evident (respectively, Wilks  $\lambda = 0.058$ ,  $p < 0.01$  and  $\lambda = 0.34$ ,  $p = 0.01$ ). Wilk's lambda tests if there are differences between group means for a particular combination of dependent variables (habitat proportions). It measures the percent variance in dependant variables not explained by differences in levels of the independent variable (between individual bats). Ranging from 0 to 1, a value of zero means that all variance is explained by the independent variable and here that individuals are not selecting habitat at random.

Overall managed grassland was the dominant habitat found within Natterer's bat foraging cores at Wallington (11/17 bats had a foraging core covered by at least 50% managed grassland, Fig. 6). In the upland landscape this land use comprised two agricultural activities: the direct use of pasture by livestock and horses and substantial areas of grass grown for silage and hay. It was notable how Natterer's bats responded to grass cutting operations by increasing their use of open field settings (JA pers. comm.). However, 'other habitats' was the most preferred habitat for the whole community (which was mainly the use of 'dwarf shrub heath' on the elevated hill and moorland areas of their foraging range, Supplementary Fig. 2).

At Low Catton 'arable' was the dominant habitat used by bats (13/17 bats had more than 50% arable in their foraging core) and it was also the preferred habitat by the community (Table 6).

There was variability in foraging habitat selection by individuals at both sites, for example the proportion of managed grassland within an individual's foraging core(s) at Wallington ranged from 10 to 98% (Fig. 6a). Also, on average, individual bats used a moderate fraction of the total population niche space (population level measure of individual specialisation = 0.63 Wallington, 0.69 Low Catton) and were more specialised than would be expected by chance at both sites (Monte Carlo analyses of individual versus population niche variation;  $p < 0.001$  Wallington,  $p < 0.001$  Low Catton). Some individual bats showed vastly different use of habitat types to others. At Wallington six bats (H1607, H1608, H1609, H1679, H1680, Y2889) used unusual habitats or exploited habitats differently to most of the group (Fig. 6a) and consequently their  $PS_i$  values were below the population mean. At Low Catton the majority of individuals had large proportions of arable in their foraging core(s), which was the most dominant habitat type in the area, except for four individuals who showed unique habitat use specialisation (Y2049, Y2106, U8558, U3941) and had large areas of unmanaged grassland, managed grassland, coniferous woodland and a mixture of habitat types, respectively (Fig. 6b).

**Table 2** Natterer's bat biometric data, tracking dates and recording information of individuals caught at Wallington (W) and Low Catton (LC)

Site	ID	Sex	Adult/juvenile	Body mass (g)	Forearm length (mm)	Reproductive condition	Tracking date	No. of observations	No. of locations
LC	U3935	F	A	7.5	37.81	Lactating	22/07/2003	33	20
				7.5		Lactating	24/07/2003	38	32
	U3938	F	A	7.9	40.7	Pregnant	11/06/2003	30	18
				7.9		Pregnant	12/06/2003	30	26
	U3941	F	A	8.1	40.6	Pregnant	03/06/2003	29	17
				8.1		Pregnant	04/06/2003	40	16
	U3947	F	A	8.2	39.07	Lactating	25/06/2003	25	20
				8.2		Lactating	26/06/2003	31	24
	U7471	F	A	7.9	39.69	Non-repro	24/06/2003	16	15
				7.9		Non-repro	25/06/2003	23	21
	U8584	F	A	7.4	41.72	Unknown	20/05/2003	34	20
	U8588	F	A	7.4	38.58	Unknown	15/05/2003	38	34
	U8590	F	A	6.3	37.52	Non-repro	29/05/2003	37	22
				6.3		Non-repro	05/06/2003	20	12
	U8592	F	A	8	39.4	Non-repro	05/08/2003	46	44
				8		Non-repro	06/08/2003	41	39
	U8890	F	A	7.5	39.0	Lactating	09/07/2003	35	31
				7.5		Lactating	10/07/2003	34	27
	Y1972	F	A	8.6	39.6	Pregnant	11/06/2003	31	27
	Y1974	M	A	6.6	38.61	Unknown	12/06/2003	29	20
				6.6		Unknown	16/06/2003	33	28
	Y1998	F	A	10.5	41.41	Pregnant	25/06/2003	29	15
				10.5		Pregnant	26/06/2003	23	14
	Y2003	F	A	7.5	40.14	Lactating	08/07/2003	36	25
				7.5		Lactating	09/07/2003	34	29
	Y2045	F	A	7.2	37.94	Non-repro	23/07/2003	36	31
				7.2		Non-repro	24/07/2003	34	34
Y2106	F	A	7	41.63	Non-repro	05/08/2003	36	34	
Y2106	F	A	7		Non-repro	07/08/2003	34	34	
W	H1607	F	A	8.8	39.90	Lactating	26/07/2013	39	17
				8.8		Lactating	28/07/2013	27	12
H1608	F	A	7.4	37.10	Post lactating	30/07/2013	40	15	
			7.4		Post lactating	31/07/2013	38	13	
			7.3		Post lactating	30/07/2014	38	13	
H1609	F	A	8.0	39.7	Pregnant	23/06/2015	35	10	
H1611	F	A	7.8	39.7	Post lactating	13/08/2014	39	12	
H1659	F	A	8.7	40.3	Lactating	08/08/2013	36	17	
			8.7		Lactating	09/08/2013	36	15	
			9.1		Post lactating	21/08/2014	44	23	
H1670	F	A	8.2	38.4	Post lactating	21/08/2013	44	17	
			9.4		Pregnant	20/06/2014	33	16	
H1672	F	A	9.2	38.9	Post lactating	19/08/2014	39	18	
H1679	F	A	9.1	39.7	Pregnant	05/06/2014	27	11	
H1673	F	A	8.0	40.1	Pregnant	15/06/2015	38	12	
H1680	F	A	8.5	40.2	Pregnant	17/06/2014	27	12	
			7.8		Post lactating	06/08/2014	36	16	
			9.0		Pregnant	02/07/2015	36	14	
H1682	F	A	8.9	40.59	Pregnant	16/06/2014	27	13	

**Table 2** (continued)

Site	ID	Sex	Adult/juvenile	Body mass (g)	Forearm length (mm)	Reproductive condition	Tracking date	No. of observations	No. of locations
				8.5		Pregnant	09/06/2015	38	14
	H1688	F	A	8.8	39.22	Post lactating	22/08/2014	39	17
	H1696	M	A	6.9	39.4	Unknown	22/06/2014	26	11
	H1700	F	A	7.6	40.9	Non-repro	13/07/2014	37	15
	H1704	F	A	8.2	39.2	Lactating	27/07/2014	34	16
	H1705	M	J	6.8	39.1	Unknown	05/08/2014	34	22
	H1713	F	A	8.9	39.0	Pregnant	02/07/2015	36	17
	Y2850	F	A	8.1	39.1	Lactating	08/07/2013	25	13
				8.1		Lactating	20/07/2014	34	15
	Y2889	F	A	9.7	39.4	Pregnant	19/07/2013	26	8
				9.7		Pregnant	22/07/2013	25	9
				8.1		Post lactating	18/08/2014	35	14

## Discussion

Foraging site fidelity in Natterer's bats was consistent across a range of intervals (days, weeks, and even years) despite contrasting landscapes and seasonal contexts. In addition, individuals exploited specific foraging locations and showed individual specialisation in their habitat use which is consistent with the behaviour of a territorial species. Bats also exhibited differences between the distance to foraging cores and the speed travelled to them which suggests individual foraging choices are being made.

### Foraging site fidelity

Individual foraging site fidelity has previously been reported or suggested for a number of bat species (Hillen et al. 2009; Rydell 1986; Encarnação et al. 2010; Hillen et al. 2009; Kapfer et al. 2008; Kerth et al. 2001; Siemers et al. 1999) albeit with variable strength of evidence. Consequently, it should not be surprising that we found

individual Natterer's bats consistently returning to unique and specific locations in the landscape and occasionally even returning to the same small foraging patches in their foraging core. More recently, novel methods have extended the suite of bat species that appear to show this behaviour as well as the quality of observations (Egert-Berg et al. 2018). Here, in common with Kerth et al. (2001) and Egert-berg et al. (2018), statistically robust quantitative evidence is provided of the reuse of the same locations by individuals, and we demonstrate this foraging site fidelity to be consistent across a range of intervals (days, months and years) within the spring and summer season. It should be noted here that along with many other studies regarding temperate bat radiotelemetry, e.g. (Bontadina et al. 2002; Dietz and Pir 2009; Divoll et al. 2022; Kerth et al. 2001; Nicholls and Racey 2006; Rossiter et al. 2002), the majority of the bats tracked were female. This is part due to the nature of summer roosting behaviour of temperate bats which typically follows that of sexual segregation, e.g. (Angell et al. 2013). We expect our results to be applicable to both sexes; however, further work would be recommended to ensure males follow similar patterns.

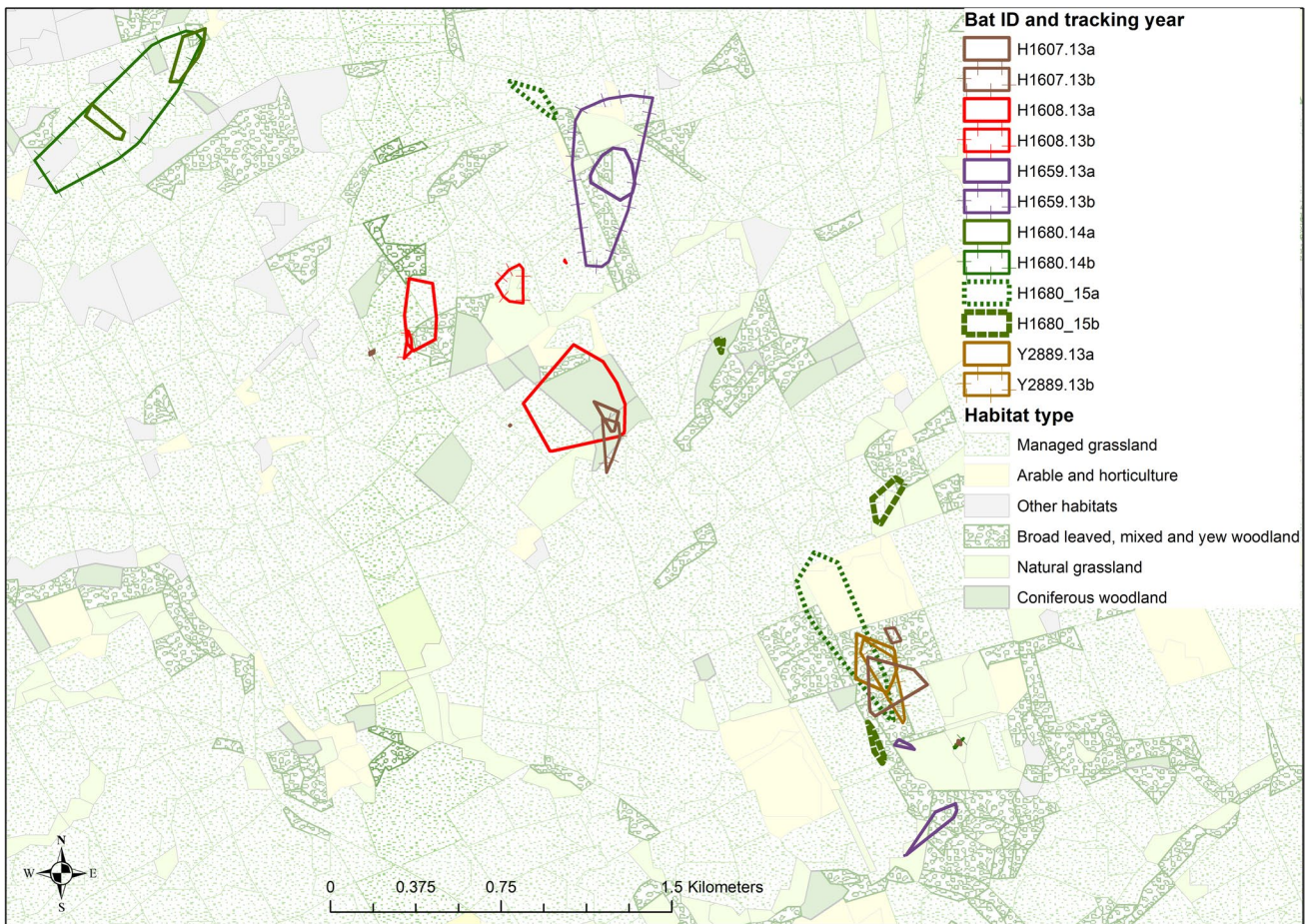
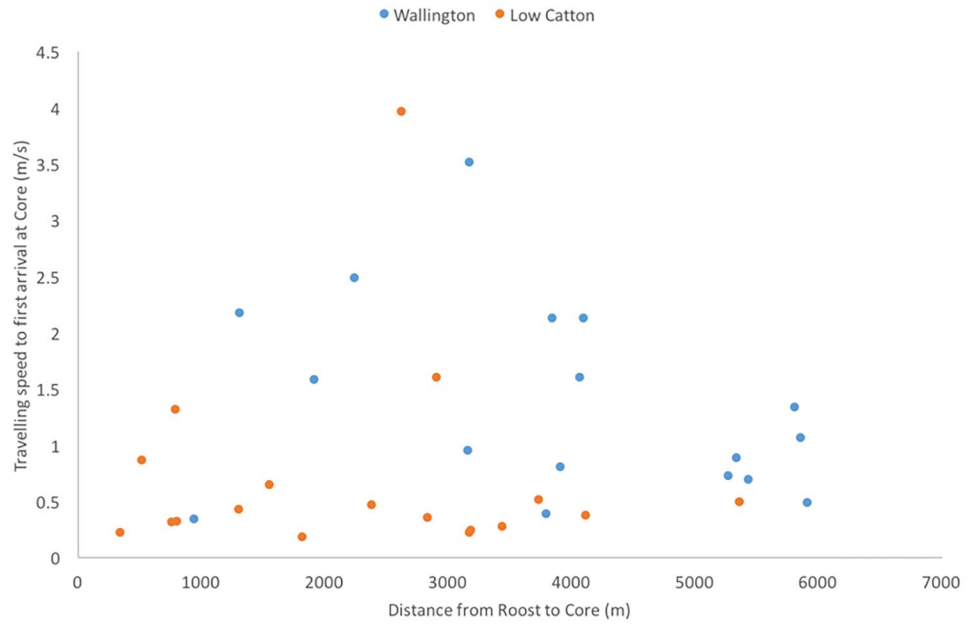
**Table 3** Number of individual bats tracked by site and year used to estimate foraging core overlap at two temporal scales, within-year (multiple foraging trips by one bat in one year) and between-year (one bat over multiple years)

Site	Year	Bats tracked	
		Within-year	Between-year
Low Catton	2003	13	0
Wallington	2013	4	4
	2014	2	4
	2015	1	4

**Table 4** Mean number of radio-tracking observations, locations and foraging time of Natterer's bats tracked at Low Catton and Wallington

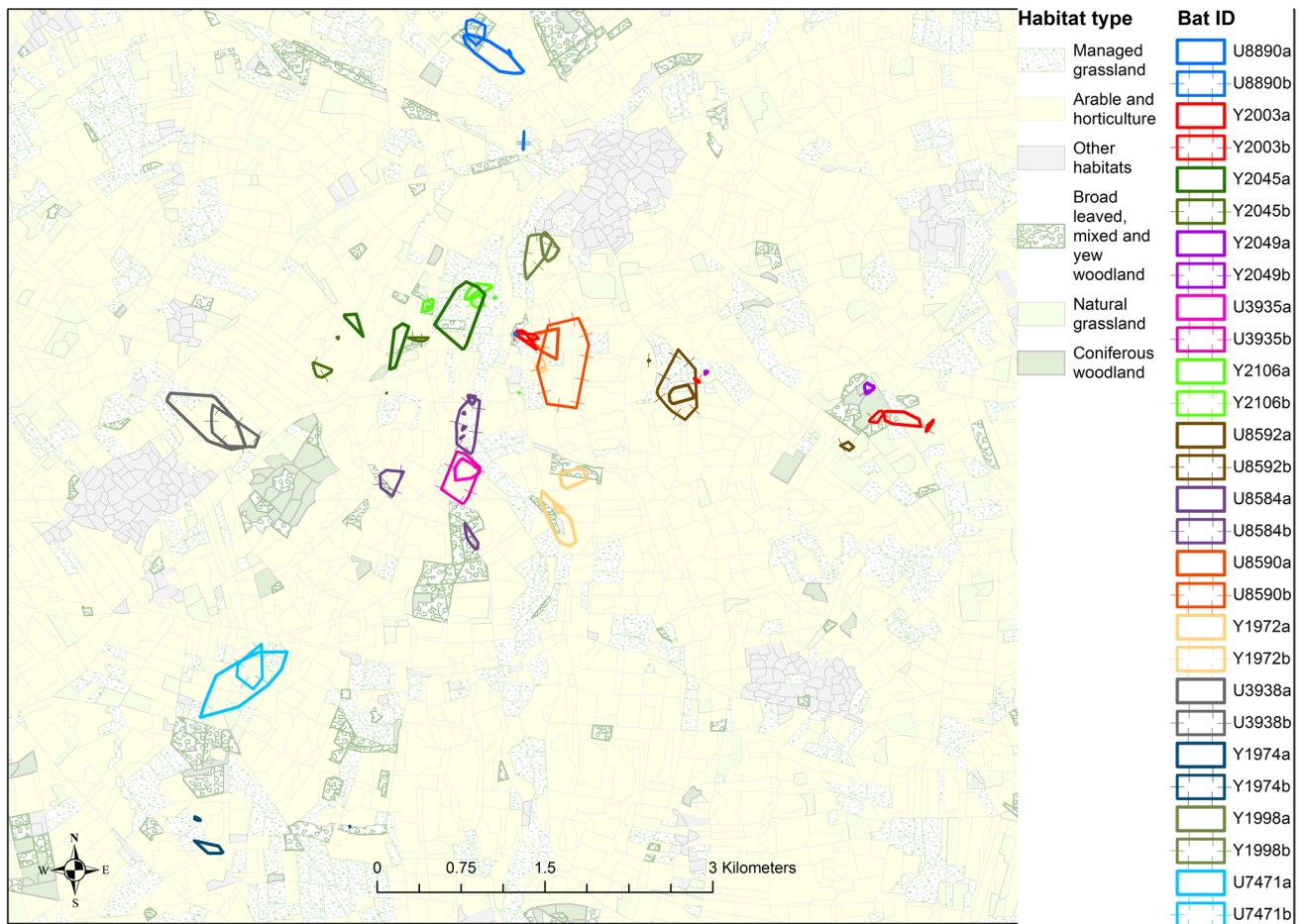
	Site	Mean	Range
Observations	Low Catton	30	16–46
	Wallington	34	25–41
Locations	Low Catton	25	12–44
	Wallington	14	8–23
Foraging time (minutes)	Low Catton	300	159.6–459.6
	Wallington	339.6	249.6–409.8

**Fig. 1** Distance from roost to foraging core and speed for bats tracked at Wallington and Low Catton



**Fig. 2** Foraging cores of bats ( $n=5$ ) tracked repeatedly at Wallington within the same year





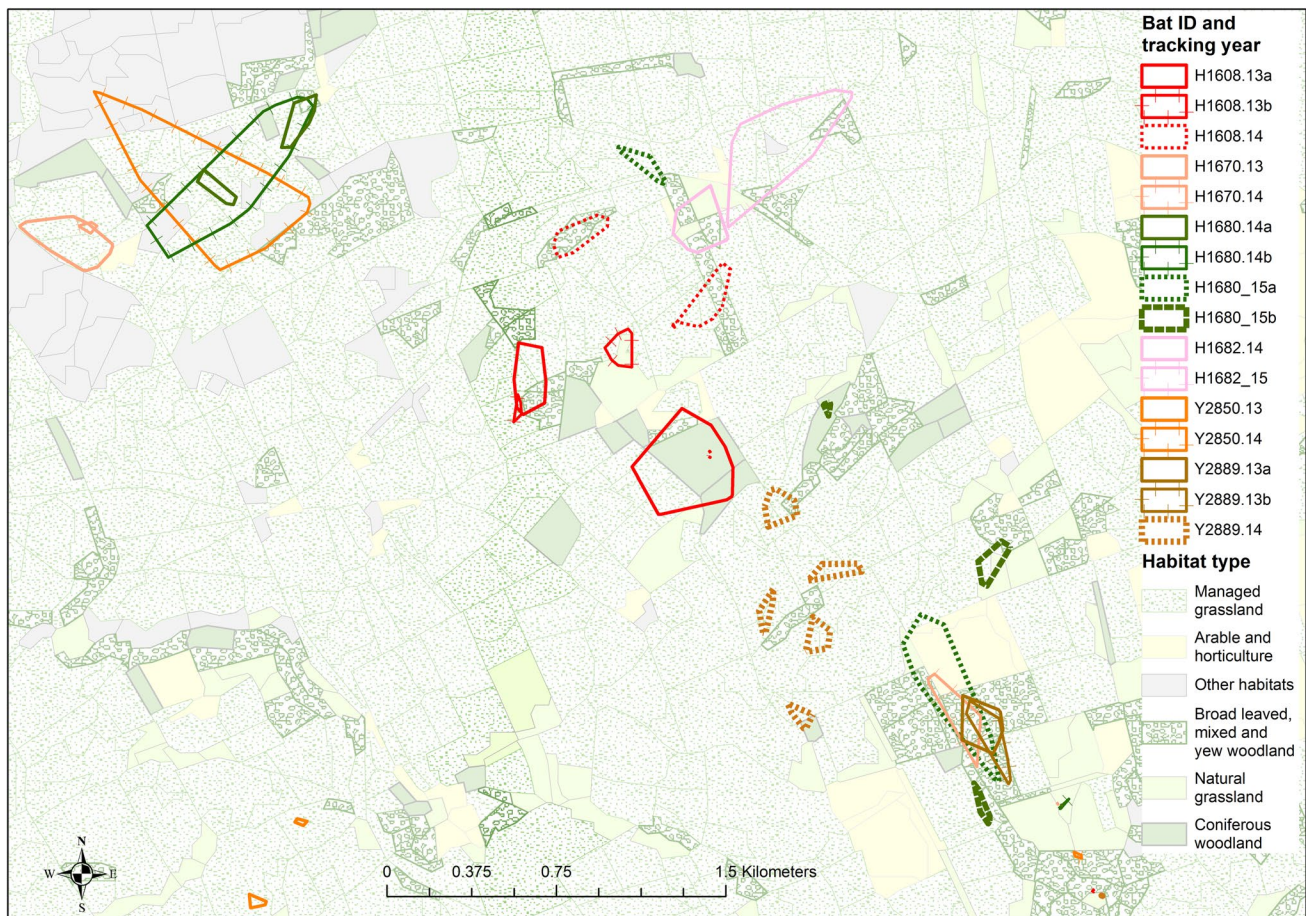
**Fig. 3** Foraging cores of bats tracked repeatedly at Low Catton ( $n = 14$ ) within the same year

The fidelity to foraging sites shown in this study extends beyond the immediate period of retracking defined by the life of currently available radio transmitters (typically  $< 10$  days for small and medium-sized species). This is potentially good news for bat conservation. Firstly, foraging site fidelity enables practitioners to be more certain of the foraging requirements of bats over time. This could help when planning areas for conservation or mitigation of anthropogenic development. Indeed home ranges (here foraging cores) could also be considered a crucial resource for survival (Kerth et al. 2001). The long life of bats suggests that their foraging cores are likely to remain valuable for some time, validating any policy investment in protecting areas of the landscape and the habitats within. Secondly, there is considerable value to scientists in knowing that descriptions of individual foraging strategies in adults represent long-lived behaviours, as this helps the integration of foraging choices into spatially explicit studies of the population dynamics of bats in anthropogenic landscapes.

### Territoriality

The behaviour of individuals repeatedly exploiting specific foraging locations whilst also showing individual specialisation in their habitat use is consistent with the behaviour of a territorial species. Here we found that not only do some individuals show foraging core fidelity but also appear to avoid overlap with other tracked bats (Figs. 2, 3, 4, and 5) which is generally considered to reflect territoriality (Chaverri et al. 2007; Encarnação et al. 2010). It should be noted here however that multiple individuals were not tracked simultaneously but our presumption is based on the knowledge that foraging cores were consistent across multiple time frames.

This is not the first time that territoriality has been suggested due to apparent foraging site fidelity in individual bats (Chaverri et al. 2007; Encarnação et al. 2010; Rossiter et al. 2002; Rydell 1986), though the difficulties in studying individual bats have previously limited authors' confidence in describing this behaviour. Territoriality has most often been suggested for bat species who have a strong connection with



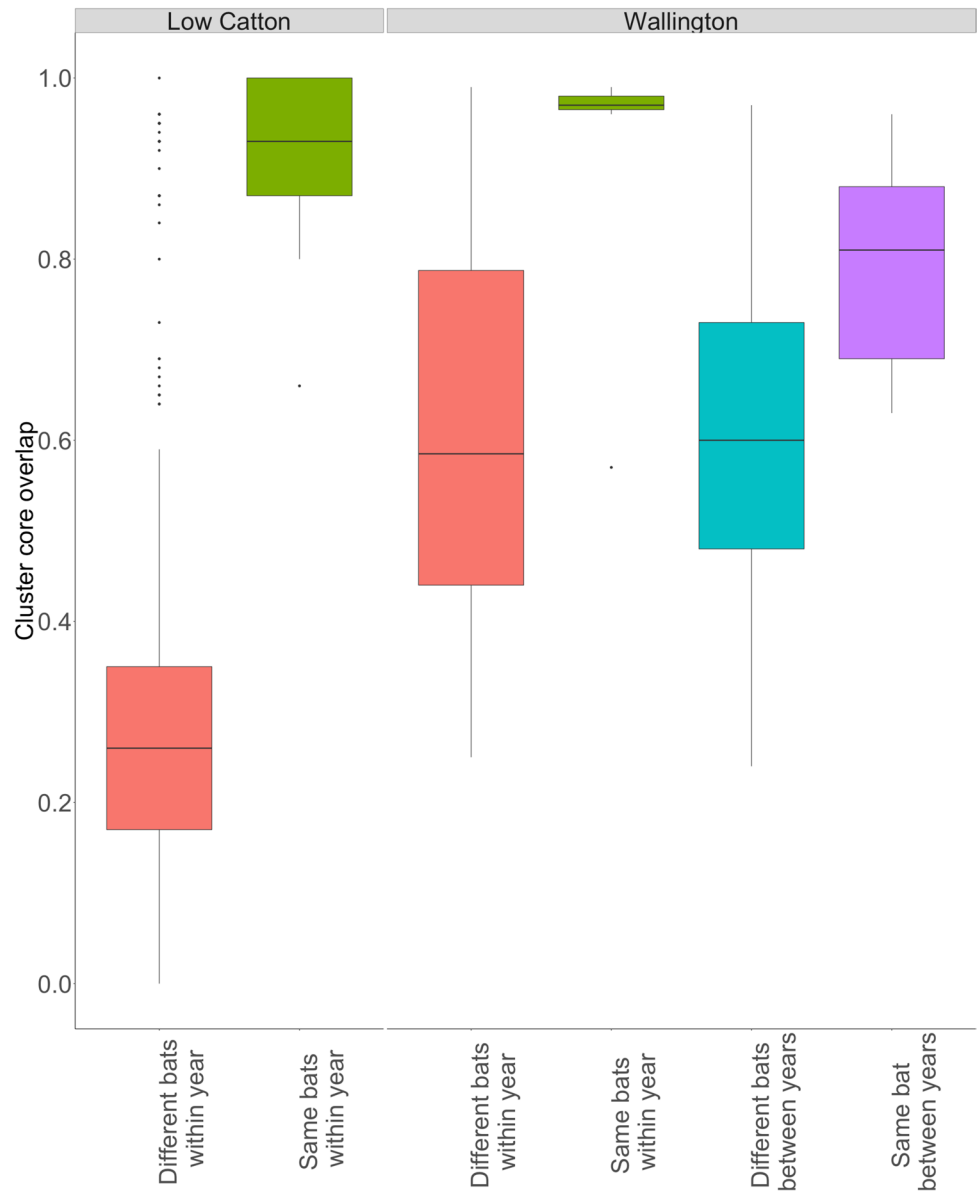
**Fig. 4** Foraging cores of bats tracked repeatedly at Wallington ( $n=6$ ) between years 2013 and 2015

the underlying landscape and therefore presumably keen to defend a static resource, i.e. gleaners or those preying weak flying prey (Gerell and Lundberg 1985; Reyes-García et al. 2008). For example, the suggestion of territoriality has often been associated with studies of Daubenton's bats foraging over water, e.g. (Encarnação et al. 2010; Kapfer et al. 2008). The suggestion arises due to Daubenton's bats strong association with riverine habitats (Warren et al. 2000), which are specific and easy to map landscape features. The distinctive features enable workers to be relatively confident in the interpretation of spatial locations from radio tracking and to directly observe the foraging behaviour of some individuals. Observed behaviour which may be considered to be territorial includes the repetitive use of space and the occurrence of social interactions (social calls and chasing) (Encarnação et al. 2010).

Sociality of temperate bats is becoming widely recognised (Altringham and Senior 2005; August 2012; August et al. 2014; Entwistle et al. 2000; Gerell and Lundberg 1985; Johnson et al. 2013; Kashima et al. 2013; Kerth et al. 2011; Park et al. 1998; Patriquin et al. 2010; Siemers and Kerth

2006; Silvis et al. 2015, 2014) and the identification of social hierarchies within groups is anticipated (Fleischmann and Kerth 2014). Whilst social dominance might only be expressed in the choice of roost (Fleischmann and Kerth 2014) or the position within the roosting group, it could also be expressed in other key activity bats undertake, e.g. foraging, with dominant individuals choosing and maintaining their preferred locations whilst subdominant bats may be left with less productive foraging choices. Food defence via social calls has been described in *Eptesicus fuscus* (Wright et al. 2014), *Vespertilio sinensis* (Luo et al. 2017) and *Myotis macrodactylus* (Guo et al. 2019), supporting the idea of bat social hierarchies. In addition, male *Hipposideros armiger* have been found to emit varying social calls correlating to information about body mass, dominance rank and individual identity. It is hypothesised that individual *H. armiger* bats are capable of perceiving information about dominance rank and body mass to make appropriate decisions during agonistic interactions (Sun et al. 2021), further supporting the theory of social dominance in relation to food resources. If social dominance does occur, understanding its effects

**Fig. 5** Comparative overlap of foraging cores at Wallington and Low Catton. Scores close to 1 indicate 100% overlap of foraging cores whilst scores close to zero indicate no overlap of space



will be important in the management or conservation of bats where pup reproduction and survival is affected by the quality of the foraging resource (Arlettaz et al. 2017). In the future workers may need to identify and protect the most

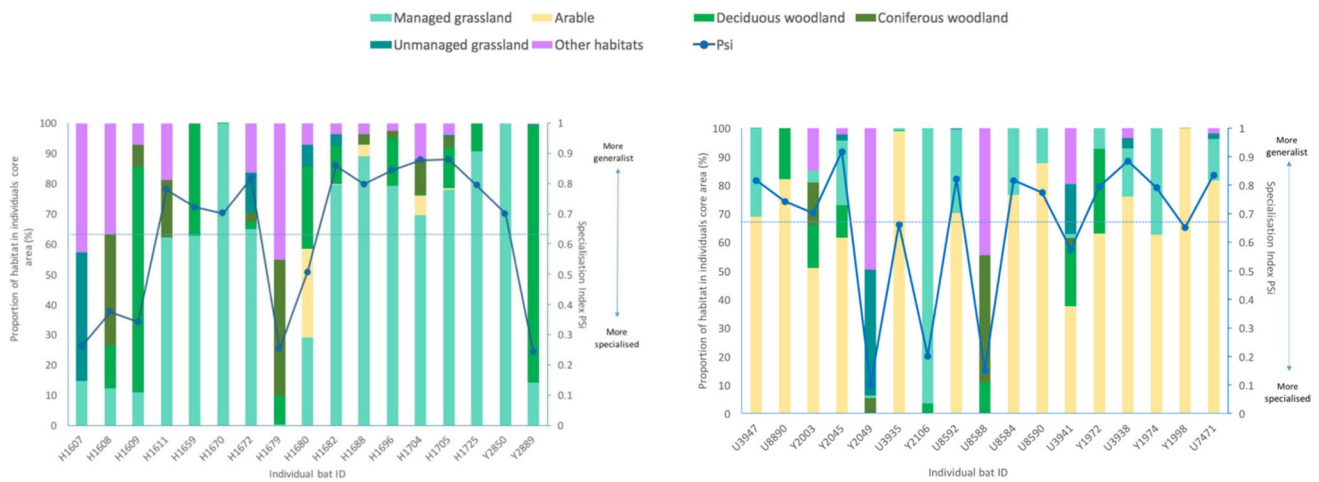
productive areas of a landscape perhaps by considering landscape geology, e.g. (Threlfall et al. 2011), and potentially distinguish this from the location of preferred habitats. It should also be noted that only approximately half of each social group at Wallington and Low Catton were tracked and there is no evidence of the functional definition of territory defence, i.e. observations of antagonistic behaviour between individuals at potential territory sites.

**Table 5** Mean repeatability score ( $\pm$  s.e.) of foraging characteristics of bats tracked at Wallington and Low Catton calculated from ‘rptR’ R package. \* indicate repeatability scores significantly higher than random permutations based on the likelihood ratio test

	Wallington	Low Catton
Distance to most used foraging core	0.979* $\pm$ 0.011	0.948* $\pm$ 0.027
Time to most used foraging core	0.698* $\pm$ 0.132	0.57* $\pm$ 0.149

**Behavioural individuality**

This study agrees with Nachev and Winter (2019) and identifies that individual bats can demonstrate distinct and divergent foraging choices compared to their peers, specifically in their choices of foraging strategy and habitats. In



**Fig. 6** Individual variation in habitat use between bats tracked at Wallington (a) and Low Catton (b). Each individual is represented by a vertical bar (x-axis), subdivided by the proportion of observations in

each habitat type in relation to the individual’s total foraging core(s) and the specialisation index  $PS_i$  (blue dots; 0 = more specialised; 1 = more generalist) along with the mean colony  $PS_i$  (dashed line)

addition, this distinct behaviour seems to have extended into groups adopting site-specific responses (or traditions) to the contrasting compositions and configurations of the habitats at our two study sites, e.g. the preferred ‘other habitat’ at Wallington compared to the preferred habitat of ‘arable’ at Low Catton. However here it should be noted that arable habitat was also the most common habitat at Low Catton so this could be a local adaptation. Further, our demonstration of foraging site fidelity suggests that these individual differences are likely to be long-lived and may represent either differences in personality (Nachev and Winter 2019) or tradition in wildlife species, examples of which are now reported for bats (Cryan et al. 2012) as well as other wildlife (Araújo et al. 2011; Knudsen et al. 2010; Patrick and Weimerskirch 2014; Robertson et al. 2014). Alternatively, individual habitat choice may just represent individual preference across the broad menu offered by these mixed landscapes. It should be also be noted that usually Natterer’s

bats are thought to be proficient at both aerial hawking and gleaning (Siemers and Schnitzler 2000; Swift and Racey 2002) and might therefore develop almost unconstrained preferences in prey and varied ways to exploit the foraging options available to them.

### Conclusions

We found that individual bats forage at specific locations, to which they repeatedly return. Whilst it is relatively easy to simply collate the land cover or habitat types represented within each foraging core into simplistic descriptions of group behaviour, individuals in this study differed greatly and showed specialisation in their foraging choices. It is possible that for some common habitats, the choice of foraging core used was unique and important and may not be replaceable at another location, even if the habitat appeared the same. Thus, studies designed to inform conservation and management of temperate bats should attempt to maximise the number of individuals from which movement data is sought and ensure that data represent a coherent and meaningful measure of behaviour such as a complete night; however, this will be costly in terms of time and resources. Maximising the number of individuals tracked may also have ethical considerations and there may be an optimum number of individuals per community to track, which, when combined with habitat use analyses, may represent the habitat specialisms of a community. This area requires further work. Further, it is not clear that any of the specific foraging space uses observed at one site (such as commuting style or habitat choices) could transfer to the second site, and our observed behaviours here could be sensitive to the characteristics of

**Table 6** Habitat ranks from compositional analysis, comparing proportional use of habitat in each community. A habitat preceding a ‘>’ symbol was preferred to that immediately following the symbol and ‘>>>’ indicates a significant selection between adjacent ranked habitats

Site	Habitat ranking
Low Catton ( <i>n</i> = 17)	Arable > managed grassland > deciduous woodland > other habitats > unmanaged grassland > coniferous woodland
Wallington ( <i>n</i> = 17)	Other habitats > managed grassland > coniferous woodland > deciduous woodland >> unmanaged grassland > arable

the landscapes, dominant habitat types or the traditions of their communities (Hillen et al. 2009).

Our finding of the strong foraging site fidelity by Natterer's bats and our speculation that this may represent some type of territorial behaviour may offset some of the effort required to collect a single full night of radio-tracking data, as a single full night of data may produce a long-lived and robust description of that bat's behaviour, justifying the additional effort in field-work hours. However it raises the concern that many of the popular analytical methods frequently used by bat workers such as compositional analysis (Aebischer et al. 1993) and selection ratios (Manly et al. 2007) may be inappropriate. Designing conservation strategies might then advocate protecting a mosaic of habitats to preserve the habitat specialisms of many individuals rather than choosing a single preferred habitat for a given bat species which may only suit a few dominant individuals.

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**Availability of data and material** The datasets analysed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Ethics approval and consent to participate** All disturbances at roosts, as well as the capture, handling and marking of bats were carried out under licence from Natural England 2014–6454-SCI-SCI.

**Consent for publication** Not applicable.

**Competing interests** The authors declare that they have no competing interests.

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