# Habitat Exploitation by a Gleaning Bat, Plecotus auritus

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# Habitat exploitation by a gleaning bat, *Plecotus auritus*

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## SUMMARY

The brown long-eared bat, *Plecotus auritus*, differs from most other Palaearctic bats in having broad wings and long ears, which are linked to its slow flight, and its ability to hover and thus glean insects from surfaces. Previous studies have suggested a relation between interspecific variation in morphology of bats, particularly the shape of the wing, and differences in foraging behaviour. It might be predicted therefore that the foraging behaviour of *P. auritus* would differ from other Palaearctic species that have been studied. To examine activity patterns and habitat use, 16 *P. auritus* were radio-tracked from six roost sites in northeast Scotland. Differences in behaviour compared to other Palaearctic species were found in the nocturnal activity pattern, habitat use and distance travelled to foraging areas. *Plecotus auritus* emerged later than other sympatric species, at around 55 min after sunset, and remained active throughout the night, with a generally unimodal activity pattern. Individual bats used a series of feeding sites, to which they returned regularly, and sometimes shared with others from the same roost. *Plecotus auritus* foraged exclusively in woodland and around individual trees. The bats displayed a preference for deciduous over coniferous woodland, probably reflecting higher insect availability in the former. Hedgerows, tree lines and fence lines were used as commuting routes between roosts and feeding sites. Bats travelled up to 2.8 km from the roost site, but spent most time foraging within 0.5 km of the roost, although males foraged further from the roost than females. The foraging behaviour of *P. auritus* reflected the morphological specializations of this species, but displayed a degree of intraspecific flexibility. Deciduous woodland in the vicinity of roost sites appeared to be key foraging habitat for *P. auritus*.

## 1. INTRODUCTION

Bats show a wide degree of morphological and sensory variation, which is mirrored by the diversity of their foraging behaviour. In particular, wing morphology and the form of echolocation calls have been linked to the abilities of different species to exploit particular habitats and prey types (e.g. Fenton 1972; Neuweiler 1984; Aldridge & Rautenbach 1987; Baagøe 1987). Such studies have revealed correlations between wing morphology, manoeuvrability, and echolocation call structure, and have led to predictions regarding foraging behaviour which can be tested under field conditions (O'Neill & Taylor 1986; Aldridge & Rautenbach 1987; Krull *et al.* 1991).

The brown long-eared bat (*Plecotus auritus*) differs in its morphology and call structure from most other Palaearctic bat species (except for the grey long-eared bat, *Plecotus austriacus*). It has a low wing-loading and short, broad wings (Norberg & Rayner 1987) which enables slow (ca. 3 m $s^{-1}$) but highly manoeuvrable flight (Norberg 1976) suitable for flying in cluttered habitats, such as woodland. The echolocation calls of *P. auritus* are of low intensity and can only be detected over a short distance, and are of a form suitable for detecting prey in cluttered habitats (Neuweiler 1989). This bat feeds predominantly on Lepidoptera and Diptera (Swift & Racey 1983; Rydell 1989) which are either gleaned from surfaces such as leaves, or are captured in flight (Anderson & Racey 1991). Low intensity calls may overcome defensive responses of tympanate moths, by enabling bats to approach close to prey without eliciting an escape response. In addition, the sensitive hearing of this species enables it to locate prey by passive listening (Anderson & Racey 1993), rather than by echolocation, which may alert some insects to the bat's presence.

Differences in morphology and echolocation calls between *P. auritus* and other Palaearctic bat species, which tend to have relatively longer wings enabling faster flight, and echolocation calls effective over longer distances, might therefore be correlated with substantial differences in the foraging behaviour of this species. For example, the slow flight may limit how far an animal can travel in a night, and may make it more at risk from aerial predators. However, the manoeuvrable flight of this species may enable bats to use cluttered areas, which are less accessible to faster flying species.

Little is known regarding the spatial and temporal aspects of foraging behaviour in *P. auritus*, or how it uses its habitat compared to other species with very different wing morphology and call structures (but see Swift & Racey 1983; Barataud 1990; Fuhrmann & Seitz 1992). Although considered primarily a woodland species, little is known about the range of habitats used, nor where the bats forage in relation to the roost, which appears to be selected on the basis of local woodland availability (Entwistle *et al.* 1996*a*). In addition, there is almost no information on intraspecific variation in foraging behaviour of *P. auritus*, and to what extent behaviour is affected by differences in environmental conditions (such as habitat and climate) or interindividual differences (such as sex or reproductive status).

As the populations of many species of bats are declining, apparently partly as a result of habitat loss, knowledge about habitat use may be particularly relevant to conservation of bats. Indeed, the protection of key foraging habitats has become recognized as an important factor in the conservation of bats in Europe, and knowledge of the habitat requirements of individual species is necessary if appropriate management plans are to be developed. This study aimed to examine temporal and spatial aspects of foraging behaviour in *P. auritus*, in relation to the wing morphology and sensory abilities of this species, while taking into account sources of intraspecific variation. We used radio-tracking to collect appropriate data from known individuals throughout the night.

## 2. METHODS

### (*a*) *Attachment of transmitters*

During the summers (May–August) of 1992 and 1993 bats were caught by hand during the day inside six maternity roosts in houses in northeast Scotland (57° N), under licence from Scottish Natural Heritage. After capture, all bats were measured and weighed (to 0.1 g, using a top-loading balance) and the heaviest individuals, of an appropriate reproductive class, were selected for radio-tracking. Bats that were tracked included males, lactating females and 'non-reproducing' females (which were not pregnant, or lactating). Pregnant females were not tracked. Transmitters weighing 0.65 g (Holohil Systems, Woodlawn, Ontario) were attached mid-dorsally using 'Skinbond' adhesive (Pfizer Hospital Products, Largo, Florida). Transmitter mass ranged from 6.4% to 9.5% of body mass. This exceeds the 5% rule for transmitter mass (Aldridge & Brigham 1988). After attachment, the tagged bat, along with the rest of the colony, was returned to the roof space.

### (*b*) *Location of radio tagged bats*

Radio tagged bats, once they had left the roost, were located using triangulation and, in addition, the bats were approached on foot and the area was circled to confirm their precise location ('homing-in' method of White & Garrott 1990). The position of the bat was determined every 5 mins, when possible. However, in certain circumstances (e.g. when a bat was commuting) a more flexible approach to recording data was taken, with bearings recorded outside a fixed time interval, but as frequently as possible (see Jones & Morton 1992). By having two observers tracking one bat each, two bats from the same roost site could be followed simultaneously.

Bats were tracked for as long as they were active i.e. from emergence until they returned to the roost before sunrise. If a bat returned to the roost earlier than expected, it was monitored until dawn to ensure that no second emergence took place. Behaviour during the night was classified as one of three activities: (i) bats flying continuously in discrete locations (termed feeding areas or feeding sites) were considered to be foraging; (ii) fast, directional flight between such areas, and to and from the roost site, was termed commuting; and (iii) when the received signal was steady, without the amplitude modulations which typified a moving animal, bats were considered to be inactive (resting).

The use of space around the roost was examined in respect to both the distance travelled from the roost site and the type of habitat used. The foraging range was described by examining how bats distributed their foraging in relation to the position of the roost site. The area around the roost was subdivided into a series of concentric 'distance bands' defined by a series of radii centred on the roost at distances of 0.5, 1.0 and 1.5 km. A time budget was devised for the time spent foraging within each distance band from the roost (i.e. $< 0.5$ km, 0.5–1.0 km, 1.0–1.5 km and $> 1.5$ km from the roost). This time budget was calculated using the average time spent in each distance band for each individual. When bats were out of contact they were included if they were known to have flown to beyond a certain distance of the roost (i.e. could not be located closer to the roost). Feeding sites were classified by predominant habitat type. The habitats found around roosts included agricultural land (both pasture and cropland), woodland, villages and areas of water.

### (*c*) *Climate records*

An Automatic Weather Station was located at the Institute of Terrestrial Ecology's Brathens research station, near Banchory, in the middle of the study area and within 15 km of the study roosts. This provided synchronous and detailed climatic information for each night of tracking from 15th July 1992, including hourly measures of temperature, rainfall, and wind speed.

Times for sunrise, sunset (defined as the depression of the sun's centre 50° below the true horizon), and civil twilight (sun's centre 6° below the horizon) were taken from Whitaker's Almanacs for 1992 and 1993.

### (*d*) *Insect captures*

During the 1993 field season, insect samples were collected on five nights, using sweep netting within different feeding sites (identified from radio-tracking), and in adjoining areas. Sites were chosen where coniferous and deciduous woodland could be sampled within the same vicinity. Insects were collected at 30 min intervals throughout the night, usually with two persons taking simultaneous samples in different habitats, and alternating between them. Sweep nets (net diameter = 0.64 m, pole length = 0.9 m) were held in front of the body and swung in a figure of eight arc (one sweep) for 200 sweeps. The catches were then sprayed with a permethrin based insecticide (Sybol) to immobilize them, identified to taxon and recorded.

## 3. RESULTS

Radio transmitters were attached to a total of 18 bats, and data were obtained from 16 of them. In the two others cases the transmitters failed before any data could be collected (table 1). Tracking was carried out for a total of 65 bat nights (emergence to re-entry) and for seven additional half nights (tracking until midnight).

### (*a*) *Activity patterns*

Bats emerged at a median of 55 min after sunset (mean = 61.7 mins, s.e. = 4.31), 1 min before the end of civil twilight (mean = 9.7 min, s.e. = 4.54). Time of emergence was highly correlated both to time of sunset and to time of civil twilight (Spearman rank correlation, $n = 67$, $r_s = 0.919$, $p < 0.005$ for both tests; figure 1). However, time of emergence (minutes after sunset) was not correlated with the length of twilight (Spearman rank correlation, $n = 56$, $r_s = -0.122$, n.s.). Bats returned to the roost in the morning at a median of 57 min before sunrise (mean = 82.68 min, s.e. = 9.19), 8 min before the beginning of civil twilight (mean = 30.82 min, s.e. = 9.26) and time of re-entry was significantly related to both time of sunrise and of civil twilight (Spearman rank correlation, $r_s = 0.64$, $p < 0.005$ for both tests; figure 2). The average time after sunset at which the bats emerged varied between roost sites (ANOVA, $F = 4.01$, d.f. = 5, $p < 0.05$), and showed a high positive correlation with the distance from the roost to the closest woodland (Spearman rank correlation, $r_s = 1.00$, $n = 6$, $p < 0.005$; figure 3).

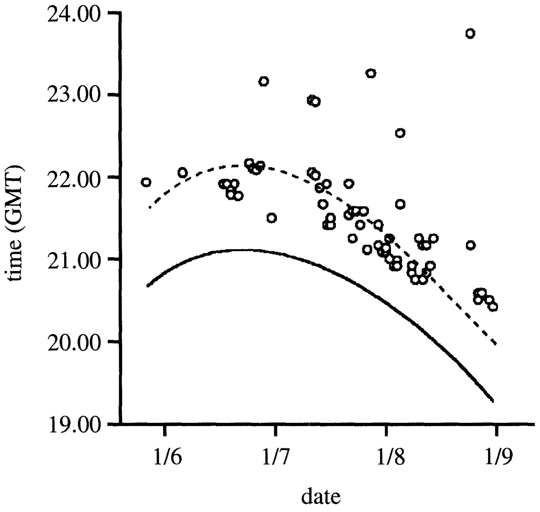

Figure 1. Emergence of radio-tracked bats (open circles) plotted against the date, with time of sunset (solid line) and the time of the end of civil twilight (dotted line).

The nocturnal activity pattern was characterized by bouts of flight, interspersed with short periods of inactivity, which ranged from 1–65 min in duration (median = 10 min), but no regular period of inactivity in the middle of the night was recorded. In general, bats hung up in trees during these rest periods, although on one occasion a wooden building (later used as a day roost by the same bat) was occupied. Because some activity was maintained at all times of night, it was assumed that this species was actively foraging throughout that time (median = 5.5 h per night).

Overall, the activity parameters of males and females did not differ significantly (table 2). Nor were significant differences found when simultaneously tracked pairs of male and female bats ($n = 3$) or lactating and non-reproducing females ($n = 2$) were compared. However, the only individuals which re-entered the maternity roost during the night were lactating females. Simultaneously tracked non-reproducing females did not display this behaviour. The number of returns made each night by lactating bats decreased through the summer (Kruskal-Wallis ANOVA, $H = 8.43$, d.f. = 2, $p < 0.05$). There was a corresponding increase in time spent inside the roost on each

Table 1. *Details of bats tracked including sex and reproductive status, roosts (indicated by a code A–G), number of nights tracked, and percentage of time spent in contact with each bat*

| bat | sex and reproductive status | roost | nights tracked | time in contact |
|---|---|---|---|---|
| 1 | female (non-reproductive) | A | 0 | no contact |
| 2 | male (mature) | B | 1 | 89 % |
| 3 | female (non-reproductive) | C | 1 | 100 % |
| 4 | male (mature) | D | 7 | 100 % |
| 5 | female (lactating) | C | 2 | 100 % |
| 6 | female (non-reproductive) | C | 2 | 100 % |
| 7 | female (lactating) | E | 2 | 100 % |
| 8 | female (lactating) | E | 7 | 97 % |
| 9 | female (lactating) | F | 5 | 96 % |
| 10 | female (non-reproductive) | F | 7 | 99 % |
| 11 | female (post-lactating) | D | 7 | 95 % |
| 12 | male (mature) | D | 5 | 77 % |
| 13 | female (non-reproductive) | C | 0 | no contact |
| 14 | male (mature) | C | 5 | 99 % |
| 15 | female (non-reproductive) | E | 2 | 100 % |
| 16 | male (mature) | E | 5 | 92 % |
| 17 | female (non-reproductive) | G | 7 | 89 % |
| 18 | male (mature) | G | 7 | 70 % |

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visit (Kruskal-Wallis ANOVA, $H = 6.25$, d.f. $= 2$, $p < 0.05$). Consequently, the total time spent inside the roost per night did not vary significantly during lactation (Kruskal-Wallis ANOVA, $H = 1.15$, d.f. $= 2$, n.s.).

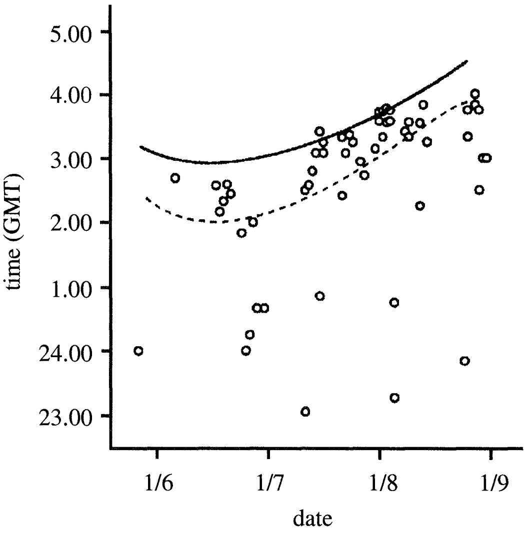

Figure 2. Re-entry time of radio-tracked bats (open circles) plotted against the date, with time of sunset (solid line) and the time of the end of civil twilight (dotted line).

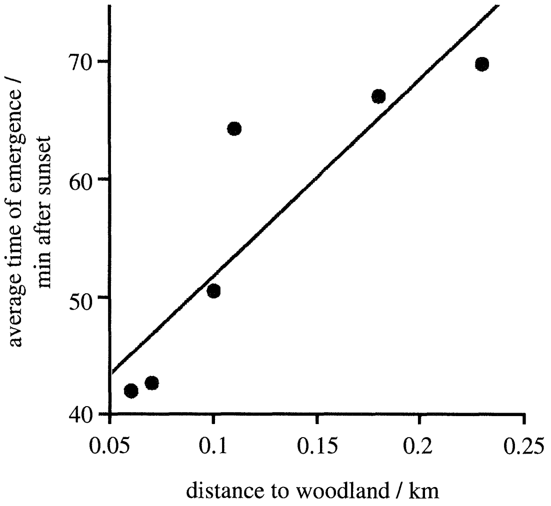

Figure 3. Average time of emergence of radio-tracked bats at six roosts, plotted against the distance to the nearest woodland. Regression equation: time of emergence = 167.8 (distance to woods) + 35.0; $F = 15.22$, $r^2 = 0.79$, $p < 0.02$.

### (*b*) *Effects of climate on activity*

Rain, during the expected period of emergence, significantly delayed the time of emergence (Wilcoxon test on all bats which experienced rain during emergence, $W = 36$, $n = 8$, $p < 0.05$). Rain also inhibited flight activity away from the roost; bats hung up and became inactive immediately as the rain started. There was a significant increase in the time spent hanging up during rain, compared to that recorded under normal flight conditions (Wilcoxon test on all bats which experienced rain, $W = 36$, $n = 8$, $p < 0.05$). Bats also returned to the roost earlier on wet nights (Wilcoxon test on all bats which experienced rain, $W = 28$, $n = 7$, $p < 0.05$). However, there was no evidence of reduced activity on nights of lower temperature (< 7 °C) excluding those nights on which it rained (Wilcoxon paired test; time of return, $W = 13$, $n = 7$, n.s.; time spent hanging up, $W = 9$, $n = 4$, n.s.; time away from roost, $W = 7$, $n = 6$, n.s.), and bats remained active at temperatures as low as 3.5 °C.

### (*c*) *Temporal use of feeding sites*

In total, 75 discrete feeding sites were located around six different roost sites. Within such areas, bats were observed flying slowly in and out of branches with a dipping flight path. Individual bats used between one and nine feeding sites each night (median = 3 sites), and the number of movements among foraging areas ranged from one to 16 (median = 6 movements), with bats returning to the same feeding site up to five times in a night. Bats appeared to use a limited number of sites in any location at any time of year and there was high night-to-night predictability in feeding site use. Of all the sites visited by bats, 77 % were used by the same individual on more than one night (males 63 % (22/35), females 87 % (42/48), difference between the sexes was significant: $\chi^2 = 6.696$, $n = 82$, d.f. $= 1$, $p < 0.05$). Sites to which females returned during the following night had been used for longer than sites to which the females did not return (median time spent in sites which were also used the following night = 50 min, median time spent in sites not used the following night = 30 min, $U = 3823.5$, $p < 0.05$). The average number of sites used per night, and the average number of movements between feeding sites during the night, by each bat, increased through the summer (Spearman's rank correlation; number of sites visited against date $r_s = 0.735$, $n = 16$, $p < 0.005$, total number of visits $r_s = 0.696$, $n = 16$, $p < 0.005$).

Table 2. *Activity parameters of males* (n = 6), *lactating* (*L*) *females* (n = 4) *and non-reproducing* (*NR*) *females* (n = 6) *compared using a Kruskal-Wallis* ANOVAS

| | median for L females | median for NR females | median for males | $H$ | significance |
|---|---|---|---|---|---|
| emergence (min post sunset) | 45.7 | 56.7 | 65.5 | 1.12 | n.s. |
| return (min pre sunrise) | 64.3 | 83.0 | 65.3 | 0.06 | n.s. |
| time active (min) | 334.1 | 349.8 | 278.3 | 2.74 | n.s. |
| time feeding (min) | 239.0 | 252.6 | 197.2 | 1.19 | n.s. |
| time resting (min) | 13.7 | 25.0 | 47.0 | 5.83 | n.s. |

Figure 4. The percentage of flight time, across all 16 bats, spent within different types of woodland, on all nights ($n = 65$ bat nights + 7 half nights).

Of the feeding sites located during periods of simultaneous tracking, 68 % were used by both bats at some time, and bats spent 11 % of their time within a feeding site at the same time as it was used by the other tracked individual. Up to five bats were observed feeding together, without any obvious interactions. Comparisons were made between the probability of a bat using a site when the other tracked individual was present, or absent. Data from eight bats using nine sites (in 18 bat-site combinations) showed that bats were significantly more likely to use a site when the other individual was also present (sign test; $n = 18$, $p < 0.05$).

### (*d*) *Habitat use*

All feeding sites were associated with either woodland or individual trees. Of the 75 feeding sites located, 13 (17 %) were in trees adjoining pasture land, but only seven (9 %) were close to any form of water. The bats spent most time (42 %) in mature deciduous woodland (excluding birch woodland), but also used mixed woodland, native, self-sown conifers (non-plantation) and birch woodland (figure 4). When plantations of non-native conifers were used, bats remained near the edges of stands, rather than entering deep into the woodland.

To test whether bats used deciduous woodland preferentially, or only in proportion to its availability (i.e. at random), a simple utilization-availability test was used, based upon time budgets. Woodland and groups of trees were classified as deciduous or coniferous from large scale maps, with mixed woodland being treated as 50 % deciduous and 50 % coniferous. This was an arbitrary classification as the exact composition of mixed woodland could not easily be determined. The area of deciduous and coniferous woodland within the range of the roost site in which each bat foraged was then calculated, and this allowed the expected time bats would spend in each woodland type to be predicted, in relation to its availability. Time spent in the two woodland types was calculated for each bat, and was compared to the predicted values. Bats spent significantly more time within areas of deciduous woodland compared to the values expected from its availability (Wilcoxon paired test, $W = 135$, $n = 16$, $p < 0.001$; figure 5). No differences in the use of habitat by males and females were identified.

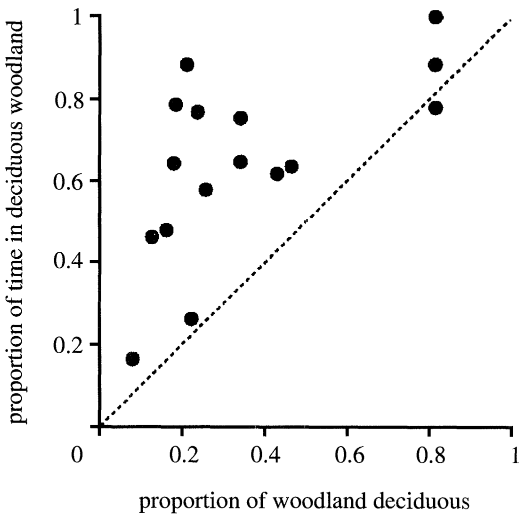

Figure 5. Comparison between the proportion of time spent by bats in deciduous woodland, and the proportion of available woodland that was deciduous. Each dot represents an individual bat ($n = 16$). The dotted line indicates the time bats would be expected to spend in deciduous woodland, if it were used at random.

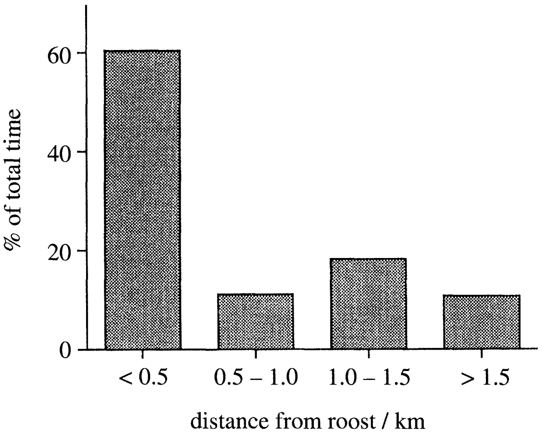

Figure 6. Percentage of total flight time spent in each distance band from the roost. Data from all 16 bats, on all nights of tracking ($n = 65$ bat nights + 7 half nights).

When commuting routes between feeding sites, and to and from the roost, could be determined, bats followed the edges of tree lines, hedges, overgrown banks, fences, rides through forests, and overgrown railway lines. Bats observed while commuting flew low and faster than within feeding areas. By using these commuting routes rather than travelling the most direct route between consecutive sites the bats travelled significantly longer distances (Wilcoxon paired test, median difference = 0.321 km, $n = 8$, $W = 36$, $p < 0.05$).

Table 3. *Comparison of time in 0.5 km band (median = 133 min) with time spent in other distance bands for all bats combined* (n = *16*), *Mann-Whitney* U *test. Initial Kruskal-Wallis* ANOVA (H = *20.25*, *d.f.* = *4*, p < *0.001*)

| | median (min) | $U$ | significance |
|---|---|---|---|
| time in 1.0 km band | 7.9 | 350.0 | $p < 0.005$ |
| time in 1.5 km band | 20.0 | 339.0 | $p < 0.005$ |
| time > 1.5 km from roost | 0.0 | 355.5 | $p < 0.001$ |
| time > 0.5 km from roost | 112.5 | 295.5 | n.s. |

Table 4. *Comparison of time in 0.5 km band (median = 189.4 min) with time spent in other distance bands for females* (n = *10*), *Mann-Whitney* U *test. Initial Kruskal-Wallis* ANOVA (H = *25.28*, *d.f.* = *4*, p < *0.001*)

| | median (min) | $U$ | significance |
|---|---|---|---|
| time in 1.0 km band | 0.00 | 151.0 | $p < 0.001$ |
| time in 1.5 km band | 10.20 | 149.0 | $p < 0.001$ |
| time > 1.5 km from roost | 0.00 | 154.0 | $p < 0.001$ |
| time > 0.5 km from roost | 36.00 | 254.0 | $p < 0.05$ |

Table 5. *Comparison of time in 0.5 km band (median = 29.7 min) with time spent in other distance bands by males* (n = *6*), *Mann-Whitney* U *test. Initial Kruskal-Wallis* ANOVA (H = *5.56*, *d.f.* = *4*, n.s.)

| | median (min) | $U$ | significance |
|---|---|---|---|
| time in 1.0 km band | 19.90 | 43.0 | n.s. |
| time in 1.5 km band | 31.70 | 40.0 | n.s. |
| time > 1.5 km from roost | 37.90 | 39.0 | n.s. |
| time > 0.5 km from roost | 152.70 | 29.5 | n.s. |

### (*e*) *Distance travelled from the roost*

The furthest feeding site used by a bat was 2.8 km from the main roost site. This was used by a male, while the greatest distance a female flew was 2.2 km from the roost site. Overall, bats spent 92% of their foraging time within 1.5 km of the roost (figure 6), and spent significantly more time within 0.5 km of the roost site, compared with any of the other distance bands (table 3). Analysis of the two sexes separately (tables 4 and 5) revealed that while females spent significantly more time within 0.5 km of the roost site when compared with other distance bands (and also when compared to time spent beyond 0.5 km of the roost site), males showed a more equal distribution of time in each distance band. Direct comparison highlighted this difference between the sexes, demonstrating that females spent more time within 0.5 km of the roost site than did males, and males spent more time beyond 1.5 km compared to females (table 6; figure 7). This difference did not reflect differences in overall flight times between the sexes, which were not significantly different (table 2). When pairs of male and female bats, which had been tracked simultaneously at the same roost, were compared similar intersexual differences in the time spent in each distance band were evident (figure 8), although the small sample size ($n = 3$) precluded statistical analysis.

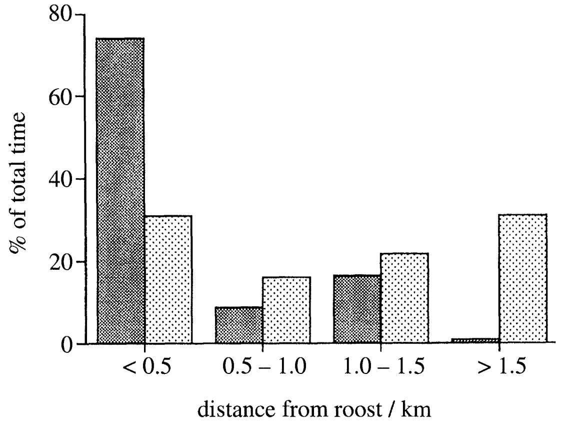

Figure 7. Percentage of total flight time spent in each distance band from the roost, comparing six male and ten female bats, across all nights of tracking. Females are represented by grey shading, and males dotted shading.

Differences in the distances travelled by bats at each roost were examined in relation to woodland availability. There was a significant positive relationship, across roosts, between the proportion of time spent by females within 0.5 km of the roost site and the area of deciduous woodland available within that distance (Spearman rank correlation, $n = 5$, $r_s = 0.98$, $p < 0.05$), but this was not found when all woodland types were considered in the analysis (Spearman rank correlation, $n = 5$, all woodland $r_s = 0.78$, n.s.) or if males were considered instead (Spearman rank correlation, $n = 5$, deciduous woodland $r_s = 0.60$, n.s.; all woodland $r_s = 0.38$, n.s.).

No relationship was found between relative transmitter loading (transmitter mass/body mass) and either the furthest distance travelled ($r_s = 0.10$, $n = 16$, n.s.), or time spent within 0.5 km of the roost by each

Table 6. *Comparison of time spent in each distance band by males* (n = *6*) *and females* (n = *10*), *Mann-Whitney* U *test*

| | median for females (min) | median for males (min) | $U$ | significance |
|---|---|---|---|---|
| time in 1.0 km band | 189.4 | 29.7 | 104 | $p < 0.05$ |
| time in 1.0 km band | 0.0 | 19.9 | 79 | n.s. |
| time in 1.5 km band | 10.3 | 31.7 | 84 | n.s. |
| time > 1.5 km from roost | 0.0 | 37.9 | 67 | $p < 0.05$ |
| time > 0.5 km from roost | 36.0 | 152.7 | 68 | n.s. |

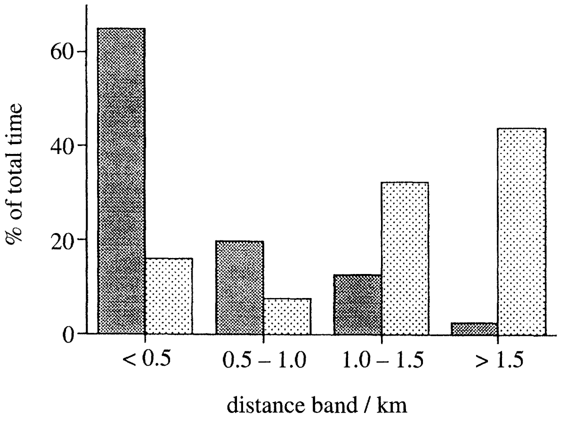

Figure 8. Percentage of total flight time spent in each distance band from the roost, comparing three pairs of male and female bats, tracked simultaneously from the same roosts. Females are represented by grey shading, and males by dotted shading.

bat ($r_s = 0.11$, $n = 16$, n.s.). Bats with lower body mass and thus higher transmitter loading ($> 8\%$ of body mass; $n = 8$), spent a median of 29.7 min within 0.5 km of the roost, less than bats with lower transmitter loads ($< 8\%$ of body mass; $n = 8$) spent within this distance (median = 152.4 mins), however this difference was not significant (Mann-Whitney U-test, $U = 0.23$, n.s.).

### (*f*) *Insect catches*

The insects caught were pooled across five nights of sweep netting. The effect of woodland type (deciduous or coniferous) and the effect of time of night on insect catches were examined using two-way ANOVAS. When all orders of insect were included, no significant effect of either woodland type or time was found (wood, $F = 3.45$, d.f. = 1, n.s.; time $F = 5.78$, d.f. = 4, n.s.). However, when only Lepidoptera were considered in the analysis there was a significant effect both of woodland type and of time through the night (wood $F = 12.41$, d.f = 1, $p < 0.05$; time $F = 13.49$, d.f. = 4, $p < 0.05$), indicating more lepidopterans were netted in deciduous woodland, and fewer were caught as the night progressed in both coniferous (linear regression $F = 16.7$, $p < 0.05$) and deciduous woodland (linear regression, $F = 109.7$, $p < 0.005$).

## 4. DISCUSSION

### (*a*) *Nocturnal activity patterns*

As in other bat species, the time of emergence of *Plecotus auritus* was highly synchronized with the time of sunset, which appears to reflect the use of light levels as a cue for emergence (DeCoursey & DeCoursey 1964; Erkert 1982). However, the relative time at which different bat species emerge differs (Jones & Rydell 1994). *Plecotus auritus*, emerged relatively late, on average half an hour later than other sympatric species (Rydell *et al.* 1996). For example, in the same region *Pipistrellus pipistrellus* emerges 35 min after sunset (Swift 1980). The time at which bats emerge may reflect a compromise between energetic requirements and the risks of predation (Speakman 1991; Jones & Rydell 1994), and the outcome of these pressures may differ between species. As a slow flying species, *P. auritus* may be more at risk from aerial predators which it cannot easily evade (Taake 1985) and may reduce such risks by emerging later, at lower light levels. In addition, the advantages of emerging early to coincide with a higher insect abundance may be reduced in *P. auritus*, because lepidopterans appear to be available for longer during the night, with a less rapid decline in activity, compared to other insects (Rydell *et al.* 1996). In addition, the ability of this species to glean non-flying prey may relieve it from the necessity of emerging to meet the peak of insect flight activity.

Intraspecific variation in the time of emergence of *P. auritus* may also reflect dangers of aerial predation. Woodland located close to roost sites may provide cover from aerial predators, enabling bats to emerge earlier, at relatively higher light levels (Jones *et al.* 1995). The use of roosts close to woodland may therefore be advantageous to bats, which can consequently extend their foraging activity by starting to forage earlier in the evening. This may explain the apparent selection for roosts located close to woodland (Entwistle *et al.* 1996). Further, roosts located close to woodland may be particularly important for bats at high latitudes, when foraging time is restricted by the duration of the night.

The nocturnal activity pattern of *P. auritus* also contrasts with many other temperate zone bat species which display a bimodal activity pattern (Erkert 1982), separated by a period of night roosting (e.g. Anthony *et al.* 1981). Bimodal activity patterns of bats are thought to parallel the nocturnal activity patterns of many insects (Swift 1980), with reduced prey activity during the middle of the night making insects more difficult to detect and thus reducing the efficiency of continued foraging. The use of passive listening and gleaning may allow *P. auritus* to overcome these apparent changes in prey availability, because non-flying insects would remain detectable (Anderson & Racey 1993). Thus, the night time variations in insect abundance may be less variable for gleaning species such as *P. auritus* compared to aerial hawking bats, allowing activity bouts to be spread over the entire night, without any substantial night roosting period.

It has been suggested that bats at northern latitudes may be forced to forego a night roosting period and continue feeding as a consequence of the limited night length (Kunz 1982). This seems an unlikely explanation for the continuous foraging behaviour in the present study because unimodal activity in *P. auritus* has also been described in a more southerly study (50° N; Fuhrmann & Seitz 1992). In the present study bats appeared to make full, symmetrical use of the night, and foraged for as long as possible within the limits set by light levels. This contrasts to activity described from Germany where activity was truncated and bats returned earlier to the roosts, although bats still foraged for an average of 6 h per night (Fuhrmann & Seitz 1992).

During lactation female bats face increased energetic demands (Kurta *et al.* 1987, 1989), linked to the costs of milk production. To meet these increased energetic requirements, females may forage for longer to increase their net energy intake (e.g. Barclay 1989; Rydell 1993), or else may change prey selection strategies to increase energy intake within the same foraging period (Belwood & Fenton 1976). Alternatively, bats may reduce their energy requirements by entering torpor for periods during the day (Speakman & Racey 1987). Data from this study showed no evidence that lactating females extended their foraging period, even when simultaneously tracked lactating and non-reproducing bats were compared. The limited hours of darkness available at northern latitudes may have precluded such an extension of foraging time. Previous investigations of *P. auritus* at roosts in the same study area suggested that the bats instead used daily torpor extensively during lactation (Speakman & Racey 1987).

Climatic conditions may have substantial effects on the activity of bats (Erkert 1982). Insect flight activity is reduced at low temperatures (Taylor 1963), and this may reduce the profitability of aerial hunting. Consequently, many bats become inactive at low temperatures (e.g. Anthony *et al.* 1981; Barclay 1982). However, *Plecotus auritus* can detect non-flying prey (Anderson & Racey 1993), and this may explain the bats' ability to continue to forage at low temperatures.

The apparent reluctance of bats to fly in heavy rain has been noted for many species (Erkert 1982) and has been explained by reduced insect availability, thermoregulatory problems, and by interference in the processing of echolocation calls (Fenton *et al.* 1977). The curtailed activity found in *P. auritus* during rain, is unlikely to reflect lowered insect activity, as non-flying prey can be detected. Also, interference in processing echolocation calls would be unlikely to affect the bats' abilities to detect prey, which can also be located using passive listening. Rather *P. auritus* may be deterred from foraging during rain due to problems linked to thermoregulation, or because the noise of raindrops interferes with the detection of prey by passive listening.

### (*b*) *Temporal use of feeding sites*

The knowledge of patches of habitat where high prey availability can be predicted may be a key benefit of remaining loyal to a foraging range and roost site (Greenwood & Harvey 1976). Many species appear to have knowledge of productive feeding sites in their range, and thus may maximize food intake by feeding in such sites. *Plecotus auritus* appears to use a series of feeding sites in the vicinity of the roost, which are used predictably night-to-night. Females appeared more likely to return to feeding patches compared to males, who may have used a more opportunistic approach to locating food.

Bats at feeding sites may interact with conspecifics in different ways, from individual defence of feeding areas (e.g. *Eptesicus nilssoni*, Rydell 1986) to group foraging (*Myotis daubentonii*, Wallin 1961). From observations of bats marked with reflective tape, Swift & Racey (1983) suggested that *P. auritus* used solitary feeding beats around trees. In the present study bats did forage in the presence of other individuals. This need not, however, imply 'group foraging' as bats may have just exploited areas of high prey availability independently, without interference. Indeed, it may be that other individuals using the same feeding site would not be detected given the short range of echolocation calls in this species (ca. 5 m, Baagøe 1987).

### (*c*) *Habitat use*

*Plecotus auritus* fed predominantly around trees and woodland, as has been described in other studies of this species (Swift & Racey 1983; Barataud 1990; Fuhrmann & Seitz 1992). The exclusive use of woodland areas and trees by *P. auritus* contrasts with the degree of flexibility in habitat use described in many other Palaearctic species, which use habitats including water bodies and pasture land in addition to woodland (e.g. *Pipistrellus pipistrellus*, Racey & Swift 1985; *Rhinolophus ferrumequinum*, Jones & Morton 1992; *Eptesicus serotinus*, Catto *et al.* 1996). Woodland is a habitat rich in lepidopterans, provides many surfaces from which insects can be gleaned, and may provide cover from aerial predation. The wing shape in *P. auritus* results in manoeuvrable flight which enables this species to exploit cluttered habitats, such as woodland, more than would be the case for species with long, narrow wings (Norberg & Rayner 1987), and quiet, clutter resistant echolocation calls allow *P. auritus* to navigate, and locate insects, within woodland. Thus, wing morphology, echolocation calls and foraging habitat appear to be features which have coevolved, allowing *P. auritus* to specialize on gleaning moths from surfaces. In addition, *P. auritus* may not be able to forage as efficiently in open areas, where fewer moths are available and could not be detected over long distances, where few surfaces are available for gleaning, and where the slow flight of this species may make it at particular risk from predation. The only flexibility in habitat use involved the use of edge habitats and single trees, which may present less clutter than woodland while still providing some degree of cover.

The clear preference of *P. auritus* for deciduous woodland is likely to reflect prey availability, because plantations of non-native pine conifers generally support fewer insects (including lepidopterans) relative to deciduous woodlands (Wormell 1977; Waring 1988, 1989). Differences in the availability of lepidopterans between deciduous and coniferous woodlands were also demonstrated in this study, where adjoining sites, some of which were used by bats, were compared. High prey availability in deciduous woodlands would result in higher encounter rates with potential prey items, and presumably higher feeding success.

The apparent reluctance of *P. auritus* to fly in open areas was further demonstrated by the use of topographical features and/or covered flyways, when commuting between feeding sites, a behaviour also described for several other bat species (e.g. *Myotis emarginatus*, Krull *et al.* 1991). Such flyways may provide cover, and reduce the risk from aerial predators, especially for slow flying species such as *P. auritus*. However, other explanations for this behaviour cannot be excluded. Species with echolocation calls of limited range, such as *P. auritus*, may rely on landscape features for orientation (Limpens *et al.* 1989). In addition, vegetated flyways such as treelines may provide *P. auritus* with the opportunity to forage while commuting, and thus balance the costs of moving between sites (see also Krull *et al.* 1991).

### (*d*) *Distances travelled from the roost*

Maximum distances travelled by the radio-tracked bats were similar to previous estimates for this species (1.1 km, Swift & Racey 1983; 1.5 km, Fuhrmann & Seitz 1992). This is a relatively short range in comparison to maximum foraging distances recorded from other Palaearctic bat species, including *Pipistrellus pipistrellus* (5.1 km, Racey & Swift 1985), *Nyctalus noctula* (26 km, Kronwitter 1988), *Rhinolophus ferrumequinum* (10 km, Jones & Morton 1992), *Eptesicus nilssoni* (30 km, de Jong 1994), and *Eptesicus serotinus* (14.1 km, Catto *et al.* 1996). The reason that bats do not travel far from the roost may reflect the slow, expensive flight of this species (Norberg 1976), a consequence of the wing shape and wing loading. Differences in wing morphology and flight abilities are considered to affect the nightly distances travelled by different species (e.g. Black 1974). Jones *et al.* (1995) suggested that distance travelled is related to the aspect ratio of the wings, and species with low aspect ratios (short, broad wings), such as *P. auritus*, may be conservative in the distances travelled from the roost site to foraging areas. This may be either because flight is costly (estimated for *P. auritus* as 0.7 kJ per km; Entwistle 1994), or because a longer time spent commuting (5.4 min per km; estimated from Norberg 1976) would restrict the time available for feeding. Maximizing the time available for feeding may be at a premium at northern latitudes when the night is short, and for lactating females which may have to return to the roost during the night. Similar restricted foraging distances have been reported from related species in America (*Plecotus* (*Corynorhinus*) *townsendii*, *P. rafinesquii*; Clark *et al.* 1993, Adam *et al.* 1994).

It has previously been demonstrated that *P. auritus* selects roosts that have abundant woodland within 0.5 km compared to random buildings (Entwistle *et al.* 1996*a*). In this study the finding that bats concentrated their foraging within 0.5 km confirms that the woodland in the vicinity of the roost is important foraging habitat. The distance travelled by females to foraging areas was affected directly by the availability of deciduous woodland within 0.5 km of the roost. Thus, the restriction of foraging distance, linked to flight characteristics, may in turn affect which roost sites are used, and otherwise suitable houses lacking sufficient foraging areas nearby may not be exploited.

During the energetically expensive period of lactation, the limited number of hours of darkness available for foraging make time, as well as energy, an important currency, especially when a bat may have to return to the roost several times each night, to suckle her young. Females may therefore benefit by remaining in the vicinity of the roost site to forage, and therefore avoid the cumulative costs of making several journeys to more distant foraging grounds. A reduction in foraging range during lactation has been reported in other mammals including voles (Madison 1978) and deer (Clutton-Brock *et al.* 1982). However, in *P. auritus* a restricted foraging range, compared to males, was also displayed by females which were non-reproducing and post-lactating. Instead, the pattern of distribution of males and females suggests that females may remain exclusively in a core area of the foraging range, whereas males travel further, similar to the pattern described in the bat *Rhynchonycteris naso* (Bradbury & Vehrencamp 1976) and in the bushbaby *Galago crassicaudatus* (Clark 1978). It is possible that males were aggressively excluded from the core area; alternatively males may benefit from travelling further from the roost site. For example, males may encounter reduced intraspecific competition further from the roost (refuging theory, Hamilton *et al.* 1967), or may reduce competition with females resulting in higher survival of related young (inclusive fitness, Hamilton 1964). Alternatively, females from neighbouring colonies might be encountered (although copulation will not occur until autumn) or males may have some territorial role in protecting a ‘colony area’ (Heise & Schmidt 1988) from outside individuals. However, differences in the distances travelled may just reflect differences in the degree to which the males are opportunistic with relation to new feeding patches, or differences in dietary preferences (although there was no evidence of differential habitat use).

There was no evidence that the restricted foraging range displayed in this species was linked to a change in behaviour due to carrying transmitters. Transmitter loading was not reflected in the distances travelled by individual bats, as would be expected if carrying the transmitter had impeded flight. In addition, the distances travelled by bats in this study were similar to those recorded from a previous, non radio-racking study, of *P. auritus* (Swift & Racey 1983). No short- or long-term effects of radio-tracking could be identified from bats tracked in this study (Entwistle *et al.* 1996*b*).

## 5. CONCLUSIONS

The foraging behaviour of *Plecotus auritus* differs from that of other Palaearctic microchiropterans which have been studied, and can be related to the morphology and sensory abilities of this species. Differences were clear with respect to the pattern of activity during the night, the way in which the bats exploit different habitats and where they forage in relation to the position of the roost site. Within the foraging behaviour described for this species some variation was identified and this could be attributed to differences in habitat availability between roost sites, interindividual differences linked to sex and reproductive status, and nightly variation in climatic conditions. The use of habitat in this species has implications for its conservation, and suggests that the protection of deciduous woodland, particularly in the vicinity of roost sites, and habitat connectivity should be key priorities.

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## REFERENCES

Adam, M. D., Lacki, M. J. & Barnes, T. G. 1994 Foraging areas and habitat use of the Virginia big-eared bat in Kentucky. *J. Wildl. Mgmt* **58**, 462–469.

Aldridge, H. D. J. N. & Brigham, R. M. 1988 Load carrying and manoeuvrability in an insectivorous bat: a test of the 5% 'rule' of radio-telemetry. *J. Mammal* **69**, 379–382.

Aldridge, H. D. J. N. & Rautenbach, I. L. 1987 Morphology, echolocation and resource partitioning in insectivorous bats. *J. Anim. Ecol.* **56**, 763–778.

Anderson, M. E. & Racey, P. A. 1991 Feeding behaviour of captive brown long-eared bats, *Plecotus auritus*. *Anim. Behav.* **42**, 489–493.

Anderson, M. E. & Racey, P. A. 1993 Discrimination between fluttering and non-fluttering moths by brown long-eared bats, *Plecotus auritus*. *Anim. Behav.* **46**, 1151–1155.

Anthony, E. L. P., Stack, M. H. & Kunz, T. H. 1981 Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density, and environmental conditions. *Oecologica* **51**, 151–156.

Baagøe, H. J. 1987 The Scandinavian bat fauna: adaptive wing morphology and free flight in the field. In *Recent advances in the study of bats* (ed. M. B. Fenton, P. A. Racey & J. M. V. Rayner), pp. 57–74. Cambridge University Press.

Barataud, M. 1990 Eléments sur le comportement alimentaire des oreillards brun et gris (*Plecotus auritus* Linnaeus, 1758 et *Plecotus austriacus* Fischer, 1829). *Le Rhinolophe* **7**, 3–10.

Barclay, R. M. R. 1982 Night roosting behaviour of the little brown bat, *Myotis lucifugus*. *J. Mammal* **63**, 464–474.

Barclay, R. M. R. 1989 The effect of reproductive condition on the foraging behaviour of female hoary bats, *Lasiurus cinereus*. *Behav. Ecol. Sociobiol.* **24**, 31–37.

Belwood, J. J. & Fenton, M. B. 1976 Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). *Can. J. Zool.* **54**, 1674–1678.

Black, H. L. 1974 A north temperate bat community: structure and prey populations. *J. Mammal* **55**, 138–157.

Bradbury, J. W. & Vehrencamp, S. L. 1976 Social organization and foraging in emballonurid bats. I. Field studies. *Behav. Ecol. Sociobiol.* **1**, 337–381.

Catto, C. M. C., Hutson, A. M., Racey, P. A. & Stephenson, P. J. 1996 Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in Southern England. *J. Zool.* **238**, 623–633.

Clark, B. S., Leslie, D. M. & Carter, T. S. 1993 Foraging activity of adult female Ozark big-eared bats (*Plecotus townsendii ingens*) in summer. *J. Mammal* **74**, 422–427.

Clark, D. A. 1980 Age- and sex-dependent foraging strategies of a small mammalian omnivore. *J. Anim. Ecol.* **49**, 549–563.

Clutton-Brock, T. H., Iason, G. R., Albon, S. D. & Guinness, F. E. 1982 Effects of lactation on feeding behaviour and habitat use in wild red deer hinds. *J. Zool.* **198**, 227–236.

DeCoursey, G. & DeCoursey, P. J. 1964 Adaptive aspects of activity rhythms in bats. *Biol. Bull.* **126**, 14–27.

De Jong, J. 1994 Habitat use, home-range and activity pattern of the northern bat, *Eptesicus nilssoni*, in a hemiboreal coniferous forest. *Mammalia* **58**, 535–548.

Entwistle, A. C. 1994 Roost ecology of the brown long-eared bat (*Plecotus auritus*) in north-east Scotland. Ph.D. thesis, Aberdeen University.

Entwistle, A. C., Racey, P. A. & Speakman, J. R. 1996*a* Roost selection in the brown long-eared bat (*Plecotus auritus*). (Submitted.)

Entwistle, A. C., Racey, P. A. & Speakman, J. R. 1996*b* No short- or long-term effects of radiotracking in the brown long-eared bat, *Plecotus auritus*. (Submitted.)

Erkert, H. G. 1982 Ecological aspects of bat activity rhythms. In *Ecology of bats* (ed. T. H. Kunz), pp. 201–242. Plenum, New York.

Fenton, M. B. 1972 The structure of aerial-feeding bat faunas as indicated by ears and wing elements. *Can. J. Zool.* **50**, 287–296.

Fenton, M. B., Boyle, N. G. H., Harrison, T. M. & Oxley, T. M. 1977 Activity patterns, habitat use, and prey selection by some African insectivorous bats. *Biotropica* **9**, 73–85.

Fuhrmann, M. & Seitz, A. 1992 Nocturnal activity of the brown long-eared bat (*Plecotus auritus* L., 1758): data from radio-tracking in the Lenneberg forest near Mainz (Germany). In *Wildlife telemetry. Remote monitoring and tracking of animals* (ed. I. G. Priede & S. M. Swift), pp. 538–548. Proc. 4th Conf. on Wildlife Telemetry. Aberdeen University, U.K.

Greenwood, P. J. & Harvey, P. H. 1976 The adaptive significance of variation in breeding area fidelity of the blackbird (*Turdus merula* L.). *J. Anim. Ecol.* **45**, 887–898.

Hamilton, W. D. 1964 The genetical evolution of social behaviour. *J. theor. Biol.* **7**, 1–52.

Hamilton, W. J., Gilbert, W. M., Heppner, F. H. & Planck, R. J. 1967 Starling roost dispersal and a hypothetical mechanism regulating rhythmical animal movement to and from dispersal centers. *Ecology* **48**, 825–833.

Heise, G. & Schmidt, A. 1988 Contribution to the social organisation and ecology of the brown long-eared bat (*Plecotus auritus*). *Nyctalus* **2**, 445–465.

Jones, G., Duvergé, P. L. & Ransome, R. D. 1995 Conservation biology of an endangered species: field studies of Greater horseshoe bats. *Symp. Zool. Soc.* **67**: 309–324.

Jones, G. & Morton, M. 1992 Radio-tracking studies on habitat use by greater horseshoe bats (*Rhinolophus ferrumequinum*). In *Wildlife telemetry. Remote monitoring and tracking of animals* (ed. I. G. Priede & S. M. Swift), pp. 521–537. Proc. 4th Confer. on Wildlife Telemetry. Aberdeen University, Aberdeen

Jones, G. & Rydell, J. 1994 Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Phil. Trans. R. Soc. Lond.* B **346**, 445–455

Kronwitter, F. 1988 Population structure, habitat use and activity patterns of the noctule bat, *Nyctalus noctula* Schreb., 1774 (Chiroptera: Vespertilionidae) revealed by radio tracking. *Myotis* **26**, 23–85.

Krull, D., Schumm, A., Metzner, W. & Neuweiler, G. 1991 Foraging areas and foraging behaviour in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). *Behav. Ecol. Sociobiol.* **28**, 247–253.

Kunz, T. H. 1982 Roosting ecology of bats. In *Ecology of bats* (ed. T. H. Kunz), p. 1–55. Plenum, New York.

Kurta, A., Bell, G. P., Nagy, K. A. & Kunz, T. H. 1989 Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). *Physiol. Zool.* **62**, 804–818.

Kurta, A., Johnson, K. A. & Kunz, T. H. 1987 Oxygen consumption and body temperature of female little brown bats (*Myotis lucifugus*) under simulated roost conditions. *Physiol. Zool.* **60**, 386–397.

Limpens, H. J. G. A., Helmer, W., Van Winden, A. & Mostert, K. 1989 Bats Chiroptera) and linear landscape elements. *Lutra* **32**, 1–20.

Madison, D. M. 1978 Movement indicators of reproductive events among female meadow voles as revealed by radiotelemetry. *J. Mammal* **59**, 835–843.

Neuweiler, G. 1984 Foraging, echolocation and audition in bats. *Naturwissenschaften* **71**, 446–455.

Neuweiler, G. 1989 Foraging ecology and audition in echolocating bats. *Trends Ecol. Evol.* **4**, 160–166.

Norberg, U. M. 1976 Aerodynamics, kinematics and energetics of horizontal flapping flight in the long-eared bat *Plecotus auritus*. *J. exp. Biol.* **65**, 179–212.

Norberg, U. M. & Rayner, J. M. V. 1987 Ecological morphology and flight in bats. *Phil. Trans. R. Soc. Lond.* B **316**, 335–427.

O'Neill, M. G. & Taylor, R. J. 1986 Observations on the flight patterns and foraging behaviour of Tasmanian bats. *Aust. Wildl. Res.* **13**, 427–432.

Racey, P. A. & Swift, S. M. 1985 Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *J. Anim. Ecol.* **54**, 205– 215.

Rydell, J. 1986 Feeding territoriality in female northern bats, *Eptesicus nilssoni*. *Ethology* **72**, 329–337.

Rydell, J. 1989 Feeding activity of the northern bat, *Eptesicus nilssoni* during pregnancy and lactation. *Oecologica* **80**, 562–565.

Rydell, J. 1993 Variation in foraging activity of an aerial insectivorous bat during reproduction. *J. Mammal* **74**, 503–509.

Rydell, J., Entwistle, A. & Racey, P. A. 1996 Timing of foraging flights in three species of bats in relation to insect activity. *Oikos*. (In the press.)

Speakman, J. R. 1991 Why do insectivorous bats in Britain not fly in daylight more frequently? *Funct. Ecol.* **5**, 518–524.

Speakman, J. R. & Racey, P. A. 1987 The energetics of pregnancy and lactation in the brown long-eared bat, *Plecotus auritus*. In *Recent advances in the study of bats* (ed. M. B. Fenton, P. A. Racey & J. M. V. Rayner), pp. 367–393. Cambridge University Press.

Swift, S. 1980 Activity patterns of Pipistrelle bats in north-east Scotland. *J. Zool.* **190**, 285–295.

Swift, S. M. & Racey, P. A. 1983 Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *J. Zool.* **200**, 249–259.

Taake, K. H. 1985 Behavioral and ecological aspects of predator-prey relationship in European bats (Chiroptera). *Z. Saugetierkd.* **50**, 202–208.

Taylor, L. R. 1963 Analysis of the effect of temperature on insects in flight. *J. Anim. Ecol.* **32**, 99–117.

Wallin, L. 1961 Territorialism on the hunting ground of *Myotis daubentonii*. *Saugetieholl Mittelungen* **9**, 156–159.

Waring, P. 1988 Responses of moth populations to coppicing and the planting of conifers. In *Woodland conservation and research in the Clay Vale of Oxfordshire and Buckinghamshire* (ed. K. Kirby & F. J. Wright). NCC, Peterborough. *Research and survey in nature conservation* **15**, 82–113.

Waring, P. 1989 Comparison of light-trap catches in deciduous and coniferous woodland habitats. *Entomol. Rec.* **101**, 1–10.

White, G. C. & Garrott, R. A. 1990 *Analysis of wildlife radio-tracking data*. Academic Press, London.

Wormell, P. 1977 Woodland insect population changes on the Isle of Rhum in relation to forest history and woodland restoration. *Scot. Forest.* **31**, 13–36.

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