Foraging Habitat Preferences of Vespertilionid Bats in Britain
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Foraging habitat preferences of vespertilionid bats in Britain

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Summary

1. The selection of foraging habitats by vespertilionid bats in Britain was quantified using a stratified sample of 1030 1-km squares.

2. Quantitative analysis of habitat preference and avoidance on a large scale indicated that bats were flexible, yet consistent in their habitat use across contrasting landscapes. Habitats associated with broadleaved woodland and water were most preferred, while arable land, moorland and improved grassland were strongly avoided. Linear vegetation features were selected in all landscapes, demonstrating the importance of habitat continuity to bats. The availability of preferred habitats was low and patchy in all landscapes, indicating that bats have specialized habitat requirements. Differences in habitat selection between landscape types and possible factors influencing habitat selection are discussed.

3. Habitat selection analysed on a local scale demonstrated the same consistent preference for woodland, riparian and corridor habitats across 19 discrete land classes.

4. Management policies for bats in Britain should endeavour to preserve and enhance the availability of woodland, water margins and linear corridor habitats. Lack of continuity of the landscape, loss and fragmentation of habitat patches plus deterioration of the quality of such patches may pose a threat to bat populations.

Key-words: corridors, fragmentation, habitat availability, landscapes, stratified survey.


Introduction

The accurate description of habitat requirements for rare species such as bats is a key part of conservation management. Bats follow an extreme ‘K-strategy’ life history, and are thus particularly vulnerable to environmental changes which lead to reduced longevity or reproductive success. Modifications to, and loss of foraging habitats may strongly affect such life history parameters, and it has been suggested that land-use change is one of several causal factors contributing to recent population declines for some species of European bats (Daan 1980; Stebbings 1988; Gerrell & Lundberg 1993).

In Britain, increasing anthropogenic pressures and changing agricultural practices have greatly altered the habitat composition of most landscapes during the past century. In some regions up to 30% of broad-leaved woodland has been lost since 1945 due to forest clearance, conifer conversion and urbanization (Stebbins 1988). During the same period, four species of bat are believed to have undergone some population decline and a further three have undergone significant declines (Harris et al. 1995). However, whether the changing status of these bat populations can be attributed directly to the changing patterns of land use in Britain remains untested. From a conservation perspective there is a clear need to evaluate this relationship, since identifying the habitat factors likely to have a significant influence on bat populations is fundamental for developing conservation management policies. However, at present one of the vital pieces of information required to quantify such a relationship is lacking; quantitative data on the relative importance of different habitats to bats.

Quantitative studies of habitat selection have been used in the design of conservation management guidelines for many endangered species (Zoellick, Smith & Henry 1989; Carey, Reid & Horton 1990; Lin-
were selected randomly within different land classes. The information provided by these is limited due to the environmental characteristics such as geology, altitude. Each 1-km square area in Britain has been allocated to one of 32 land classes defined on the basis of this, each 1-km square area in Britain has been allocated (Hutson 1993). Whilst there are some published studies on habitat use by bats resident in Britain (Swift & Racey 1983; Racey & Swift 1985; McAney & Fairley 1988; Walsh & Mayle 1991; Jones & Morton 1992), the information provided by these is limited due to the small number of species, sites and habitats investigated. Elsewhere, attempts to quantify habitat use are more numerous (see, for example, Fenton 1970; Barclay 1985; Lunde & Harestad 1986; Brigham, Aldridge & Mackey 1992), but few studies have been made on species resident in Britain (de Jong & Ahlen 1991; Rachwald 1992; Rydell 1992). Also, extrapolation from these studies may be of doubtful validity since widely varying survey methodologies were employed and because animals may alter their patterns of habitat utilization in different landscapes (Mann & Putman 1989). For a small island, Britain has a highly diverse landscape structure, and so a landscape-scale approach was needed to quantify the fundamental habitat requirements of bats in Britain.

This paper presents an analysis of foraging habitat selection by vespertilionid bats based on data collected during a national survey. Comparisons of the patterns of habitat use on both large and local scales are used to highlight the fundamental habitat requirements of bats, and to explore the differences in habitat use between contrasting landscapes. The primary aim was to identify key bat foraging habitats and to rank these in order of priority so that the results could be incorporated into basic conservation management plans. This would also provide quantitative base-line data on the use of foraging habitats to facilitate future research into the impact of land-use change on bat populations.

**Methods**

**DATA COLLECTION**

The data were derived from the results of a national survey of bats and their habitats in Britain carried out over three consecutive summers from 1990 to 1992. The survey was stratified using the land class system (Bunce, Barr & Whittaker 1981a, 1981b, 1983). For this, each 1-km square area in Britain has been allocated to one of 32 land classes defined on the basis of environmental characteristics such as geology, altitude, land use and climate. Squares to be surveyed were selected randomly within different land classes approximately in proportion to the abundance of that land class. The data were collected by experienced volunteers, who recorded ‘bat passes’ registered on a bat detector tuned to 45 kHz whilst walking a pre-selected transect across the 1-km square. Transects were completed on four occasions during defined date periods: 16 June–7 July, 8–28 July, 29 July–18 August and 19 August–8 September. One ‘bat pass’ was defined as a sequence of at least two echolocation pulses of a passing bat (Thomas & West 1989). The position of all bat passes detected were marked onto a separate map for each walk, and data on prevailing weather conditions and time spent monitoring also recorded. Bat passes were coded as either trains of echolocation calls heard indicating a bat in transit or trains of rapidly repeated calls heard indicating a bat feeding. In addition a letter code was added to indicate the species if this could be identified with certainty. For each 1-km square, the vegetation types occurring along the transect line were marked onto a separate map of the square; 49 vegetation types were recorded similar to those described in Cresswell, Harris & Jeffries (1990). The completed maps were then all checked by one person (A.L.W.) to ensure uniformity of approach, and for data extraction. A full description of the sampling protocol is given by Walsh, Hutson & Harris (1993) and Walsh, Harris & Hutson (1995).

**DATA ANALYSIS**

Habitat availability in each 1-km square was determined by measuring the length of each habitat type along both sides of the transect line to the nearest 50 m with an opisometer and expressing it as a proportion of the total length of all habitats measured. Where linear features such as hedgerows or streams were perpendicular to the transect line, they were assigned a distance of 50 m. The habitat types for which availability was calculated are listed in Table 1. To reduce the number of habitat variables from 49 to a more manageable number, similar categories were combined into the broad habitat categories listed. The total number of bat passes marked within each habitat type in each square were counted to calculate the percentage use of each habitat. Bats were frequently recorded in a combination of two habitat types. In such cases a bat pass was assigned to both habitat types. Where the bat pass was recorded in a single habitat type, it was counted twice. In this way the proportion of activity recorded in different habitats remained consistent, allowing direct comparisons to be made. The number of feeding passes counted constituted c. 20% of the total passes counted and was strongly correlated to the total number of bat passes (Spearman Rank $r = 0.56$, $P < 0.001$). Furlonger, Dewar & Fenton (1987) similarly found the incidence of feeding passes to parallel total bat activity but at a reduced level. Thus, numbers of total bat passes were...
Foraging habitats of bats in Britain

Table 1. Non-coastal habitat types for which availability was measured

<table>
<thead>
<tr>
<th>Code</th>
<th>Habitat type</th>
</tr>
</thead>
<tbody>
<tr>
<td>HG</td>
<td>Hedgerow</td>
</tr>
<tr>
<td>TR</td>
<td>Treeline</td>
</tr>
<tr>
<td>DO</td>
<td>Open ditch – no vegetation cover</td>
</tr>
<tr>
<td>DC</td>
<td>Covered ditch – vegetation cover</td>
</tr>
<tr>
<td>SW</td>
<td>Stone wall</td>
</tr>
<tr>
<td>SR</td>
<td>Stream</td>
</tr>
<tr>
<td>BE</td>
<td>Broadleaved woodland edge – semi-natural plus plantation</td>
</tr>
<tr>
<td>CE</td>
<td>Coniferous woodland edge – semi-natural plus plantation</td>
</tr>
<tr>
<td>ME</td>
<td>Mixed woodland edge – semi-natural plus plantation</td>
</tr>
<tr>
<td>BO</td>
<td>Broadleaved woodland opening – semi-natural plus plantation</td>
</tr>
<tr>
<td>CO</td>
<td>Coniferous woodland opening – semi-natural plus plantation</td>
</tr>
<tr>
<td>MO</td>
<td>Mixed woodland opening – semi-natural plus plantation</td>
</tr>
<tr>
<td>FL</td>
<td>Felled and newly planted woodland</td>
</tr>
<tr>
<td>SB</td>
<td>Scrub – included low scrub, tall scrub and bracken</td>
</tr>
<tr>
<td>PK</td>
<td>Parkland – included amenity grassland such as golf course</td>
</tr>
<tr>
<td>RI</td>
<td>River and canal</td>
</tr>
<tr>
<td>PO</td>
<td>Pond</td>
</tr>
<tr>
<td>LK</td>
<td>Lake and reservoir</td>
</tr>
<tr>
<td>MR</td>
<td>Moorland – included heather moor, blanket bog and lowland heath</td>
</tr>
<tr>
<td>AB</td>
<td>Arable land – including grassland ley</td>
</tr>
<tr>
<td>IG</td>
<td>Improved grassland</td>
</tr>
<tr>
<td>SG</td>
<td>Semi-improved grassland</td>
</tr>
<tr>
<td>LG</td>
<td>Lowland unimproved grassland</td>
</tr>
<tr>
<td>UG</td>
<td>Upland unimproved grassland</td>
</tr>
<tr>
<td>UR</td>
<td>Urban land – built-up land, mainly residential</td>
</tr>
</tbody>
</table>

assumed to accurately reflect levels of foraging bat abundance and were used in all analyses.

Throughout the survey, species identification was limited by the demand for continuous steady procession and by having the detector tuned only to 45 kHz. Of the bat passes, 71.6% were unidentified. Of the 24.4% identified to a particular bat species or species group, 71.0% were Pipistrellus pipistrellus, 17.0% Myotis spp., 7.6% Nyctalus noctula, 2.7% Plecotus spp. and 1.7% Eptesicus serotinus. Due to the low incidence of positive identifications, analyses were undertaken to examine broad trends in habitat use for all species combined.

Data were screened and observations with high potential influence were re-examined to detect outliers and possible errors in the data. Selection analyses were used to identify preferred and avoided habitat types across squares in each date period and over all four date periods pooled for both land class groups and individual land classes. Initially, large-scale patterns of selection were examined by combining all 32 land classes into seven major land class groups (Table 2). Coastal squares were combined in a separate analysis to examine selection of coastal habitats. More localized patterns in habitat selection were then outlined in 19 separate land classes. These were the most common and widespread land classes for which we had an adequate sample size (n > 24 squares), this figure being determined by plotting increasing sample size against mean bat activity (Walsh et al. 1995). Absence or selection of particular habitat types was determined using the z statistic with Bonferroni adjustment and a confidence level of 90% (Neu, Byers & Peek 1974; White & Garrott 1990). For this test, simultaneous confidence intervals using Bonferroni’s inequality were calculated for the percentage use of each different habitat. Where the percentage availability of a habitat fell below the relevant confidence interval, it was considered to have been significantly selected (P < 0.10) and where habitat availability was above the confidence interval, a habitat was significantly avoided. Since large numbers of comparisons were being made, it was necessary to reduce the probability of Type II errors by using a less stringent criterion for statistical significance, namely setting the confidence limits at 90% (Cresswell et al. 1990; Bright & Morris 1993). In all analyses only habitat variables occurring in more than 10 squares and with five or more bat passes were used (Hayes & Winkler 1970).

Results

Of the 1030 1-km squares surveyed, 120 (11.7%) were not included in the analysis because the sheets were either incorrectly or inadequately completed. Only one influential outlier was identified in the screening process and discarded on the assumption that this was an incorrectly completed sheet. Thus, the analysis is based on data from 910 squares which were of uniform approach. In total nearly 30,000 bat passes were counted in the 9000 km walked, involving 2700 hours of search effort. Only 6% of 1-km squares had no recorded bat activity, and these were mostly in Scotland at the northern limit of the range of many species in Britain.

TEMPORAL PATTERNS IN HABITAT SELECTION

There were no temporal shifts in habitat use in either large- or local-scale analyses, since very few differences in habitat selection were found between the four date periods. Hence, all the results presented were pooled across date periods.

LARGE-SCALE PATTERNS IN HABITAT SELECTION

Bats were observed in a diverse range of habitats and were rarely totally absent even from less favoured habitats. However, they did not use all habitats in proportion to their availability and showed some very
Table 2. Land class composition, typical physiogeography, land use and distribution of the seven major land class groups (I-VII) used in the analyses. Based on Bunce et al. (1981b)

<table>
<thead>
<tr>
<th>Land class type and group</th>
<th>Land classes included</th>
<th>No. of 1-km squares included in the analyses</th>
<th>Description of topography and land use of land class group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arable I</td>
<td>2</td>
<td>68</td>
<td>Open gentle slopes with land at medium low or low altitude. Mainly open or wooded downland with few hedges. Varied agriculture but extensive cereals and built-up land. S England and SW Midlands.</td>
</tr>
<tr>
<td>Arable II</td>
<td>3, 4, 9, 11, 12</td>
<td>184</td>
<td>Flat mainly low altitude alluvial plains. Open, intensively farmed lowland and fenland areas with large cereal fields and little native vegetation. East Anglia, S and mid to NE England, and SE Scotland.</td>
</tr>
<tr>
<td>Pastural IV</td>
<td>1, 5, 6, 7, 8</td>
<td>222</td>
<td>Medium to low altitude, often coastal areas. Undulating lowland farmland, intricate in composition with small fields, many hedges and small woods. Predominantly pasture. S England, SW Midlands and Wales.</td>
</tr>
<tr>
<td>Marginal upland VI</td>
<td>17, 18, 19, 20, 28, 31</td>
<td>86</td>
<td>Moderate slopes, medium to high altitude river valley hillsides and exposed coast. Transitional farmland with walls and fences. Mainly rough grassland and moorland vegetation, often afforested. SW and N England and Scotland.</td>
</tr>
<tr>
<td>Upland VII</td>
<td>21, 22, 23, 24, 29, 30, 32</td>
<td>55</td>
<td>Steep sloping ridges, high altitude. Bleak moorland and upland bog with scattered lochs and large areas of afforestation. Mainly mountainous landscapes and rocky coasts with much bracken. N England and Scotland including the Western Isles.</td>
</tr>
</tbody>
</table>

Clear preferences. Figures 1, 2 and 3 show the relative availability of habitats preferred and avoided in the seven land class groups. Despite the wide variation in distribution and habitat composition between the land class groups, there was a high degree of uniformity in preferred foraging habitats. Across all land class groups bats tended to forage selectively in edge and linear habitats and avoided more open and intensively managed habitat types. Some major trends in selection are discussed below.

In all land class groups, bats showed a far stronger preference for woodland edge and all water bodies than for any other habitat type, emphasizing the important role of these habitats as key foraging sites. Within woodland categories, edges tended to be more strongly selected than openings within woodlands, and semi-natural broadleaved woodland was more strongly selected than either mixed or conifer woodland. Felled and newly planted areas were selected when present, but this may represent a selection for the woodland edge surrounding the felled area rather than for this habitat itself. The only woodland category that was avoided was openings in conifer woodlands in upland landscapes where plantation woodland often occurs in large blocks. The strong selection exhibited for streams, rivers/canals, ponds and lakes/reservoirs in all land class groups confirms the great importance of water bodies for foraging bats. There was, however, a weak selection and lack of preference for rivers/canals observed in arable land class groups I and II, respectively. Urban areas were positively selected in three land class groups. The urban areas surveyed were most often residential areas of villages and small towns, although the suburbs of some large cities were also included.

Bats were consistent in their positive selection for linear vegetation corridors, though selection of these was less strong than for woodland and riparian habitats. Treelines were selected in all land class groups and hedgerows in all but arable groups I and III. Only covered rather than open ditches were positively selected in two land class groups and stone walls were avoided in all groups. Thus, connectivity appears to be an important part of the landscape infrastructure.
Fig. 1. Selection of habitats by bats in arable land class groups I, II and III. Habitat codes as in Table 1. Percentage habitat availability, and hence expected use, is shown by bars, the percentage use by bats of each habitat by solid circles. Solid bars denote that a habitat was significantly selected, an open bar that a habitat was used in proportion to its availability, and a hatched bar that that habitat was significantly avoided. All tests of significance used 90% Bonferroni confidence intervals. The absence of a bar denotes that the scarcity of that habitat in the land class group precluded analysis. A cross indicates that < 5 bat passes were recorded in that habitat, thereby also precluding analysis, but that the habitat was sufficiently common to infer avoidance.

for bats, although the types of linear features are important.

Habitats strongly and consistently avoided in all land class groups were the more exposed and more intensively managed habitats; these included moorland, improved grassland, semi-improved grassland, upland unimproved grassland and arable land. This avoidance is particularly evident in marginal upland and upland landscapes (Fig. 3). The only grassland type not consistently avoided was lowland unimproved grassland where prey availability may be higher than in the improved grassland types.

Fig. 2. Selection of habitats by bats in pastural land class groups IV and V. Legend as in Fig. 1.
A separate analysis was carried out on the 44 coastal squares surveyed and the results for three main types of coastal habitat are shown in Table 3. In these squares, coast-line in the form of sandy, shingle or rocky beaches and estuarine coastal marsh were significantly selected as foraging sites and, surprisingly, even cliff tops were not avoided.

The sorts of habitats preferentially utilized by bats were also those which were comparatively rare within each land class group (Figs 1, 2 and 3). For instance, woodland edge, hedgerows, treelines and water bodies were optimal habitats that were selected in either all or the majority of land class groups. However, their sum percentage availability in each land class group ranged from 13.5% to 30.8%, with a mean of 24.7%. In contrast, stone walls, moorland, arable and all grassland categories except lowland unimproved grassland were consistently avoided as foraging habitats. Yet their sum percentage availability in each land class ranged from 40.4% to 54.2%, with a mean of 47.2%. This difference is even greater when the relative areas of habitats covering an entire square are considered. Optimum habitats tend to be the perimeter of blocks of habitat or linear strips of habitat, and so in comparison with contiguous blocks of pasture or arable land, for instance, their area is proportionately smaller. Thus, the optimal habitats for bats are rare and patchily distributed.

LOCAL-SCALE PATTERNS IN HABITAT SELECTION

A similar examination of habitat selection using the Bonferroni confidence interval technique between individual land classes (numbers 1–11, 13, 15, 16, 17, 22, 25, 26 and 27) demonstrated the same consistent preference for woodland habitats, water bodies and linear vegetation corridors, and an avoidance of arable, moorland and most grassland habitats. Because the patterns in selection proved to be highly similar between individual land classes, the results are summarized in Table 4 by habitat type rather than by land class. For each habitat, the number of land classes within which it was selected, used in proportion to availability and avoided were summed and used to designate a selection rating ((i)-(v)) for that habitat. Habitats were then grouped according to selection rating and hence Table 4 ranks bat foraging habitats based on local scale analyses; groups (i) and (ii) represent habitats of high importance to bats, whereas groups (iv) and (v) represent habitats of low importance. Group (iii) represents habitats of differential importance to bats, depending on the land class under examination.

The local selection trends shown in Table 4 are the same as for the large-scale analysis. Since land classes used in this analysis included representatives from the arable, pastoral, marginal upland and upland groups,
Foraging habitats of bats in Britain

Table 4. Summary of habitats significantly selected, used in proportion to availability or avoided in 19 discrete land classes. All tests of significance used 90% Bonferroni confidence intervals. The proportion of land classes in which each habitat was selected (+ Ps) or avoided (−Ps) is shown together with the number of land classes for which a test was conducted (n).

<table>
<thead>
<tr>
<th>Group (i)</th>
<th>Group (ii)</th>
<th>Group (iii)</th>
<th>Group (iv)</th>
<th>Group (v)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Selected in all land classes</td>
<td>Selected in some land classes, never avoided</td>
<td>Selected in some and avoided in other land classes</td>
<td>Avoided in some land classes, never selected</td>
<td>Avoided in all land classes</td>
</tr>
<tr>
<td>+Ps = 1.00</td>
<td>+Ps(n)</td>
<td>−Ps(n)</td>
<td>−Ps(n)</td>
<td>−Ps = 1.00</td>
</tr>
<tr>
<td>n = 19</td>
<td>n = 19</td>
<td>n = 19</td>
<td>n = 19</td>
<td>n = 19</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Selected in all land classes</th>
<th>Selected in some land classes</th>
<th>Avoided in some land classes</th>
<th>Avoided in all land classes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treeline</td>
<td>+0.83 (18)</td>
<td>−0.30</td>
<td>+0.20 (10)</td>
<td>−0.84 (19)</td>
</tr>
<tr>
<td>Broadleaved woodland edge</td>
<td>+0.084 (19)</td>
<td>−0.39</td>
<td>+0.07 (14)</td>
<td>−0.84 (19)</td>
</tr>
<tr>
<td>Lake and reservoir</td>
<td>+0.67 (12)</td>
<td>−0.69</td>
<td>+0.15 (13)</td>
<td>−0.42 (19)</td>
</tr>
<tr>
<td>Mixed woodland edge</td>
<td>+0.81 (16)</td>
<td>−0.20</td>
<td>+0.40 (10)</td>
<td>−0.05</td>
</tr>
<tr>
<td>Broadleaved woodland opening</td>
<td>+0.50 (18)</td>
<td>−0.63</td>
<td>+0.05 (19)</td>
<td>−0.25</td>
</tr>
<tr>
<td>Mixed woodland opening</td>
<td>+0.50 (6)</td>
<td>−0.25</td>
<td>+0.13 (16)</td>
<td>−0.42 (19)</td>
</tr>
<tr>
<td>Felled woodland</td>
<td>+0.50 (6)</td>
<td>−0.25</td>
<td>+0.13 (16)</td>
<td>−0.42 (19)</td>
</tr>
<tr>
<td>River and canal</td>
<td>+0.88 (8)</td>
<td>−0.42</td>
<td>+0.42 (19)</td>
<td>−0.05</td>
</tr>
<tr>
<td>Pond</td>
<td>+0.82 (11)</td>
<td>−0.42</td>
<td>+0.42 (19)</td>
<td>−0.05</td>
</tr>
</tbody>
</table>

Good habitats > Poor habitats

Discussion

Data Interpretation

A full discussion on the limitations of the survey technique is given in Walsh et al. (1995), but a brief outline of the two main limitations is required prior to a discussion of the results. The sampling procedure worked well in that the proportion of each species in the identified sample compares well with the relative abundance of that species/group of vespertilionids (using the figures in Harris et al. 1995). Thus, Pipistrellus pipistrellus constituted 71.0% of the identified sample in this study cf. 76.8% of the total vespertilionid population, 17.0% vs. 12.4% for Myotis spp., 7.6% vs. 1.9% for Nyctalus noctula, 2.7% vs. 7.7% for Plecotus spp. and 1.7% vs. 0.6% for Eptesicus serotinus. Thus, the habitat preferences and the recommended conservation measures reported here apply to the family as a whole and to Pipistrellus pipistrellus in particular, but there may be detailed habitat requirements for some of the rarer species that are masked by this analysis. A second limitation is that due to safety considerations, our sample of marginal upland and upland landscapes was slightly biased towards areas of lower altitude and with less steep slopes. Consequently, measures of habitat availability and use are skewed towards those habitats more associated with these areas, and so this may introduce a slight bias in the relationships described for these landscapes.
Bats were observed in a diverse range of habitats but a clear and consistent pattern in the preferred and avoided habitats was common to all landscapes. This pattern strongly reflects potential prey availability within habitats. Bats preferred to forage in habitats associated with woodland and water and also made selective use of linear vegetation corridors connecting these habitats.

A number of small-scale studies have already identified woodland sites as preferred foraging areas (Racey & Swift 1985; Furlonger et al. 1987; Rachwald 1992; Clark, Leslie & Carter 1993). This study shows that the strongest selection was for semi-natural broad-leaved woodland, a finding also reported for a study on *Pipistrellus pipistrellus* and *Eptesicus nilssonii* in central Sweden (de Jong & Ahlen 1991). More bats were recorded along the edges of woodlands than within woodland gaps, probably because they have higher insect densities (Lewis 1970) and offer a suitable flying zone free from too much clutter. Fewer bats were recorded in coniferous woodlands (in this study mainly plantations) in relation to other types of woodland, indicating that this represents a less optimal woodland type. Conifer plantations contain low numbers of insect species (Winter 1983) and an avoidance of gaps in large contiguous conifer blocks in the uplands confirms their low value to foraging bats. Smaller block size and the enhancement of plantation edges, rides and glades to include shrub and broad-leaved species in lowland areas may boost insect availability (Carter & Anderson 1987) and enhance their suitability for foraging bats.

Where available, bats showed a strong preference for all water bodies, from small streams and ponds to larger rivers, canals, lakes and reservoirs. Fenton (1970), Bell (1980) and Walsh & Mayle (1991) also recorded high activity over ponds. In Scotland both *Pipistrellus pipistrellus* and *Myotis daubentonii* favour riverine habitats (Swift & Racey 1983; Racey & Swift 1985), and in Poland Rachwald (1992) found that *Nyctalus noctula* fed most often at riversides. Water bodies offer high insect densities since many insects have aquatic larval stages. However, one important finding was a weak or lack of preference for rivers in some intensively agricultural land classes. The quality of rivers as a foraging site for bats may be reduced in these areas if higher pollution levels, such as from agricultural insecticide run-off, leads to a decrease in insect availability. Further studies into the relation between aquatic pollution, insect prey and bats are needed to quantify the relationship between aquatic pollution and bat foraging activity.

A very strong relationship exhibited in all landscapes was an avoidance of arable land and improved grassland categories. Other authors have recorded comparatively low bat activity over farmland and pasture (Fenton 1970; Lunde & Harestad 1986; Rydell 1986; Walsh & Mayle 1991), and this may be a reflection of the lower insect densities associated with such intensively managed land. Less managed grasslands, such as hay meadows, appear to be of greater value to foraging bats, since unimproved pasture was the only grassland category that was often used in proportion to its availability. However, its importance is probably underestimated in this study, since the results are biased towards habitat preferences exhibited by *Pipistrellus pipistrellus*, a species known to avoid open fields (Racey & Swift 1985). Other studies have shown that larger species of vespertilionid bat, such as *Eptesicus nilssonii* and *Eptesicus serotinus*, and *Rhinolophus ferrumequinum*, readily exploit old pasture, where they forage for beetles and moths (Rydell 1986; Jones & Morton 1992; Robinson & Stebbings 1993).

Optimal habitats for bats are rare within all landscapes; for instance, water bodies generally represent less than 1% of the available habitat, and broad-leaved woodland edge ranges from 3 to 4%. In contrast, very poor habitats such as arable land and improved grassland are common, constituting c. 40% of the available habitat. Furthermore, optimal habitats are highly patchy in their distribution, thus emphasizing the specialist nature of the habitat requirements of bats. It is hardly surprising, therefore, that vegetation corridors in the matrix between favoured foraging patches were also favoured by vespertilionid bats. The positive selection of hedgerows and treelines implied that they were not only used as commuting routes but also as linear foraging sites. Limpens & Kapteyn (1991) proposed that small bats, particularly *Myotis* spp., preferred commuting along linear landscape elements because of the availability of insects, shelter from wind and predation and a reliance on these features for orientation within the landscape. Kalko & Schnitzler (1993) concluded that pipistrelle bats were not reliant on linear elements for orientation purposes, since their use of open space is not restricted by constraints of their echolocation system. In this study, bats demonstrated an avoidance of stone walls without vegetational cover and a lack of selection of hedgerows in two arable land class groups, where they are most likely to be low cut heavily managed hedges. This suggests that while linear structures may facilitate the orientation of bats, the association of cover and/or high insect densities are important factors influencing the suitability of different linear landscape elements as flight routes.

A requirement for patchily distributed habitats within large suboptimal areas reinforces the prediction that bats are highly susceptible to habitat fragmentation (Bright 1993). Much emphasis has been placed on the theoretical impact of insularization on the fauna confined to fragments of habitat. Bats commute between roosting sites and feeding areas, which may be quite distant. Thus, bats are confined to fragments of habitat within a predetermined area. Flight
Foraging habitats of bats in Britain and foraging on the wing is known to be very energy-consuming (Thomas 1987), and so the further feeding areas are situated from roost sites the more energetically expensive foraging is likely to become. Ransome (1990) has shown how increased foraging distances decrease maximum bat colony sizes in Rhinolophus hipposideros, and Tuttle (1976) demonstrated that in a colony of Myotis grisescens greater distances to feeding grounds were correlated with decreased growth rate and survivorship of young. Since habitat fragmentation leads to the further dispersion of feeding patches, this may have a profound effect on the long-term survival of local bat populations. Corridors such as hedgerows and treelines may enable the chances of long-term survival for a bat population in a fragmented landscape by linking patches, thereby providing access to additional feeding areas, or by providing an additional food supply that enables the bats to travel over a wider area in search of profitable feeding areas.

Roosting requirements may also influence habitat utilization (Kunz 1982; Geogie & Fenton 1985). For instance, urban areas may have been selected because of the high availability of roost sites in houses. However, it could also be related to the availability of gardens, hedges and streetlamps as possible feeding sites (Rydell 1992), and may also in part reflect an adaptation by vespertilionid bats to feeding in less optimal habitats as these increase in their relative availability whilst optimal habitats decrease.

LAND-USE RELATIONS AND IMPLICATIONS FOR THE CONSERVATION MANAGEMENT OF KEY HABITATS FOR BATS

If recent changes in land use have contributed to the decline of some species of bat in Britain, then the habitats identified in the selection analyses as being most favourable to bats should have suffered the largest reduction during the past century. Examination of published figures lend convincing support to this hypothesis. During the 20th century the overall trend in agricultural land use has been the expansion of arable farming and a loss of semi-natural habitats. For instance, 75% of Britain’s ponds have been lost since 1880 (Oldham & Swan 1993), thereby substantially reducing one of the habitats identified as being of prime importance to bats. Similarly large reductions in the length of hedgerows and number of old hedgerow and farmland trees have taken place (Pollard, Hooper & Moore 1974), and despite a high conversion rate to broadleaved plantations, a loss in the area and size of ancient, semi-natural broadleaved woodland has occurred (Peterken & Allison 1989). Although total woodland cover has increased during the 20th century, the increases are mainly due to widespread conifer afforestation in the uplands (Peterken & Allison 1989), which we have demonstrated is a woodland type of particularly low value to foraging bats.

The present trends in land-use change outlined by Barr et al. (1993) indicate that the future prospect for foraging bat populations remains fairly bleak. From 1984 to 1990 there has been a continued loss of hedgerows, despite a shift from cut to relict hedgerows which may provide a better quality feeding habitat than short managed hedges. While there has been little woodland loss, there was a general trend in loss of plant biodiversity in woodlands, pasture and arable land and in streams in most landscapes, which could affect insect prey availability and hence the quality of these habitats for bats. A small decline in the area of water bodies and coastal marsh was reported, coupled with an increase in the area of conifer plantation and urbanized land. Thus there is continued loss, deterioration and fragmentation of those habitats which we have identified as preferred foraging habitats for bats. One exception is the apparent stabilization of broadleaved woodland loss and the increase in the area of broadleaved plantations across lowland Britain. However, broadleaved plantations lack many of the semi-natural plant species that ancient woodlands possess, and may thus have lower associated insect availabilities.

The analyses in this study have shown that over-intensive use of the rural environment and changes relating to prime foraging habitats could substantially affect the suitability of an area for foraging bats. It has provided objective criteria on which to base conservation management decisions which may have a profound influence on bat populations, and has clarified the need for positive action towards habitat conservation measures for bats. Immediate recommendations are that management policies consider the continuity of the landscape for bats in the form of treelines and other corridors such as hedgerows and streams, and should preserve and minimize the further fragmentation of woodland and water bodies. In addition, active management of habitats for bats (e.g. pond creation schemes) should be encouraged. Further research is required to assess the relative quality of different foraging areas and the potential effects of quality change. Woodenland diversity and water quality of riparian sites in particular may have a profound effect on the quantity and type of prey available to foraging bats, affecting the quality and hence conservation value of these important habitats. Further studies quantifying the habitat requirements of individual species are also required if we are to identify the potentially more specialized requirements of target species.

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