

Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland

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Abstract

Over the past 50 years European populations of the lesser horseshoe bat *Rhinolophus hipposideros* have severely declined, probably because of the loss of foraging habitat. To date, studies of the foraging behaviour of this species have been limited as its low mass (4–8 g) precluded the use of radio-telemetry because commercially available radio-transmitters exceeded 10% of its body mass. In this study, radio-transmitters weighing < 0.35 g were built. These increased the body mass of the animals from 4.5% to 8.1%, with no demonstrable adverse effect on their flight behaviour. The habitat selection of eight female lesser horseshoe bats was studied in Monmouthshire, U.K. The bats had foraging ranges between 12 and 53 ha (100% kernel). Although one bat foraged 4.2 km from the roost, for 50% of the time tracked bats were recorded within 600 m of the nursery roost. The estimated density within 200 m of the roost was 5.8 foraging bats/ha. This decreased to 0.01 bats/ha at 1200 m. Compositional analysis revealed that this species used woodlands, predominately broadleaf, more than any other habitat. In addition, the bats foraged in areas of high habitat diversity. Conservation management of this species should concentrate on such areas within 2.5 km of the nursery roost.

Key words: *Rhinolophus hipposideros*, population decline, habitat use, spatial use, conservation, management

INTRODUCTION

The lesser horseshoe bat *Rhinolophus hipposideros* is one of the most endangered European bat species (Stebbins, 1988). It was once widespread and common in most countries of Western and Central Europe, e.g. the Netherlands (Voûte, Sluiter & van Heerdt, 1980), south Poland (Kokurewicz, 1990), Germany (Rudolph, 1990) and Switzerland (Stutz & Haffner, 1984). A dramatic population decline occurred in the 1950s and 1960s, which led to the loss of large areas of its former distribution.

Several causes for this decline have been suggested; roost destruction, pesticide contamination of prey and roosts, habitat alterations and competition with other bat species (overview in Stebbins, 1988; Kulzer, 1995; Arlettaz, Godat & Meyer, 2000). However, it is believed that habitat destruction and the effects of pesticides are the main causes of the population decline (Bontadina, Arlettaz *et al.*, 2000).

In order to plan and implement adequate protection measures for this species, a basic knowledge of its habitat selection is required. To date several attempts have been made to study habitat use in lesser horseshoe bats either using ultrasound detectors or by light-tagging animals (McAney & Fairley, 1988; Schofield, 1996). However, the very weak and highly directional echolocation calls of this bat make it difficult to detect in the field. In addition, light-tagged animals quickly disappear into dense vegetation making them hard to follow. Consequently, data collected by these methods has been limited.

Since the 1980s, radio-tracking has developed as one of the main techniques for studying many aspects of bat ecology (Kenward, 1992; see overview in Bontadina, Scaravelli *et al.*, 1999). However, the small body mass of many species, including the lesser horseshoe bat, has precluded the use of radio-telemetry as the smallest transmitters exceeded the justifiable surplus weight they added to these animals (Aldridge & Brigham, 1988). Recent advances in transmitter technology have reduced the mass of radio-tags to the point at which it is feasible to radio-track species such as lesser horseshoe bats. In this study new lightweight

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transmitters were used to investigate the habitat use of this species in Wales.

The aims of our study were: (1) to investigate the performance of the new lightweight radio-tags; (2) to collect data on range and habitat use for the species for the first time by radio-tracking and to compare these results with those obtained by other methods; (3) to make proposals for the conservation of lesser horseshoe bats based on the results of the study.

METHODS

Study site, capture methods and selection of study animals

The study was conducted during July and August 1997, and May and June 1998 at a nursery colony of *c.* 300 animals roosting in the roof void of an old church in the Lower Wye Valley, South Wales, U.K. (51°48'N, 2°42'W) (Warren, 1998). The roost is situated 600 m from the River Wye at an altitude of 160 m on a wooded side of the valley. Although some large intensively managed agricultural fields do exist, traditional pastoral farming methods predominate in this area. Copses at the edges of fields have been retained as well as many hedgerows and tree-lines enclosing fields of grazing pasture.

To minimize the disturbance to the colony, the bats were caught in mist nets along flight lines at points between 10 and 30 m from the church when they left the roost at dusk. After capture, bats were held in catch bags before biometric data was obtained. Mass was recorded to an accuracy of 0.1 g and forearm length to 0.1 mm. Animals were sexed and the reproductive condition of the females was assessed. Parous females were identified by the presence of large pelvic nipples (Gaisler, 1963) and palpably pregnant animals were recorded. Bats were assigned to 1 of 3 age classes: class 1, yearlings identified by their grey pelage (Gaisler, 1963); class 2, bats > 1 year but which showed no sign of extensive tooth wear; class 3, estimated as older animals from extensive tooth wear. Only females were used for the tracking study as sex differences in habitat selection would have been difficult to determine with a small sample size. The females were selected for tagging depending on their reproductive condition and size. Heavily pregnant females were avoided. Larger animals (in terms of their forearm length) were selected to reduce possible adverse effects of carrying the transmitter mass.

Radio-transmitters and tracking methods

The bats were tagged with transmitters that were based on the design in Naef-Daenzer (1993), these ranged in mass from 0.332 to 0.440 g, including zinc-air batteries. In the second year, 4 bats were tagged with 0.4 g Titley LTM transmitters (Titley Electronics, New South

Wales, Australia, www.titley.com.au). The transmitters were attached to the back of the bats between the scapulae, the fur was trimmed and the tag was glued close to the skin using surgical cement (SkinBond, Smith & Nephew United Inc., Largo, Florida, U.S.A.). The transmitter batteries had a minimum life of 8 and 11 days, respectively. Bats were tracked using TRX-1000 (Wildlife Materials Inc., Illinois, U.S.A., www.wildlifematerials.com) and modified YEASU FT-290 receivers (adapted by Karl Wagener, Telemetrie-Material, Köln, Germany) with hand-held H-aerials.

The locations of the tagged bats were recorded in 5-min intervals throughout the night by triangulating the signal direction. Two field workers co-ordinated their simultaneous bearings using trigger signals from Casio DB-31 watches, and they remained in contact with one another using hand-held FM-radios. If one person lost contact with the bat, the other either tried 'homing-in on the animal' (White & Garrott, 1990), or simulated cross-triangulation by taking a bearing in one position and then moving 50 m in < 30 s before taking the second bearing. This was only possible with any reasonable accuracy when the animal was foraging in a small area. Locations were assigned to 1 of 3 accuracy classes (50, 100 and 250 m) depending on confidence in the estimated location. The highest accuracy class (50 m) could only be assigned when we were in close proximity to the bat. The accuracy of these classes was determined during a field test at night with a transmitter being moved around in a foraging area by a colleague. A test of the deviation of the estimated locations from exactly known locations (location error method; Zimmermann & Powell, 1995) gave a location error of $\pm 9.3^\circ$ (SD) with the estimated locations bivariately normally distributed around the 'true' transmitter positions. The locations of the estimated accuracy classes of 50, 100 and 250 m had their centre not significantly different (*t*-test, $P < 0.01$) from the 'true' centre, the standard deviations of the normally distributed location errors were 44, 85 and 162 m, respectively.

Time, location of observers, bearings on the bats, accuracy data and general observations were recorded in the field on a Dictaphone and later transcribed onto data sheets. The positions of the bats in the field were calculated from the bearings and their estimated location written into a geographical information system (GIS) MapInfo (MapInfo, New York, U.S.A., www.mapinfo.com).

Analysis of ranging behaviour and habitat use

The habitat in the area was divided into 11 categories: broadleaf woodland, mixed woodland, conifer woodland, tree-lines, hedgerows, bare areas (including roads), water, riparian vegetation, settlements, arable, pasture. These habitats were mapped into the GIS using 1:25 000 Ordnance Survey Maps and aerial photographs.

The foraging ranges of the tagged bats in Table 3 were determined by 2 methods: (1) using a minimum

Table 1. Morphological and reproductive measurements of the 12 radio-tagged *Rhinolophus hipposideros* bats. Age class 1 animals are yearlings (for detailed definition see Methods)

Date of capture	Animal code	Forearm (mm)	Mass (g)	Breeding status	Pelvic nipples	Age class
15 Jul 97	F5	39.2	6.2	Post-lactating	yes	2
16 Jul 97	F4	39.2	6	Post-lactating	yes	2
24 Jul 97	F7	38.8	6	Post-lactating	yes	2
24 Jul 97	F9	38.6	6	Post-lactating	yes	2
28 Jul 97	F8	37.3	7.4	Post-lactating	yes	2
12 Aug 97	F6	38.1	6	Post-lactating	yes	3
13 Aug 97	F16	38.1	6.1	Post-lactating	yes	2
31 May 98	F3	36.4	4.7	Not pregnant	no	1
31 May 98	F15	39	5	Not pregnant	no	1
7 Jun 98	F17	37	5.1	Not pregnant	no	1
7 Jun 98	F2	37.7	4.8	Not pregnant	no	1
15 Jun 98	F14	37.4	4.9	Not pregnant	no	1

convex polygon (MCP) of all locations; (2) the 100% contour line of a kernel estimation (Harris *et al.*, 1990). For better comparability, the smoothing factor h was set to 100 m (Naef-Daenzer, 1994). To determine the polygon, the tracking locations were buffered by circles with radii of 44, 85 or 162 m depending on the SD of their assigned accuracy class, and the MCP was calculated around these buffered locations for each tracked bat. The areas covered by these ranges and the distances at which individuals foraged from the roost were determined in the GIS. The relationship between the number of locations and foraging range was computed using the animal movement extension in ArcView (Hooge & Eichenlaub, 1997). The estimation of foraging density was calculated based on the utilization density of the radio-tracking locations and a colony size of 300 bats was assumed.

Habitat selection was investigated on 2 levels.

(1) On a broad scale, the selection of foraging ranges was compared to the available habitat. The available foraging area was taken as that falling inside the MCP around all tracking locations of all bats. The habitat within this available area was compared with the habitat within the MCPs of individual bats.

(2) On a fine scale, the habitat selected by individual bats within their foraging range was studied. This was done by comparing the core foraging areas used within the MCP of every bat with the habitat available within that individual MCP. Core foraging areas were defined by the 50% contour lines of the fixed kernel estimation (Worton, 1989) in the program GRID (Naef-Danzer, 1994) and on the GIS ArcView (Environmental Systems Research Institute Inc., California, USA, www.esri.com; Hooge & Eichenlaub, 1997). Least square cross-validation LSCV as recommended by Seaman *et al.* (1999) was not used because different smoothing factors for different animals make comparisons unfeasible. To take account of the different accuracies of the locations, the standard deviation of the accuracy class (44, 85, 162 m respectively) was used as the estimator h and the resulting densities adjusted according to n to achieve correct information from all accuracy classes (Bontadina & Naef-Daenzer, in press).

One problem in habitat selection analysis is that the area of a specific habitat class is inversely correlated with the area of the other classes (Otis & White, 1999). To avoid this constraint compositional analysis was used to investigate habitat selection (Aebischer & Robertson, 1992; Aebischer, Robertson and Kenward, 1993). This non-parametric technique uses the single animal instead of the locations as sample unit. Statistics were computed with an Excel macro (P. Smith, pers. comm., pgsmith@aber1.fsnet.co.uk, beta version of an unpublished program), which also carried out the randomization procedure recommended by Aebischer *et al.* (1993).

For the calculations of habitat diversity, the Levins Index (Krebs, 1989) was used, where

$$B = 1/\sum(p_i^2).$$

This index ranges from 1 to n , where n is the number of habitat classes. In our study, 11 was the theoretical maximum. The indices of the bats were compared with the habitat diversity of 428 generated random locations and tested these with the Dixon Sign Mood Test (Sachs, 1992) according to Kenward (1992).

General observations

Throughout the study, general observations of the bats behaviour were recorded both visually and with Pettersson D240 mini bat detector (Pettersson Elektronik AB, Uppsala, Sweden, <http://www.batsound.com>). Notes were also taken of any other buildings or structures used by the tagged bats.

RESULTS

Ninety lesser horseshoe bats were caught during the study, of which 24.4% were males. Twelve of the largest non-pregnant or post-partum females were selected and fitted with radio-transmitters. The non-pregnant animals were all young from the previous year (age class 1), the remaining tagged animals were age class 2;

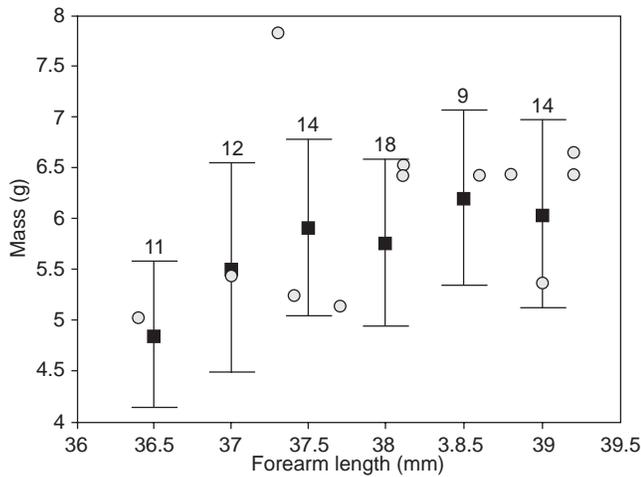


Fig. 1. Mass of the lesser horseshoe bats *Rhinolophus hipposideros* in relation to forearm length. The body mass of $n = 78$ untagged lesser horseshoe bats caught when emerging from the roost is given as error bars (mean \pm SD) for weight categories. The weight of the 12 radio-tagged bats (including transmitter and attachment cement) are marked with circles.

only one animal had excessive tooth wear and was classified as age class 3 (Table 1).

The use of small transmitters for tracking lesser horseshoe bats

The transmitters increased the body mass of the animals by 4.5–8.1%. With one exception, this increase in mass was within 1 SD of the mass of all bats caught in the respective category of forearm length (Fig. 1). The weight of one post-lactating female, which was caught returning to the roost after 1 h of foraging was 35% higher than the mean mass in the relevant category of size. She was fitted with one of the smallest available transmitters (0.332 g).

After the attachment of the transmitters, most bats either immediately returned to the roost or hung in trees close to the release site and spent time trying to groom off the tags. This period lasted between 20 and 150 min, after which they left to forage. One tagged animal flew back to the roost and did not emerge again to forage that night.

A total of 309 locations was collected from eight bats during tracking sessions that lasted between 1 and 4 nights. Another four tagged bats either left the area or the transmitters failed before sufficient data could be collected. During the sessions, our mean contact time with the animals while they were foraging was $47 \pm 22\%$. The transmitters remained attached to the bats between 2 and 16 days and had a maximum range of 1150 m. This range dropped to < 100 m in wet woodlands, when the animals flew in dense vegetation or when they flew close to the ground.

The bats showed multimodal phases of activity with two to four foraging bouts (mean 2.4 of 13 nights with

Table 2. Availability of habitats around the roost of *Rhinolophus hipposideros*. COR, habitat types marked with the same letter are significantly positive correlated with each other ($P < 0.05$, two-tailed)

Habitat	Availability in %	COR	Classes regrouped to
Pasture	59.0	A	Pasture
Arable land	13.4	B	Arable
Broadleaf woodland	8.5		Woodland
Settlement	4.9	C	Rest
Coniferous woodland	4.8		Woodland
Bare areas	2.9	C	Rest
Tree-lines	1.7	B	Arable
Hedgerows	1.6	A	Pasture
Mixed woodlands	1.5		Woodland
Riparian vegetation	1.0	D	Rest
Water	0.7	D	Rest

complete data). Analysis of the time at which location data were taken during three periods of the night (22:00–24:00, 24:00–02:00 and 02:00–04:00) showed no difference in our sampling efficiency over the night (Friedman-test, $n = 8$, d.f. = 2, $P = 0.88$, NS), therefore the location data was treated as representative samples of foraging activity during the night.

Ranging behaviour and habitat selection

The colony range was predominantly grazing pasture (59%) with woodlands (14.8%) and arable fields making up 13.4% of the available habitat (Table 2). Although there were long lines of hedgerows and treelines in the study area, they both accounted for $< 2\%$. The following pair of habitats were significantly correlated ($P < 0.05$): pasture and hedgerows, arable land and treelines, settlement and bare areas, riparian vegetation and water. This means that the resolution of the radio-tracking locations does not allow discrimination between, for example, hedgerows and pastures, which always were adjacent to each other. To reduce the number of variables for compositional analysis, correlated habitats were combined.

Range sizes determined by radio-tracking increase depending on the number of locations. At the beginning of a session this relationship is very steep and then approaches an asymptote when the maximal area is reached. Asymptotes for foraging range were achieved in four of the eight animals (three at 30 locations and one at 90). Therefore we calculated the absolute foraging range area for these four bats, for the others the calculated area is a minimum foraging range. The bats had foraging ranges between 1 and 368 ha using the MCP method, but the more precise 100% kernel method gave areas of 12–53 ha (Table 3). The three non-pregnant sexually immature animals tracked in May and June all had larger foraging areas than the

Table 3. Radio-tracking data of eight successfully tracked *Rhinolophus hipposideros*. The size of foraging areas is given by minimum convex polygons (MCP) and by 100% contour lines of kernel estimation (kernel)

Animal code	Breeding status	Number of locations	Foraging area (MCP, ha)	Foraging area (kernel, ha)	Maximum distance to main roost (m)
F3	Not pregnant	8	25.7 ^a	32.5 ^a	994
F17	Not pregnant	63	368.4	52.5	2488
F14	Not pregnant	36	229.5	52.3	4177
F5	Post-lactating	11	1 ^a	12.8 ^a	249
F4	Post-lactating	9	2.6 ^a	11.9 ^a	282
F7	Post-lactating	96	20.4	28.4	882
F8	Post-lactating	30	8 ^a	15.2 ^a	560
F16	Post-lactating	56	57.9	32.2	273

^a Minimum used area, curve of area in relation to sample size reaches not an asymptote.

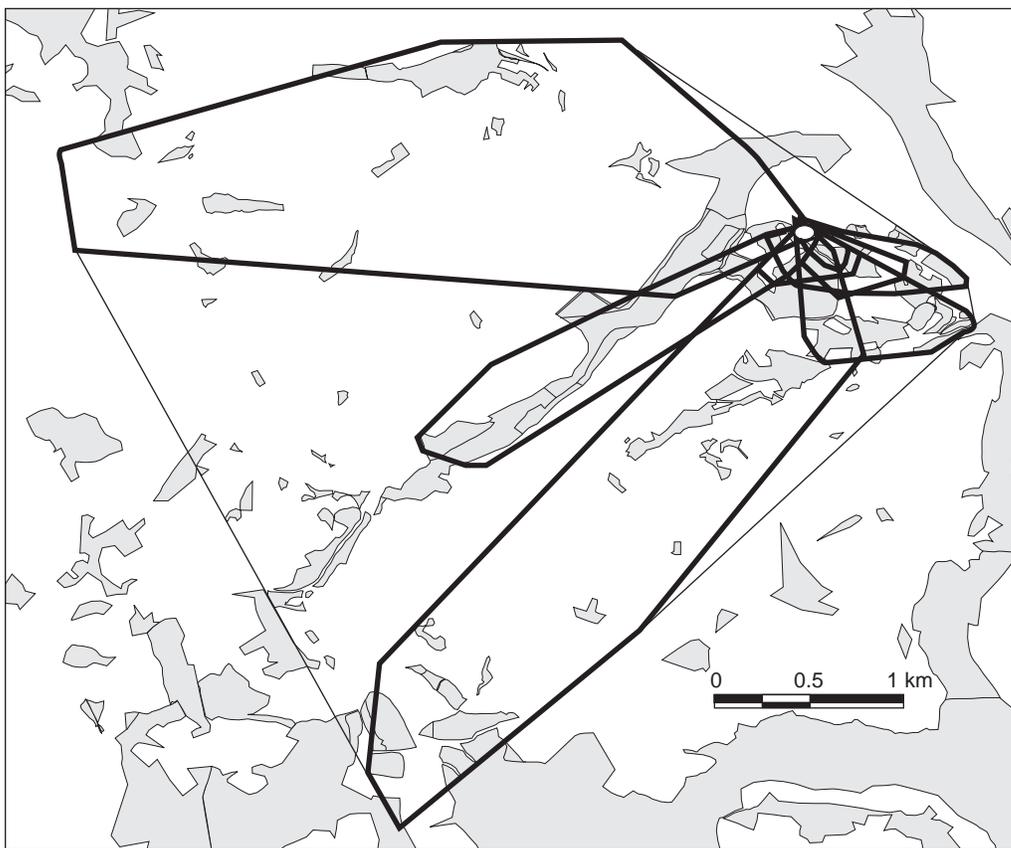


Fig. 2. Foraging ranges (MCP) of eight radio-tracked female *Rhinolophus hipposideros* bats caught near the nursery roost (white dot). The colony range is given as the MCP around all foraging ranges. Woodlands are marked in grey.

post-partum females tracked in July and August. The foraging ranges extended in all directions around the nursery roost (Fig. 2). Fifty per cent of the tracking locations were made within 600 m of the maternity roost. If a random sample of the studied bats is assumed, this indicates that bats from the colony foraged half of their time within this distance of the roost. The maximum distance a bat was recorded from the roost was 4.2 km. Within 200 m of the maternity roost, the estimated density of foraging lesser horseshoe bats was 5.8 bats/ha, decreasing to 1 bat/ha at 390 m

and 0.01 bat/ha at 1200 m (Fig. 3a). If the utilization pattern is compared to a uniform distribution, foraging areas up to 2.3 km from the roost are used more than expected (Fig. 3b).

Habitat selection was investigated in two steps. The first step shows which habitats the bats selected for foraging (see the individual foraging ranges in Fig. 2). Compositional analysis of the foraging ranges of the bats compared with the overall colony range revealed woodlands as significantly selected over all other habitat types ($\chi^2 = 10.86$, d.f. = 3, randomized $P < 0.05$; Fig. 4a).

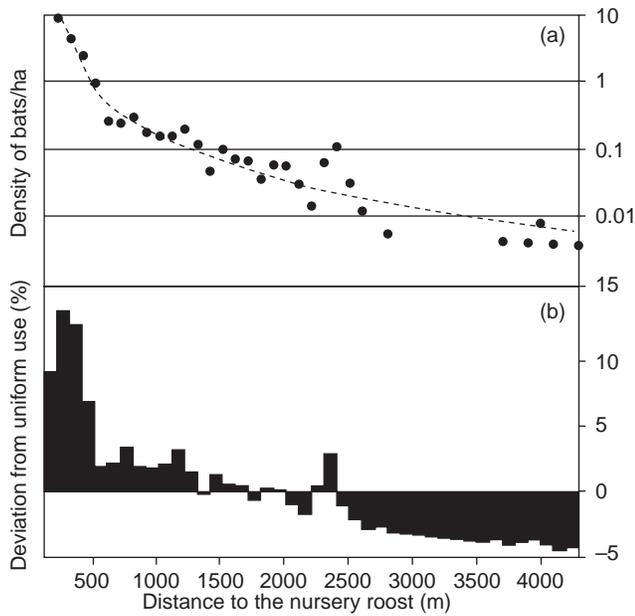


Fig. 3. (a) Variation in estimated logarithmic density of lesser horseshoe bats *Rhinolophus hipposideros* with distance from the roost. Dotted line, regression power function. (b) Deviation of the observed frequency of locations ($n = 309$) when compared with a model of uniform spatial use.

Pasture and arable areas were the habitats least used by foraging bats.

In the second step, how bats selected their core foraging areas was investigated. The comparison of core foraging areas with individual foraging ranges again showed woodlands ranking in first place, being significantly selected over pasture and arable ($\chi^2 = 13.98$, d.f. = 3, randomized $P < 0.05$; Fig. 4b). The rest, composed of settlement, bare areas, riparian vegetation and water, was selected over pasture.

Woodland in the core foraging areas accounted for $58.7 \pm 5.2\%$ (mean \pm SE) of the habitat. In contrast, the amount of woodland in the foraging ranges was $40.8 \pm 4.2\%$ and in the colony range it was only 14.8%. In the core foraging areas of all eight bats, broadleaf woodland predominated over other woodland types. One bat foraged in riparian vegetation 4.5 times more frequently than expected from the proportion of available habitat.

The habitat diversity was larger in the foraging areas (used) than in the colony range (available) of all eight bats ($B = 2.39$ (median, interquartile range: 1.87–2.98) and $B = 1.48$ (1.14–2.03, respectively, sign test, $n = 8$, $P < 0.01$).

General observations

The tracked bats used three night roosts: one in a derelict ice-house, another in an outbuilding of a farm and the third in an old deserted building with a large attic space. This building was also used as an alternative day roost by one bat during the study.

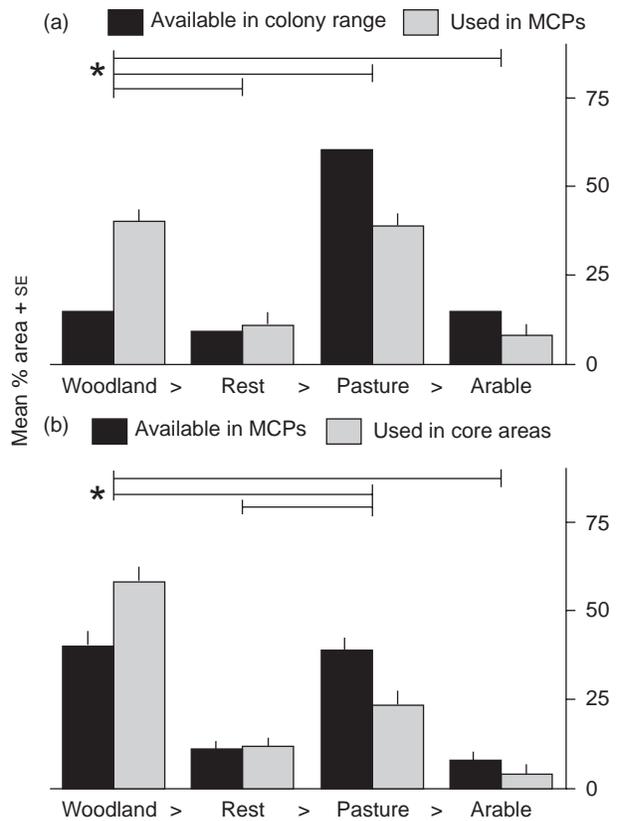


Fig. 4. Habitat selection by *Rhinolophus hipposideros*: comparisons of habitat available vs habitat used (mean percentage area \pm SE). Classes to the left of the symbol > are selected over those to the right. *, significant differences ($P < 0.01$, compositional analysis) between those habitat classes connected by a line. (a) Selection of foraging ranges: comparison of the habitat available in the colony range (defined as the minimum convex polygon MCP of all animals; see Fig. 2) with the mean foraging ranges (MCP). (b) Selection of core foraging areas: comparison of the individual foraging ranges (available area, defined as MCP) with individual core foraging areas (defined as 50% kernel density contours).

Direct observations of the tracked bats were difficult. However, on two occasions it was possible to observe the foraging behaviour of tagged bats. One bat was observed foraging high in the canopy of a tree. Its behaviour suggested it was catching insects flying within foliage or gleaning them off the outer edge of the canopy leaves. It was not possible to detect the echolocation calls of this bat on a heterodyne detector. The other bat was observed repeatedly flying a beat along the side of woodland track just below the canopy.

DISCUSSION

Relevance of the new lightweight transmitters

To date the smallest bat species studied by radio-tracking have had a mass between 8 and 15 g, e.g. *Myotis bechsteinii* (Schofield & Morris, 1999), *Myotis*

emarginatus (Krull *et al.*, 1991), *Myotis nattereri* (Smith, 1999), *Eptesicus nilsonii* (e.g. De Jong, 1994), *Plecotus auritus*. (e.g. Fuhrmann & Seitz, 1992) and *Plecotus townsendii* (Adam, Lacki & Barnes, 1994). Eight of the 31 European bat species weigh between 4 and 8 g (Schober & Grimmberger, 1987). This study has shown that their foraging and ranging ecology can now be investigated by radio-tracking.

The main drawback in using transmitters trimmed for minimum weight was their very short transmitting ranges, making it difficult to detect the bats in dense vegetation or when they were close to the ground. This may place limitations on their use in some species.

The additional weight of carrying radio-tags on flying animals has consequences for both their energetic costs and their manoeuvrability (Caccamise & Hedin, 1985; Hughes & Rayner, 1991). It is recommended that tags should add < 5% of the mass of flying animals (Aldridge & Brigham, 1988). However, small bats can carry larger loads relative to their body mass than larger species (Norberg & Rayner, 1987). This is similar to the situation in birds where Caccamise & Hedin (1985) showed that for a 5% reduction in surplus power, a 10 g bird could carry a transmitter weighting > 25% of its body mass, while a 100 g bird can carry only about 8% of its body mass. In addition, the mass-carrying capability may also be greater in species with a low wing loading, such as the lesser horseshoe bat (Norberg & Rayner, 1987).

The body weight of small flying animals changes following feeding and during pregnancy by much more than 5%: Hughes & Rayner (1993) found short-term differences of 17% in mean body mass of pipistrelles, and Kurta & Kunz (1987) report that the foetal mass of heavily pregnant bats represents 30–40% of their body mass. Female lesser horseshoe bats have been observed carrying young weighing up to 50% of their body mass (Kokurewicz, 1997).

Consequently, as the bats were not tagged when heavily pregnant, the tracking sessions should not have artificially altered their foraging behaviour. Moreover, if the surplus weight had reduced manoeuvrability, then the bats would be expected to forage less in cluttered vegetation (Aldridge, 1985–86). As our results indicate that the habitat class with the most cluttered vegetation was selected over all the others, any reduction in manoeuvrability did not mask this selection.

Carrying the weight of the tag could limit the bats foraging stamina and hence their food intake with consequences for their fitness. However, as the transmitters are only attached for a few days, this effect is probably fairly limited.

Habitat selection in accordance with morphological predictions

Bats of the rhinolophid family are specialized having broad wings with narrow tips resulting in a generally slow but highly manoeuvrable flight (Neuweiler, 1989)

and also having high and constant frequency echolocation calls with a high duty cycle. This enables them to detect fluttering insects amongst cluttered vegetation (Von der Emde & Menne, 1989) and is probably a prerequisite for selective foraging (Jones, 1990). Both of these specializations can be seen as an adaptation to foraging in highly cluttered environments (Schnitzler & Oswald, 1983). This is supported by our results on habitat use, which revealed that lesser horseshoe bats foraged mainly in woodland. The lesser horseshoe bat is the smallest member of the 69 rhinolophid species (Nowak, 1994). Its wings have the smallest aspect ratio within the family (Norberg & Rayner, 1987) and other morphological traits that enhance its wing camber (Stockwell, 2001). From a morphological point of view it should be the most capable of all the rhinolophids at foraging in cluttered vegetation. Schofield (1996) reported seeing lesser horseshoes flying in the canopy of trees. However, in this study only one animal was observed foraging within the foliage of the crown of a free-standing tree. Only two direct observations were made, even though observers were often very close to the tracked animals, and this reinforces the assumption that they often forage within vegetation and are therefore hidden from view.

The habitat choice of female bats is mainly determined by the selection of the nursery roost (second order selection in Johnson, 1980). Schofield (1996) analysed roost sites with respect to their surrounding landscape and found deciduous woodlands to be the main habitat class associate with lesser horseshoe roosts. Our results support these findings.

Earlier landscape studies indicated that broadleaf woodland may be the key foraging habitat of this species. This study of individual bats from one colony has quantitatively confirmed these indications. Moreover, correlative evidence was found that areas with high habitat diversity were the most favoured foraging grounds. It is not known whether areas of high habitat diversity are selected because of enriched food resources or an enlarged foraging space.

The habitat selection determined in this study only partly supports the predictions made from dietary analysis of this species. Beck, Stutz & Ziswiler (1989) found Diptera, Lepidoptera and Neuroptera in faecal pellets from Swiss populations of lesser horseshoe bats. They suggested this might indicate foraging in riparian vegetation or along well-structured hedgerows. In this study no overall selection for riparian vegetation was found. This discrepancy could be derived from different habitat selection in different geographical areas, as documented in the greater horseshoe bat *Rhinolophus ferrumequinum*. In Wales and England this bat species foraged mainly in ancient woodlands and along vegetative structures in pastures (Jones & Morton, 1992; Duvergé, 1996), whereas in Luxembourg, Switzerland and Italy it foraged along the riparian vegetation of rivers and streams (Pir, 1994; Bontadina, Hotz *et al.*, 1997; Bontadina, Scaravelli *et al.*, 1999).

Flight performance in bats is influenced by wing

morphology (Norberg & Rayner, 1987). Jones, Duvergé & Ransome (1995) used this to predict the foraging range of several species. In their model, the lesser horseshoe bat (aspect ratio 5.7; Norberg & Rayner, 1987) was predicted to have a foraging range of 1.3 km, which agrees closely with our results. However, the distances flown by the non-lactating females showed that these individuals could forage at a much greater distance.

If the results revealed by radio-tracking are compared with those of former studies, it becomes apparent that some types of data cannot be recorded using other methods. This is particularly true in determining the range use of bats where their low foraging density away from the nursery roost and the difficulty in detecting their echolocation calls in the field makes any ultrasound detection study unfeasible.

This study was based on one of the largest colonies of lesser horseshoe bats known in Western Europe (Ohlendorf, 1997). Our results revealed that the colony was foraging half of the time within a radius of 600 m around the nursery roost. If large colony size increases the foraging range of individuals (Jones *et al.*, 1995), the average foraging distances in smaller colonies may be even smaller. Densities of up to 5.8 bats/ha foraging near to the nursery roost were estimated. In comparison, Rydell (1992) found about 1.8 bats/ha along illuminated streets where street lamps artificially attract moths and lead to insect densities hardly ever found in nature. The high densities of foraging bats around large nursery roosts must result in a high predation pressure on insects and strong competition between individual bats. Therefore the amount of woodland around maternity sites could determine colony size.

An understanding of the causes of the large-scale decline in this species is needed if the success of long-term conservation measures are to be realized. This study may help to explain this decline. If woodland is the key habitat of this species and if habitat destruction has caused its large-scale decline, a reduction in woodland cover in the same geographical areas and at the same time as the populations declined would be expected. However, the greatest loss of woodlands in Britain occurred in the 18th and 19th centuries (Rackham, 1980), long before the populations of this bat species collapsed after the 1960s (Stebbing, 1988). In the second half of the 20th century the amount of woodland has even increased in some areas (Smout, 1997). As the bats seem to exploit the habitat immediately surrounding their roost, there could be individual colonies of lesser horseshoe bats affected by small-scale reductions of woodland in their vicinity. However, it seems implausible that the large-scale reduction in population was caused by the destruction of woodland. An alternative hypothesis is that the quality of the habitat in woodlands has been reduced, resulting in a reduction in the availability of suitable prey and the decline in the bat population. To determine this would require further study of micro-habitat selection and prey availability within woodlands.

Recommendations for conservation

From this study the following recommendations can be made.

(1) Conservation measures for lesser horseshoe bats should be undertaken within 2.5 km of nursery roosts, with special consideration to the area within 600 m of the roost.

(2) The quantity of woodland and the diversity of habitats within these areas should be maintained and where possible enhanced, especially close to the roost.

(3) Further studies should be undertaken to determine whether the habitat selection found in this population of lesser horseshoe bats is consistent with populations in other regions of Europe. Further study is also needed both to derive more detailed information on the woodland microhabitats used by this species, and to investigate seasonal variation in habitat selection.

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