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Contrasting home-range size and spatial partitioning in cryptic and sympatric pipistrelle bats

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Abstract The extent of spatial partitioning in insectivorous bats, whose prey is patchily distributed and transient in nature, remains a contentious issue. The recent separation of a common Palaearctic bat, the pipistrelle, into *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*, which are morphologically similar and sympatric, provides an opportunity to examine this question. The present study used radio telemetry to address the spatial distribution and foraging characteristics of *P. pipistrellus* and *P. pygmaeus* in northeast Scotland, to test the hypothesis that coexistence between these species is facilitated through spatial segregation. We reveal large and significant differences in the spatial distribution and foraging characteristics of these two cryptic species. Individual *P. pipistrellus* home ranges were on average three times as large as that of *P. pygmaeus*, and they foraged for approximately an hour longer each night. Inter-specific spatial overlap was minimal (<5%) and core foraging areas of either species were essentially mutually exclusive despite the proximity of the two roosts. Inter-specific differences in range size were associated with the spatial dispersion of productive foraging sites within individual foraging ranges. *P. pipistrellus* foraging sites were highly dispersed, necessitating larger ranges. It is predicted that the spatial segregation revealed by the present study is a result of selection favouring the avoidance of competition in these species through differential habitat use.

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Introduction

The accurate description of an animal's home-range size, shape and pattern of utilisation is often a fundamental precursor for ecological or behavioural studies, particularly those concerned with foraging behaviour, habitat selection, distribution of resources, spacing of individuals and their interactions (Harris et al. 1990). Animals are expected to utilise home ranges that represent the minimum economically defensible area (Pyke et al. 1977; Maher and Lott 1995; Johnson et al. 2001) but which are large enough to satisfy their metabolic needs over time (McNab 1963; Reiss 1988). Therefore, inter-specific variation in home-range size and shape has typically been related to body size-dependent metabolic requirements (Reiss 1988; Lindstedt et al. 1986), species overlap (Damuth 1981) and rate of home range use (Swihart et al. 1988).

Carr and Macdonald (1986), through the Resource Dispersion Hypothesis (RDH) offer an alternative view, suggesting that intra- and inter-specific variation in home-range size can be determined by the spatial dispersion, patchiness and variation of food resources, and that group size is independent of range size and is instead limited by the resource value of available patches and their pattern of availability.

Colonial species, such as bats, typically congregate at roosting sites, and individuals move elsewhere to forage. Little is known about whether bats partition their foraging ranges, or how they space themselves to minimise potential

competition. Although there is evidence for inter-specific partitioning of space in bats (Herd and Fenton 1983; Aldridge and Rautenbach 1987; Saunders and Barclay 1992; Arita and Fenton 1997; Arlettaz 1999), studies investigating intra-specific behaviour have been equivocal (Fenton and Bell 1979; Bell 1980), and there remains a great deal of contention regarding the requirement for spatial partitioning in insectivorous bats whose prey is both patchily distributed and transient in nature (Schum 1984; Willig and Moulton 1989; Arita 1997; Barlow and Jones 1997).

Spacing patterns identified in aerial feeding insectivorous bats include territoriality (Bradbury and Emmons 1974; Rydell 1986, 1989) and use of exclusive feeding areas through mutual avoidance (Vaughan 1976). Alternatively, no spacing occurs and there is considerable overlap among individuals in foraging areas where prey density is high, or there is active aggression at shared food patches (Racey and Swift 1985; Rydell 1986). This level of territoriality may be directly linked to resource availability, as territoriality at foraging sites increases as insect density decreases (Racey and Swift 1985; Rydell 1986). However, the spacing patterns of pipistrelle bats remain poorly understood, particularly in light of the recent discovery of cryptic species within the genus *Pipistrellus*.

For more than 200 years, *Pipistrellus pipistrellus* the most widespread bat in Europe (Avery 1991), and probably the most abundant, was considered to be a single species. However, in recent decades, analysis of echolocation calls revealed that pipistrelle calls fall into two discrete frequency bands with average frequencies of maximum energy of 45 and 55 kHz (Ahlen 1981; Miller and Degn 1981; Weid and von Helversen 1987; Zingg 1990; Jones and van Parijs 1993). Subsequent ecological and morphological studies led to the discovery that *P. pipistrellus* is comprised of two cryptic species with considerable genetic divergence (Jones and van Parijs 1993; Barratt et al. 1995, 1997). The suggested name for the 55 kHz phonic type of *Pipistrellus pygmaeus* (Jones and Barratt 1999) was accepted in 2003 with the 45 kHz phonic type retaining the name *P. pipistrellus* (Anon 2003).

P. pipistrellus and *P. pygmaeus* occur across a wide geographic range throughout Europe (Hulva et al. 2004). They largely overlap in their distribution, although their relative abundance varies locally. They are widespread and abundant in Britain (Jones and van Parijs 1993), Northern Ireland (Russ 1996) and Switzerland (Zingg 1990), and more recently both species have been recorded in Germany (Haussler et al. 1999; Mayer and von Helversen 2001), Spain (Ruedi et al. 1998; Mayer and von Helversen 2001), Greece (Mayer and von Helversen 2001) and Italy (Russo et al. 2002). Such widely overlapping distribution indicates that they may differ in aspects of their ecology. Otherwise,

displacement of the less well-adapted species would be expected due to competitive exclusion (Mayer and von Helversen 2001).

This view is supported by the findings of Barlow and Jones (1997) who used playback experiments to investigate the use of social calls in these species. It had previously been believed that such calls served an agonistic function, in the defence of transient food patches (Miller and Degn 1981; Racey and Swift 1985). Barlow and Jones (1997) confirmed that production of these social calls increased as insect density decreased, and that they reduced feeding activity in conspecifics, thereby reflecting a degree of intra-specific competition. However, neither species responded to playback calls from the other species, suggesting a lack of inter-specific competition, which may reflect the partitioning of resources in time or space between the two species.

Although the sympatry of *P. pipistrellus* and *P. pygmaeus* has been described over a broad geographical range, there is no quantitative information on their spatial distribution at a more local scale. This is primarily due to the absence of relevant telemetry data because their small size (4–8 g) has precluded the use of radio transmitters. However, recent advances in the miniaturisation of electrical components, has facilitated the production of a radio transmitter light enough (0.33 g) to be used on pipistrelles. This study will use radio telemetry to address the spatial distribution and foraging characteristics of *P. pipistrellus* and *P. pygmaeus*, to test the hypothesis that these species segregate spatially to an extent that prevents inter-specific competition.

Materials and methods

Study area

The study was carried out near the town of Kemnay in northeast Scotland (latitude 57°23′ N, longitude 02°45′ W, National Grid Ref: NJ 728 159) from May to September 2002 and 2003. This area is comprised primarily of improved agricultural land. The river Don lies to the southeast of the study area and is bordered by riparian woodland along much of its length and tributaries. Woodland is well represented in the area, comprising both broadleaved woodland and conifer plantations. The primary criterion for this choice of study site was the location of maternity roosts of both species within close proximity of each other (straight-line distance of 1.5 km). Pipistrelle maternity roosts are comprised almost exclusively of female bats although occasionally pre-pubertal males are tolerated (Swift 1980). Until the formation of mating roosts in early August, males are typically found roosting alone or in small

bachelor roosts, and given the difficulty in locating these roosts the present study was limited to describing the foraging behaviour of female bats. A comprehensive survey was carried out on all buildings within the area to ascertain that no other maternity roosts were present in the vicinity. All individually tracked bats were initially residents of the maternity colony, although alternate roosts were used throughout the study.

The *P. pipistrellus* colony was estimated to consist of ca. 100 bats, originally found roosting in the wall cavity of a converted schoolhouse, in an area surrounded by intensively managed agricultural land. In the second year, the maternity colony moved to an adjacent residential building, where they again roosted within the wall cavity. The *P. pygmaeus* colony consisted of ca. 250 bats and was located in the apex of an old stable building close to the river Don.

Radio telemetry

Bats were caught individually in a hand net as they emerged from the roost. Each animal was sexed, weighed to 0.01 g with a digital balance and its forearm length measured to 0.1 mm with dial callipers. Reproductive condition was assessed, with the presence of large pectoral nipples, surrounded by bare patches, indicating lactation. All bats were fitted with a 2.5-mm (closed internal diameter) aluminium alloy bat ring (The Mammal Society). Only adult females were chosen for tagging, and unfused phalangeal epiphyses readily distinguished juveniles (Racey 1974). The hair between the scapulae was trimmed and a radio transmitter (model LB-2N, Holohil systems, Ontario, Canada) attached using Skinbond surgical cement (Smith & Nephew, Largo, Florida, USA). The mass of the transmitter plus adhesive never exceeded 7% of body weight (Aldridge and Brigham 1988; Wilkinson and Bradbury 1988) with a mean of 6.1%.

The rapid movement of the bats made cross bearings for positional fixes inaccurate; therefore, using Mariner 57 radio receivers, in conjunction with fixed and collapsible three element Yagi antennae, individual bats were tracked continually using the close approach method (White and Garrott 1990). When the signal was lost, a vehicle with a roof-mounted antenna was used to relocate the bat.

Location, activity and accuracy of the fix were recorded on a hand-held tape recorder every 10 min, and fixes were transferred directly to a 1:10,000 Landline Ordnance Survey (OS) map. Telemetry locations were transferred daily to a geographical information system (GIS ArcView 3.2) together with date, activity, time and accuracy of fix. Individual bats were followed until the transmitter either fell off or ceased to function (mean 5.3 days). Data from the night of transmitter attachment was not used in the subsequent analysis.

Analyses of range use

With the advent of radio-tracking techniques, there has been a considerable increase in the amount of data that can be collected and used to analyse home-range size, shape and internal configuration. As a result, a wide variety of methods of home-range analysis have subsequently evolved, each with their own assumptions and limitations (Wray et al. 1992; Kenward 1987; Harris et al. 1990; White and Garrot 1990; Kenward and Hodder 1996). Therefore, in the present study, the analysis of home-range size and structure was approached in a hierarchical fashion using a combination of GIS ArcView 3.2 (ESRI GIS and Mapping Software) and Ranges 6 software (Kenward et al. 2002).

Fully revealed home ranges (where plots of home-range size vs number of fixes had reached an asymptote) were expressed as 100% minimum convex polygons (MCP's) (Mohr 1947; Southwood 1966). This is the oldest and simplest method for estimating home-range size and as such facilitates comparison with other studies (Harris et al. 1990). However, as with any peripheral contour technique, its dependence on outliers leads to an overestimation in range size and provides no information on range use or internal range structure. Therefore, 100% MCPs were recalculated using only fixes that had been accurately described as foraging. A signal fluctuating within a defined area clearly indicated foraging (Russo et al. 2002). This was further corroborated by the use of bat detectors (S-25 Ultrasound advice, London), to record feeding buzzes. These characteristic increases in pulse repetition rate are produced by aerial hunting, insectivorous bats, when prey capture is attempted (Griffin et al. 1960). The use of foraging MCPs provides a more accurate estimate of an animal's foraging range, but is still likely to be an overestimate, and for bats, which typically utilise discrete foraging patches, will include areas never actually visited.

For more detailed analysis, core areas of activity were identified using kernel analysis (Worton 1989) which is able to assess an animal's probability of occurrence at each point in space, or its utilisation distribution. The level of inclusion was determined for each bat by plotting locational fixes against home-range size on a utilisation plot and determining the inflexion point on the curve. The mean percentage of fixes within this core area was not significantly different between species (mean±SD: *P. pipistrellus* 73±13; *P. pygmaeus* 78±9. Mann–Whitney $U=183.0$, $p=0.29$, $df=23$). Therefore, a 75% core area estimate was calculated for each species. Least squares cross validation as recommended by Worton (1989) was used to determine the smoothing parameter which produces estimates with small variance and bias (Bowman 1985).

Range overlap

The degree of intra and inter-specific spatial overlap was assessed by calculating the proportional overlap of all individual home ranges using the three estimators outlined above (100% MCP, foraging MCP and 75% kernel). An index of the degree of overlap at each level was recorded for each bat by calculating the mean percentage overlap between all possible combinations of individuals (i.e. percentage overlap between bat A and bat B, bat B and bat A, bat A and bat C, etc.).

Data analyses

Variation in range size, range overlap and foraging characteristics were analysed using three-way ANOVAs, to test for the effects of species, reproductive status and year of tracking. Data were checked for assumptions of normality and homogeneity of variance. When these conditions were not met, non-parametric tests were applied. When comparing the magnitude of inter- and intra-specific spatial overlap, randomization procedures were used to avoid statistical pseudo-replication inherent in pairwise comparisons (Manly 1991). For all three home range estimators, mean intra-specific overlaps were calculated for both species, as well as mean inter-specific overlap. To test for differences between means, the following two-step procedure was repeated 10,000 times: (1) random permutations of rows and columns of the spatial overlap matrix (as would be done for a Mantel test; Manly 1991); (2) calculation of the intra- and inter-specific means of the shuffled matrix. The test probability was then the proportion of shuffled matrices where the difference between inter- and intra-specific spatial overlap was as large as or larger than the observed.

Results

Radio-tracking effort

Fourteen *P. pipistrellus* and 12 *P. pygmaeus* were radio-tracked from May to September 2001/2002 (Table 1). Mean tracking effort did not differ significantly between species (mean±SD: 21.14±7.08 h for *P. pipistrellus* and 20.01±5.53 h for *P. pygmaeus*, Mann–Whitney $U=194.5$, $p=0.79$, $df=23$), and tracking sessions typically ended before battery failure when the tag became separated from the bat, probably as a result of grooming. There was no significant difference in contact time between the observers and the two species (mean±SD: 85.6±7% for *P. pipistrellus*, and 80.2±17% for *P. pygmaeus*, Mann–Whitney $U=192.0$, $p=0.89$, $df=23$), and asymptotes of home-range size were achieved for all individuals tracked. Range-size plots of

five randomly selected bats of either species are shown in Fig. 1 and reveal that for both species range size begins to level off after only thirty consecutive fixes, and reaches a stable estimate after ca. 60 fixes.

Colony home ranges, defined as the minimum convex polygon enclosing all accurately recorded radio locations for all bats tracked from that colony, reached an asymptote after seven radio-tracked bats for *P. pipistrellus* and eight for *P. pygmaeus*. These data indicate that all records included in further analyses provide a robust estimate of the foraging characteristics of these species.

Home-range size

The *P. pipistrellus* colony home range was approximately three times as large as that of *P. pygmaeus* (Fig. 2), and individual home-range sizes for *P. pipistrellus* were also significantly larger than *P. pygmaeus*, regardless of which type of range estimator was used (three way ANOVA species effect for 100% MCP: $F=19.39$, $p<0.001$; foraging range: $F=21.04$, $p<0.001$; 75% kernel: $F=7.32$, $p=0.013$, all $df=1,25$, Fig. 3). The year of tracking and reproductive status (lactating/non-lactating) had no significant effect on range size at any level.

Foraging characteristics

Both species showed a shift in foraging behaviour at different stages of reproduction. Bats tracked outwith the lactating period typically engaged in a single foraging bout per night, (mean±SD: 1.05±0.13 flights for *P. pipistrellus* and 1.28±0.41 flights for *P. pygmaeus*). During lactation, this changed to two or even three foraging bouts each night (mean±SD: 2.31±0.38 flights for *P. pipistrellus* and 2.65±0.53 flights for *P. pygmaeus*).

Although there was no significant difference in the number of foraging flights recorded for either species, time spent actively foraging away from the roost was significantly different. *P. pipistrellus* consistently foraged for longer across all years and reproductive stages (mean±SD, 258.4±45.8 min/night for *P. pipistrellus*; 204.0±42.9 min/night for *P. pygmaeus*, three way ANOVA, species effect, $F=8.36$, $p=0.008$, all $df=1,25$) and the year of tracking and reproductive status had no effect on foraging time. No difference was observed in the time spent in the roost during return visits (mean±SD, 71.2±30.23 min/night for *P. pipistrellus* and 87.68±22.67 min/night for *P. pygmaeus*, Mann–Whitney $U=67.0$, $p=0.19$, $df=23$).

Distance to core areas

Kernel analysis revealed a total of 51 core areas of activity for all bats tracked throughout the study. Although a greater

Table 1 Date of capture, sex, biometry, percentage ratio tag/body mass and tracking details of the bats studied

Species	Bat ID (ring number)	Date of capture	Sex	Reproductive status	Mass (g)	Ratio	Days tracked	Time tracked (min)	Max distance
P. pipistrellus	U7233	May 27, 2002	F	Pre-lactating	6.7	5.6	5	1,450	2,778
	U7203	Jul 8, 2002	F	Lactating	6.2	6.3	4	1,420	3,732
	U7204	Jul 8, 2002	F	Lactating	6.8	5.4	3	1,025	2,488
	U6204	Jul 21, 2002	F	Lactating	6.1	6.5	6	2,280	2,653
	U6245	Jul 21, 2002	F	Lactating	6.0	6.3	4	1,230	2,140
	U6235	May 18, 2003	F	Pre-Lactating	4.99	7.4	4	1,395	1,574
	U6061	Jun 16, 2003	F	Lactating	5.75	6.6	5	1,435	2,969
	U6092	Jul 3, 2003	F	Lactating	5.9	6.7	3	980	1,163
	U6054	Jul 6, 2003	F	Lactating	5.78	6.2	5	1,675	2,801
	U6066	July 14, 2003	F	Lactating	5.71	6.4	4	1,370	3,166
	U6074	Jul 21, 2003	F	Post-lactating	6.48	5.8	4	940	3,396
	U6070	Jul 21, 2003	F	Post-lactating	6.0	6.6	3	760	2,596
	U6069	Aug 12, 2003	F	Post-lactating	6.58	5.6	3	715	3,204
	U6152	Aug 13, 2003	F	Post-lactating	6.12	6.2	3	830	1,923
P. pygmaeus	U7206	Jun 10, 2002	F	Pre-lactating	7.5	5.3	6	1,230	1,292
	U6240	Aug 5, 2002	F	Post-lactating	5.85	6.4	6	1,485	2,332
	U6244	Aug 17, 2002	F	Post-lactating	6.51	5.8	6	1,365	2,073
	U6243	May 27, 2003	F	Pre-lactating	5.99	6.0	4	1,185	802
	U6231	Jun 3, 2003	F	Pre-lactating	6.5	5.6	4	1,270	1,154
	U60969	Jun 8, 2003	F	Lactating	7.85	4.9	5	940	903
	U6058	Jun 23, 2003	F	Lactating	5.6	6.6	5	1,515	914
	U6078	Jun 23, 2003	F	Lactating	5.99	6.3	3	795	698
	U6075	Jul 7, 2003	F	Lactating	6.02	6.4	4	1,205	1,147
	U6065	Jul 14, 2003	F	Lactating	6.33	6.0	4	1,235	745
	U6151	Jul 30, 2003	F	Post-lactating	6.35	5.8	5	1,560	2,149
	U6162	Aug 31, 2003	F	Post-lactating	6.1	6.5	4	475	1,658

Time tracked is the total tracking effort, including lost contact. Max distance is the maximum straight-line distance the bat was recorded from the roost of occupancy.

number of core areas were recorded for *P. pipistrellus* (*P. pipistrellus* 32, *P. pygmaeus* 19), this to some extent reflects the difference in sample size between the species, and there was no significant difference in the numbers of core areas utilised by individuals of the two cryptic species (mean± SD, 2.28±0.99 areas for *P. Pipistrellus* and 1.58±0.52 areas for *P. pygmaeus*, Mann–Whitney $U=223.5$, $p=0.089$, $df=23$). The core areas utilised by *P. pipistrellus* were also located much further from the roost than those of *P. pygmaeus* (mean±SD: 1.44±0.55 km for *P. pipistrellus*; max: 3.24 and 0.69±0.18 km for *P. pygmaeus* max: 1.33 km, three-way ANOVA species effect, $F=16.95$, $p<0.001$, all $df=1,25$). The year of tracking and reproductive status had no effect on the distance travelled to core areas.
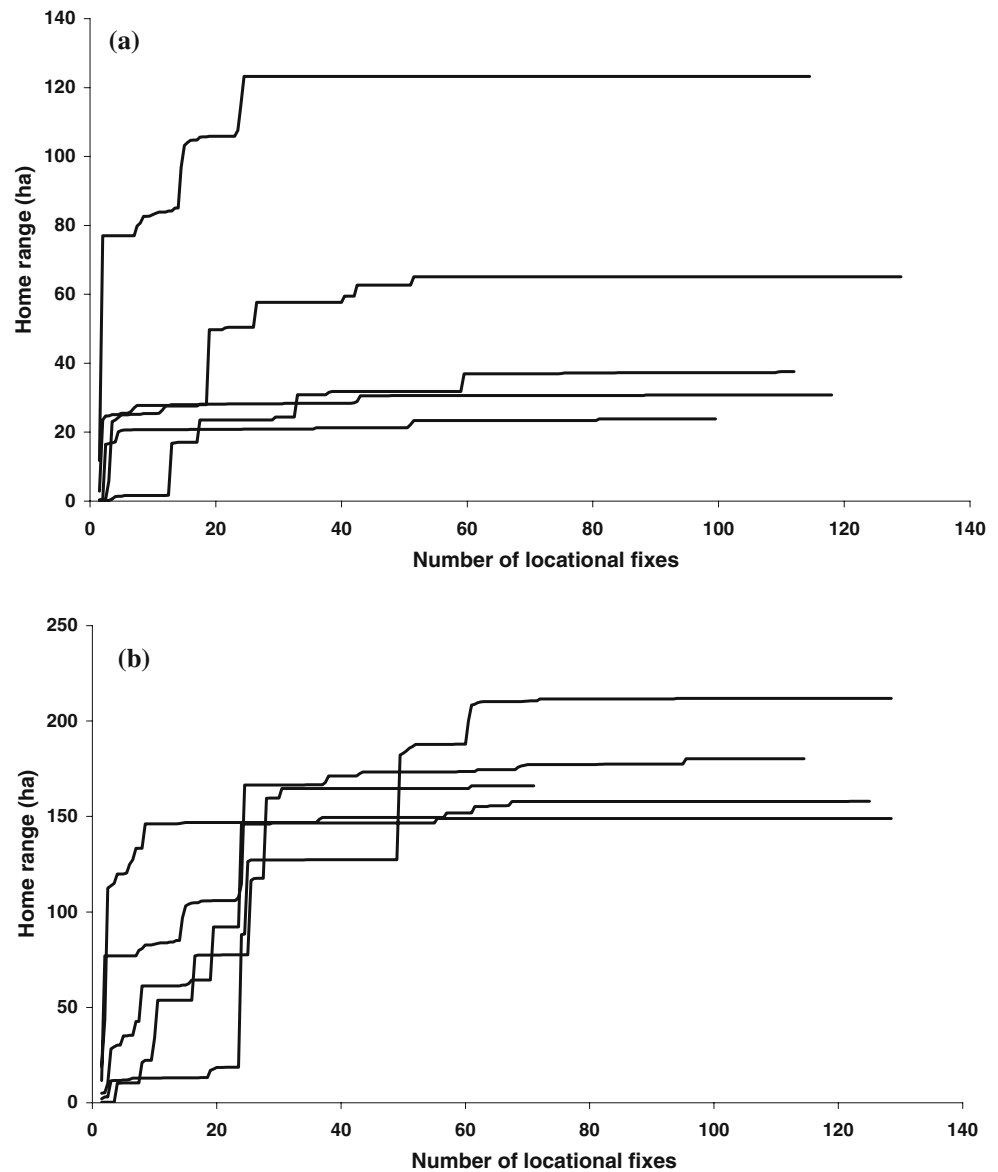
Range overlap

A high level of intra-specific overlap was recorded for both species and for all range estimators (Fig. 4), with certain locations within the study area being utilised on a regular basis by several radio-tracked bats (Fig. 2). Throughout the

radio-tracking period, seven discrete sites were identified within the *P. pipistrellus* colony home range, where core foraging areas of individual bats overlapped. At four of these sites, the core foraging areas of three or more bats overlapped and at two of these sites, the core foraging areas of four or more bats overlapped. These sites clearly represent important foraging areas for this colony and although bats were not recorded foraging at the same place at the same time, observational records and sound recording data confirmed that these sights were being utilised by conspecifics on the nights radio-tracking locations were obtained. Within the *P. pygmaeus* colony home range, core areas of activity were located closer to the roost and were less spatially dispersed. Core foraging areas of individual bats overlapped at four discrete sites and at two of these sites the foraging areas of four or more bats overlapped. Once again, observational and sound recording data confirm the use of these sites by conspecifics on the night of tracking.

At all levels of range estimation, the degree of intra-specific overlap for both species, greatly exceeded the degree of inter-specific overlap (randomization tests:

Fig. 1 Cumulative home-range
size against number of consecu-
tive locations for: **a** five ran-
domly selected, adult female
P. pygmaeus; **b** five randomly
selected, adult female *P. pipis-
trellus*, tracked from May–Sept
2002/2003. Estimates of range
size are based on 100% mini-
mum convex polygons

$p<0.0001$ for 100% MCP; $p<0.0001$ for foraging range;
$p<0.0001$ for 75% kernel. Fig. 2). Even using 100% MCPs,
where range size is likely to be a gross overestimate, the
mean overlap between species was only 2.7% and within
core areas this overlap drops to 0.5%. The core foraging
sites of these two colonies are essentially mutually
exclusive with inter-specific overlap recorded at only two
sites, and even then only at the periphery of cores (Fig. 2).
This is a striking result given the proximity of the two
maternity roosts and suggests almost complete spatial
segregation in the use of foraging areas by these colonies.

Foraging behaviour and general observations

In the present study, the colony home range of *P. pygmaeus*
effectively bordered the river Don, a broad slow flowing
river with deciduously wooded banks, with large tracts of
broadleaved and riparian woodland, and sites where core
areas of this species overlapped incorporated both the river
and adjacent woodland. These sites were in close proximity
to the roost and locally dispersed along a 1-km stretch of
river.

The colony home range of *P. pipistrellus* was spread out
over a much larger area comprised of intensively managed
agricultural land. Broadleaved woodland within this area
was scarce, represented by small tree lines running along
the edge of roads. The only forests were large conifer
plantations that are unlikely to support high insect densities
(Winter 1983). Core foraging areas of this colony over-
lapped in a wider variety of habitat types. Two small
broadleaved tree lines, a forestry road dissecting a conifer
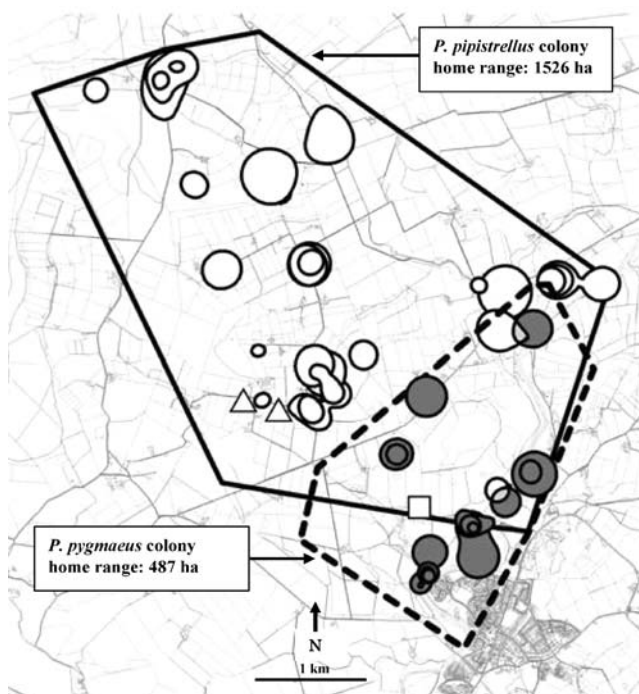plantation adjacent to the maternity roost and a patch of

Fig. 2 Spatial distribution of 14 *P. pipistrellus* and 12 *P. pygmaeus* radio-tracked from May–Sept 2002/2003. Colony home ranges are expressed as 100% MCPs enclosing all accurately recorded locations from all individuals tracked from that colony. Individual range size is expressed as 75% kernel core areas (*P. pipistrellus*: *white*; *P. pygmaeus*: *dark grey*; areas of inter-specific overlap are *highlighted in light grey*). Maternity roosts are represented by *triangles* (*P. pipistrellus*) and *squares* (*P. pygmaeus*)

riparian woodland on the very edge of the colony's range were all used extensively. These sites were interspersed by large areas of improved agricultural land, and consequently

distances travelled from the roost to foraging sites were significantly greater than those of *P. pygmaeus*, and distances between sites were comparable with the maximum distances flown in this species.

Discussion

Studies of ecomorphology in bats predict partitioning of resources linked to differences in echolocation call structure and wing morphology (Fenton 1990). However, studies investigating differences in the wing morphology of *P. pipistrellus* and *P. pygmaeus* have been equivocal (Jones and van Parijs 1993; Haussler et al. 2000), and intraspecific variation in their echolocation calls mean that analysis of call parameters is also subject to a degree of inter-specific error (Vaughan et al. 1997). Therefore, differences in the foraging ecology of these species would be expected to be subtle. However, the results of the present study reveal large and significant differences in the spatial distribution and foraging characteristics of these two cryptic species.

Variation in home-range size

Individual home-range size for *P. pipistrellus* was approximately three times larger than *P. pygmaeus* irrespective of which range estimator was used. For animals that forage by flying, which is estimated to raise energy expenditure by 14.5 times above the basal metabolic rate (Racey and Speakman 1987), this is a substantial difference. Further-

Fig. 3 Mean±standard error of home-range size, for 14 *P. pipistrellus* and 12 *P. pygmaeus*, radio-tracked from May–Sept 2002 and 2003, expressed as 100% minimum convex polygons (MCPs), foraging MCPs (utilising only foraging fixes) and 75% fixed kernel core areas
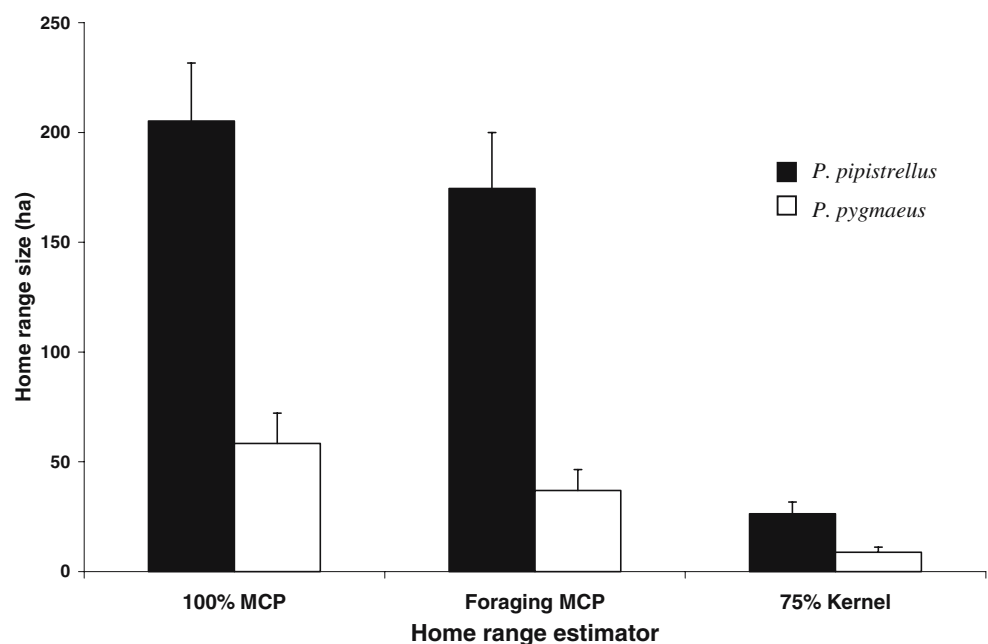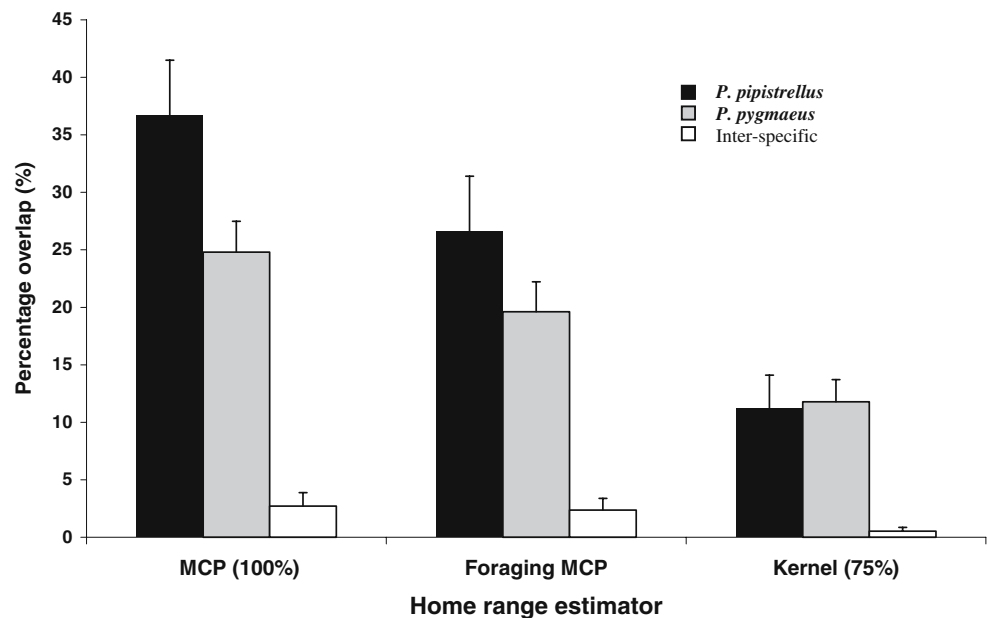
Fig. 4 Mean±standard error of intra- and inter-specific range overlap, for 14 *P. pipistrellus* and 12 *P. pygmaeus*, radio-tracked from May–Sept 2002 and 2003. Estimates of range overlap based on 100% minimum convex polygons (MCPs), foraging MCPs (utilising only foraging fixes) and 75% fixed kernel core areas

more, although the *P. pygmaeus* colony was approximately 2.5 times larger than the *P. pipistrellus* colony, it occupied an area approximately three times smaller, resulting in a higher density of bats per unit area. This is a striking result between two morphologically similar and sympatric species. Intuitively, it would be expected that a larger colony would require a larger home range to meet the energetic demands of more individuals. However, it has been demonstrated for several species that home-range size does not necessarily increase with group size (Macdonald 1983). The Resource Dispersion Hypothesis (RDH) predicts that if there is spatial or temporal heterogeneity in resource availability, then home-range size is predicted to be dependant on the spatial dispersion of resource patches, whereas group size is independent of range size and is instead limited by the richness of available resource patches.

Several studies have identified differential habitat use in the two cryptic pipistrelle species (Vaughan et al. 1997; Russ and Montgomery 2002; Nicholls and Racey 2006), with *P. pygmaeus* foraging preferentially in riparian habitats, over water and in adjacent riparian woodland. *P. pipistrellus*, however, has been recorded foraging over a wider range of habitats, including rivers, lakes, woodland and cattle pasture. The foraging sites used by *P. pipistrellus* in the present study are unlikely to support comparable resources, in terms of insect abundance, as the riparian habitat used by *P. pygmaeus* (Jackson and Fisher 1986; Iwata et al. 2003). Although this would explain the difference in numbers of foraging bats per unit area, the difference in range size is likely to be not only a function of patch richness but of the spatial dispersion of these patches, as predicted by the resource dispersion hypothesis.

One of the main tenets of this hypothesis is that a certain number of resource patches must be included in an animal's home range to ensure a critical probability that sufficient food is available over time (Carr and Macdonald 1986). In an environment where prey availability may vary considerably in time and space, additional food or habitat patches must be included in the home range to reach this critical probability. Consequently, patterns of resource dispersion have a greater influence than resource richness on home-range size (Macdonald 1983). Increasing home-range size with increasing resource dispersion has been reported for a wide variety of species, including high-density badger populations (Doncaster and Woodroffe 1993), red foxes (Macdonald 1981), kinkajous (Kays and Gittleman 2001) and arctic foxes (Eide et al. 2004).

It is therefore plausible that the dramatic difference in range size between these morphologically similar and sympatric species is due to the difference in the spatial dispersion of suitable foraging patches. The open agricultural landscape utilised by the *P. pipistrellus* colony has a higher degree of habitat fragmentation, with a higher patch dispersion necessitating larger range sizes to encompass enough resources to satisfy daily metabolic requirements.

Activity patterns

Temperate zone bats typically have two principal peaks in foraging activity, at dusk and dawn, with a reduction in activity during the night (Anthony and Kunz 1977; Anthony et al. 1981; Barclay 1982; Hayes 1997; Waters et al. 1999), which is attributed to the return of lactating females to the roost to suckle their young, coinciding with a nadir in the density of aerial insects. Similar activity

patterns has been reported for pipistrelle bats (Swift 1980; Maier 1992), with the bats timing their two foraging flights during lactation to coincide with the peaks of insect abundance that occur at dusk and dawn (Lewis 1969a,b; Swift 1980). However, these studies were carried out using roost-monitoring techniques, and the present study is the first that allows the foraging patterns of individual pipistrelle bats to be recorded continually.

The results of the present study broadly confirm those of Swift (1980) and Maier (1992). During pregnancy, bats of both species typically engaged in a single uninterrupted foraging flight returning to the roost before dawn. However, during the lactation period, foraging patterns were not strictly bimodal. There was a high degree of variation in this pattern both between and within individuals, nevertheless three foraging flights per night were common, particularly in *P. pygmaeus*, with the bats returning twice to the roost during the night. Similar trimodal patterns have been recorded for other temperate bat species (Kronwitter 1988; Rydell 1990), with the number of flights being correlated with temperature; and it seems likely that the high degree of variation seen in the present study is due to environmental conditions. In accordance with Swift (1980) and Maier (1992), once the young had been weaned and adult females began to leave the roost, leaving their young to increase body mass, there was a return to a unimodal pattern of activity with a single foraging bout per night.

This increase in the number of flights between the roost and foraging sites must increase the amount of time and energy allocated to flight. Income breeders (those that cover breeding costs by daily feeding), such as bats, cannot forego foraging during the critical lactation period (Kurta et al. 1989; Mclean and Speakman 1999; Racey and Speakman 1987) and may therefore have to increase food intake to compensate. This is accommodated by coinciding the period of highest energetic costs during June and July (Racey and Speakman 1987) with the time of maximum insect abundance.

It is often predicted that the energetic demands of nightly return visits to the roost are further facilitated by a shift to foraging sites closer to the roost, and a reduction in home-range size, a pattern recorded in several species of temperate zone bats (O'Donnell 2001; Shiel et al. 1999; Henry et al. 2002). However, in the present study, no difference in activity time or home-range size between reproductive stages was seen and similar results have been reported elsewhere (Adam et al. 1994). This is not surprising; the hypothesis that bats will have smaller home ranges during lactation (Henry et al. 2002) makes the implicit assumption that foraging resources are dispersed across a homogenous environment, which in the case of insect prey is unlikely to be the case. Bats are clearly unable to shift to foraging closer to the roost during lactation if closer foraging sites are not available. In a fragmented landscape, foraging decisions made by individual bats are clearly constrained by the spatial distribution and resource richness of available sites. In such an intensively managed landscape, the *P. pipistrellus* colony had access to a finite number of productive foraging sites. Similarly, although foraging resources for the *P. pygmaeus* colony were abundant along the river, sites of a similar quality closer to the roost are likely to be limited.

Although there was no difference in activity time between reproductive periods, a significant difference was recorded between species, with *P. pipistrellus* active for approximately an hour longer each evening. This is a substantial difference between two morphologically similar and sympatric species. Foraging pipistrelles can feed at a rate of 10 catches per minute when insect density is high (Racey and Swift 1985). At this rate, pipistrelles are likely to fill their stomachs in 2–3 h of feeding (Stebbings 1986). In the present study, the mean activity time for *P. pygmaeus* was 203 min, which is comparable with this estimate, but the mean activity time of 258 min for *P. pipistrellus* is substantially higher. In many species, time spent foraging is inversely linked to relative food abundance (Schoener 1971). It is therefore possible that the difference in activity times between these species is directly related to the difference in insect availability within their respective foraging sites, with *P. pipistrellus* having to forage for longer to satisfy daily energy requirements.

Previous studies on pipistrelles have also reported large differences in activity time. Monitoring the activity of pipistrelle bats from a roost only 10 km from the present study area, Swift (1980) reported average activity time outside the roost of 225 min. Maier (1992), using similar techniques in Oxford, reported a mean activity time of 321 min. It is impossible to confirm which of the cryptic species was being studied in these cases but the times reported by Maier (1992) are excessive regardless of species. This difference may be due to climactic variation with decreasing latitude or the use of night roosts in an environment where conditions are favourable (Anthony et al. 1981). Kunz (1982) suggested that in more northerly latitudes, where summer nights are shorter, bats tend to avoid an extended night roosting period, and no night roosting was recorded throughout the present study.

Range overlap

Perhaps the most surprising result to emerge from the telemetry data was the extent of the spatial segregation between these two colonies. The core foraging areas of either species are essentially mutually exclusive, despite

the proximity of the two maternity roosts, which are well within the commuting distances recorded for these species (Racey and Swift 1985). Although our results are restricted to a single colony of each species, the absence of *P. pipistrellus* from foraging sites along the river strongly corroborate the results from acoustic surveys carried out across England and Northern Ireland, which revealed differential habitat use between these species (Vaughan et al. 1997; Russ and Montgomery 2002). The similarity in morphology and echolocation call structure between the two cryptic species suggests that they are likely to select for similar habitats and prey items. It is therefore plausible that the spatial partitioning observed in the present study may be driven by inter-specific competition. However, without further study on additional colonies, it cannot be discounted that the observed segregation may simply reflect colony-specific foraging ranges rather than inter-specific spatial partitioning.

The playback experiment of Barlow and Jones (1997) suggests that there is no evidence of inter-specific competition between these two species. However, the absence of current competition does not mean it is unimportant as a structuring force. It is possible that these species do not compete at present because selection in the past favoured an avoidance of competition and subsequent differentiation of niches, commonly referred to as the 'ghost of competition past' (Connell 1980). Whether the nature of this competition was direct or exploitative is difficult to determine. However, if this niche separation was based on selection for different sized insects, then a higher degree of spatial overlap would be expected. It is more likely that selection has favoured the avoidance of competition through differential habitat use, and evidence for this is mounting (Vaughan et al. 1997, Russ and Montgomery 2002).

It is possible that the results presented in this study represent an extreme situation. The study area represents the northern edge of the distribution for these species. A strong correlate of latitude is climate, with increasing latitudes subject to an increase in rainfall, reduced ambient temperatures, shorter night length and higher winds, all of which inhibit the foraging activity of bats and the abundance of insects. If niche partitioning between these species is being driven by competition, then at the extreme edge of their range, competition between these species would be heightened, leading to an increase in habitat partitioning, and spatial segregation between the species. One obvious prediction of this is that the degree of spatial overlap between the two cryptic species would increase with decreasing latitude. Similarly, if as predicted, the difference in range size is linked to a difference in the spatial dispersion of available patches, which in the present study is exacerbated by the intense habitat modification for agriculture in the north east of Scotland, we could predict that in an area

subject to less habitat fragmentation the difference in range size between these species would be lower.

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