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Importance of night roosts for bat conservation: roosting behaviour of the lesser horseshoe bat *Rhinolophus hipposideros*

Tessa Knight, Gareth Jones*

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

ABSTRACT: Safeguarding day roosts is of key importance in bat conservation. However, little emphasis has been placed on the conservation of night roosts, although these may act as refuges close to foraging grounds. We studied the roosting behaviour of the lesser horseshoe bat *Rhinolophus hipposideros*, a species that has declined over large areas of Europe, and radio-tracked 54 bats from 3 maternity roosts in contrasting landscapes in Britain. The bats exhibited multimodal patterns of overnight activity (mean ind.$^{-1}$: 2.1 to 4.5 night roosting bouts). More than 75 % of bats used night roosts away from the maternity roost, typically in buildings. Up to 5 different night roosts were used by individual bats, with the number of night roosts correlated with home range and core area. Night roosts were significantly nearer to core foraging areas than were maternity roosts, with 64 to 86 % contained within core nuclei. Multimodal activity patterns and frequent use of night roosts are important aspects of *R. hipposideros* behaviour that need to be considered in management strategies. We postulate that minimisation of distance to feeding sites may be the primary function of the night roosts, with roosts being used for resting and digestion between foraging bouts. Night roosts are therefore an integral part of core foraging areas and require protection.

KEY WORDS: Rhinolophidae · Habitat management · Nocturnal activity · Multimodal

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INTRODUCTION

Bats spend a large proportion of their lives roosting, and insectivorous species have a wide diversity of roosting habits (Kunz & Lumsden 2003). Many bats form maternity roosts where large numbers of females congregate to give birth and raise their young. These roosts are arguably sites of prime conservation concern. Disturbance and destruction of day roost sites is a major factor in bat population declines (Kunz 1982), and as such the protection of day roosts may be of great importance in modern bat conservation efforts (Fenton 1997). However, much less emphasis has been placed on the use and conservation of roosts used during the night (night roosts), and yet occupation of night roosts between foraging flights is a common habit of temperate insectivorous bats (Anthony et al. 1981, Barclay 1982, Lewis 1994, Jaberg & Blant 2003).

To help define the needs of night roosting bats in a rural setting we studied the roosting behaviour of the lesser horseshoe bat *Rhinolophus hipposideros*. Although this species is listed in the category of 'Least Concern' globally in the latest IUCN Red List of Threatened Species (www.iucnredlist.org) its numbers are decreasing; the species underwent a dramatic decline in western Europe, where it is now regarded as endangered in many areas (Stebbings 1988, Ohlendorf 1997). In northern Europe *R. hipposideros* generally roosts in buildings during the summer and uses caves and mines during the hibernation period. Although the use of night roosts by *R. hipposideros* has been reported previously (Gaisler 1963a, McAney & Fairley 1988), research has focussed on maternity roosts and hibernation sites. For example, within Britain the general characteristics of *R. hipposideros* maternity roosts have been well documented (McAney & Fairley 1988), and

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ongoing monitoring of colony counts at maternity roosts and hibernation sites is widespread (Warren & Witter 2002). However, much less is known about use of roosts at night.

Early studies of overnight activity of the species failed to describe any overall pattern (Gaisler 1963a, McAney & Fairley 1988). However, more recent exploratory work using radio-telemetry has indicated multimodal phases of activity, with 2 to 4 foraging bouts (Bontadina et al. 2002). This multimodal pattern is unusual. A review by Erkert (1982) found that insectivorous bats characteristically follow a bimodal pattern of activity, whereby a peak in activity is recorded following emergence from the roost at dusk, with a second smaller peak at the end of the night before dawn. During lactation female bats often return to maternity roosts in the middle of the night to suckle offspring (Swift 1980, Maier 1992). The pattern of overnight activity in *Rhinolophus hipposideros* may suggest that night roosting behaviour is of greater importance than previously believed and therefore warrants more extensive study.

Kunz (1982) suggested 5 possible functions of night roosts: energy conservation, digestion, predator avoidance, information transfer and social interactions. Roost switching to conserve energy may reflect the selection of optimal microclimate, for example during sub-optimal foraging conditions or to enable torpor, or the minimisation of distance to feeding sites (Kunz & Lumsden 2003, Lausen & Barclay 2003). We used radio-telemetry to investigate the behaviour of *Rhinolophus hipposideros* to test the following predictions: (1) that night roosts are significantly nearer to foraging grounds; (2) that the species exhibits multimodal patterns of activity through the night; and (3) that temporal variation in overnight patterns relates to weather conditions. We discuss the importance of night roosts as refuges in close proximity to key foraging sites and suggest that this has significant implications for the conservation value of such roosts. Our results will directly aid the development of management plans and may also be more widely applicable to other bat species in rural and semi-rural landscapes.

MATERIALS AND METHODS

Study sites and land use mapping. The study was conducted during early to late May (defined as early pregnancy), late May to early June (late pregnancy), late July to mid-August (lactation) and late August to mid-September (post-lactation) in 2003 to 2005. We radio-tracked bats from 3 maternity roosts in contrasting landscape types. The 'lowland landscape' roost was a colony of ~160 animals (including juveniles) lo-

cated in the attic space of a converted barn in Upper Langford, North Somerset, England (51° 19′ N, 2° 46′ W, ~40 m above sea level [a.s.l.]). The surrounding landscape is predominantly lowland pastoral farmland (about 30% of land cover within 2 km of the roost), with <10% arable, and an extensive wooded scarp to the southeast (about 23% woodland cover, including about 5% broad-leaved woodland within 2 km). The colony was typical of many found in lowland areas in southwest England and south Wales.

The second maternity colony studied was in what we considered a 'high quality' landscape situated in the Wye Valley. The roost was a maternity colony of ~750 bats within a small barn in Brockweir, Gloucestershire, England (51° 43′ N, 2° 40′ W, ~120 m a.s.l.). The Wye Valley and Forest of Dean (Wales/England border) support 26% of the British population of *Rhinolophus hipposideros*. This area is designated a Special Area of Conservation (SAC; EU code UK0014794) and comprises 26.2% broad-leaved deciduous woodland, which is considerably higher than the national average (5.8% in England, 6.1% in Wales). Broad-leaved woodland is a key foraging habitat for *R. hipposideros* (Bontadina et al. 2002). Other important habitats within 2 km of the roost included >40% pastureland and the River Wye. On the basis of the nature of the surrounding habitat and the large roost size, we classified this landscape *a priori* as 'high quality' for the species.

Our third study site was a colony of ~130 animals within a large barn in Llanbedr, Brecon Beacons National Park, Wales (51°53′ N, 3°06′ W, ~247 m a.s.l.). The roost was in a valley characterised by numerous small streams, pasture farmland and sizeable areas of forestry plantation. Above the valley the landscape was dominated by open moorland. Indeed, about 50% of the habitat within 2 km of the roost site was moorland dominated by bracken or heath vegetation. The presence of large areas of moorland and coniferous non-native forestry plantation (about 15%) in the area, and the relatively high altitude of this site led us to consider it *a priori* as being of relatively low quality for the species. We refer to this landscape as the 'upland landscape'.

We undertook Phase 1 habitat surveys (JNCC 1993) of the study sites and mapped all areas of settlement, defined as built-up areas with associated gardens and infrastructure, which included roads, individual scattered properties and villages/towns. Base maps (Ordnance Survey Land-Line.Plus, multi-scale) were obtained from Digimap (© Crown Copyright Ordnance Survey, EDINA Digimap/JISC) and converted for use in the GIS software ArcView GIS 3.2 (ESRI GIS and Mapping Software) with Map Manager (ESRI). Landuse maps were then generated with ArcView so that

the dominant habitat types around each roost could be quantified.

Radio-telemetry. We caught bats in a static hand net as they emerged from the roost, except for 18 ind. which we caught in the roost. Bats were assigned a reproductive class, defined as juvenile (yearlings with grey fur and lacking ossification of the epiphyseal joints in the finger bones [Anthony 1988]), nulliparous (females lacking pelvic nipples) (Gaisler 1963b) or adult (parous females with pelvic nipples). Forearm length was recorded to 0.1 mm, using callipers and bats were weighed to 0.1 g in a small plastic bag using a Pesola (Baar) Micro-Line 30 g scale. Between 2 and 6 bats were selected per session for radio tagging. Emphasis was placed on studying female bats, and any males caught were disregarded unless juvenile. Larger bats were selected to minimise risk of adverse effects of carrying extra weight, using forearm length as a measure of skeletal size, following Bontadina et al. (2002).

The fur between the scapulae was clipped and a radio transmitter (<0.35 g PIP3, Biotrack) attached using Skinbond (Smith and Nephew, supplied by Alana Ecology). Tagged bats were ringed (banded) using 2.9 mm magnesium-aluminium flanged rings (Mammal Society). The transmitters increased the body mass of adult females by mean 6.2% (range 4.9 to 8.1%), of nulliparous females by mean 7.1% (range 6.5 to 8.8%) and of juveniles by mean 7.2% (range 6.7 to 7.8%). The increased body mass recorded in adult females is comparable with the 4.5 to 8.1% increase documented by Bontadina et al. (2002) in their study on *Rhinolophus hipposideros* in which they concluded that the transmitters had no demonstrable adverse effect on flight behaviour.

We located bats using a Lotek Suretrack STR_1000 receiver (Lotek Wireless) connected to either a hand-held directional 3-element Yagi aerial or a magnetic whip aerial on the car roof. Locations were recorded at 5 min intervals on a Garmin GPSmap76 Global Positioning System (minimum accuracy ± 10 m) using the 'homing-in' method (Kenward 2001). Homing-in has been used successfully to radio-track flying greater horseshoe bats *Rhinolophus ferrumequinu*m (Duvergé & Jones 2003, Flanders & Jones 2009). Lesser horseshoe bats fly more slowly than greater horseshoe bats and we are confident that homing-in was an appropriate method to use in this study. On the small number of occasions when access to sites was restricted, we took bearings using a prismatic compass, and distance to the bat was estimated from the minimum signal strength, knowledge of the terrain and observer experience (O'Donnell 2000). Each location (hereafter termed a fix) was recorded on maps with an estimated accuracy of ±100 m. If we felt there was poor resolution

of a fix (signal faint, i.e. high gain or direction uncertain, e.g. due to signal bounce) then we omitted the fix from the analysis. Although bats were followed continuously, analysis was undertaken using fixes recorded at 15 min intervals to minimise autocorrelation (Harris et al. 1990).

An activity category was assigned for each fix: commuting (rapid, directional movements between distant sites), foraging (sustained activity within a defined area of variable size), perching (typically a period of inactivity <10 min where the bat was hanging from a tree), night roosting (typically a period of inactivity >10 min within a building) or day roosting (see Russo et al. 2002).

Weather conditions were recorded at dusk and dawn and at hourly intervals in between: air temperature (°C), wind speed (Beaufort scale) and rainfall (ranked descriptively as 0 = none, 1 = spots, 2 = drizzle, 3 = fine, 4 = moderate, 5 = heavy, 6 = torrential).

Data analysis. We used Ranges 7 v1.0 (South & Kenward 2006) (Anatrack) to calculate seasonal home ranges as 100% minimum convex polygons (MCPs) (Mohr 1947) of all fixes. We then used cluster analysis (Kenward 2001) to remove outlying fixes and describe core areas (Harris et al. 1990). We created 85% cluster cores (i.e. based on 85% of fixes) using only commuting, foraging and perching fixes, hereafter termed as 'active core' areas. As commuting fixes are generally removed by the use of cluster cores, the active cores typically represent core foraging areas, comprising one or more distinct nuclei. This therefore allows comparison between core foraging areas and night roost locations.

Correlations between different response variables were tested using the non-parametric Spearman's rank-order correlation (Dytham 1999). General linear modelling (GLM) was used to analyse the radio-tracking data. The following response variables were tested: mean number of night roosts used, mean number of night roosting bouts per night, mean length of average night roosting bout and minimum distance between the night roosts and nearest nuclei. The mean nightly value of the first 4 response variables over the number of nights that each bat was tracked was used to avoid pseudoreplication. Explanatory categorical variables were reproductive status and landscape type (i.e. locality) and, where appropriate, minimum night temperature, average nightly rainfall and average nightly wind speed (continuous variables). The model simplification process using the GLM approach as advocated by Grafen & Hails (2002) was employed to reduce multiplicity of p-values. The assumptions of the GLM (independence, homogeneity of variance, normality of error and linearity/additivity) were tested using histograms of residuals, normal probability plots

and plots of standardised residuals against the fitted values/continuous variables, and transformations (square root and natural log) were used where required. Multiple comparisons among the means of significant categorical explanatory variables were undertaken using Tukey's method.

Statistical analyses were carried out on Minitab version 13.32 for Windows (Minitab) with a significance level of 5%.

RESULTS

Data were obtained from 54 *Rhinolophus hipposideros* radio-tracked in May to September during 2003 to 2005 (Table 1). The mean (± SD) number of nights with full data was 2.7 ± 1.2, 2.8 ± 1.0 and 2.7 ± 0.9 in the lowland, high quality and upland landscapes, respectively. Sampling effort was similar for each reproductive class and landscape. Two-way ANOVA with replication showed that the mean number of fixes per bat did not vary significantly among reproductive classes ($F_{3,36} = 2.75$, not significant [ns]) and landscape ($F_{2,36} = 1.85$, ns) whilst ANOVA showed that between localities, bats were radio-tracked on similar dates (using Julian days) ($F_{2,142} = 0.119$, ns). The range of minimum night temperatures was 4.3 to 20.3°C.

The majority of bats were recorded night roosting in one or more locations away from the maternity roost. Night roosting activity was restricted to the maternity roost in only 19% of the bats sampled (lowland: n = 6, high quality: n = 2, upland: n = 2). These were adult females during late pregnancy and lactation, and juveniles, although use of alternative night roosts was recorded in each group. We identified a total of 55 night roost sites, although the exact structure of 7

roosts could not be determined due to lack of access. The remaining roosts were predominantly within a variety of man-made structures: outbuildings associated with domestic properties (n = 15), old barns (n = 10), garages (n = 9), stables (n = 2), a porch (n = 1), and derelict buildings (n = 3). Seven barns were 2-storey, whereas other buildings were typically single-storey. Roof structure was varied and included flat felt roofs (on garages and outbuildings) and sloping or pitched tiled/slate/corrugated iron roofs. A feature of all of the buildings was their open-aspect, with an often sizeable opening ranging from an open window/doorway to open front. A further 6 roosts were in underground structures: caves (n = 2), cellars (n = 2), former railway tunnel (n = 1), former lime kiln (n = 1). Roosting in trees was seldom recorded (n = 2) and was believed to be opportunistic, as use was not repeated. Of the roosts occurring within the 'settlement' habitat type (built-up areas with associated gardens and infrastructures), 93%, 57% and 75% were in the lowland, high quality and upland landscapes respectively (Fig. 1). The mean (± SD) distance of the night roosts from the maternity roost was 1.71 ± 0.98 km (range 0.03 to 3.44 km, n = 29) in the lowland landscape, 2.40 ± 1.44 km (range 0.32 to 3.50 km, n = 14) in the high quality landscape and 1.34 ± 0.86 km (range 0.82 to 3.05 km, n = 12) in the upland landscape.

The maximum number of different night roosts recorded being used by any bat was 5, with a mean of 1.3 ± 0.9, 1.6 ± 1.6 and 1.8 ± 1.2 different night roosts (excluding the maternity roost) per bat in the lowland, high quality and upland landscapes, respectively. The number of night roosts (square-root transformed) did not vary among landscapes ($F_{2,46} = 0.89$, ns) or according to reproductive status ($F_{5,46} = 0.32$, ns). There was a positive correlation between the number of night roosts used (excluding and including the maternity

Table 1. *Rhinolophus hipposideros.* Sampling effort for radio-tracked individuals during summers of 2003–2005 in 3 different landscape types in Britain. See 'Materials and methods' for details of 'lowland', 'high quality' and 'upland'. Blanks indicate no data available

|	No. of individuals tracked			Mean total no. of fixes per bat (± 1 SD)		
	Lowland	High quality	Upland	Lowland	High quality	Upland
Adult female						
Early pregnancy	6			36.2 ± 8.6		
Late pregnancy	6	3	3	57.7 ± 28.5	54.0 ± 32.1	59.3 ± 28.5
Lactation	6	3	3	57.0 ± 29.7	63.7 ± 13.7	66.0 ± 33.7
Post-lactation	6	3	3	43.0 ± 24.7	73.0 ± 2.0	100.7 ± 23.2
Nulliparous female	6			59.8 ± 25.9		
Juvenile						
Female	2			99.0 ± 7.1		
Male	4			101.0 ± 16.7		
Totals	36	9	9	59.0 ± 29.8	63.6 ± 19.3	75.3 ± 31.5
Overall total	54				62.5 ± 28.8	
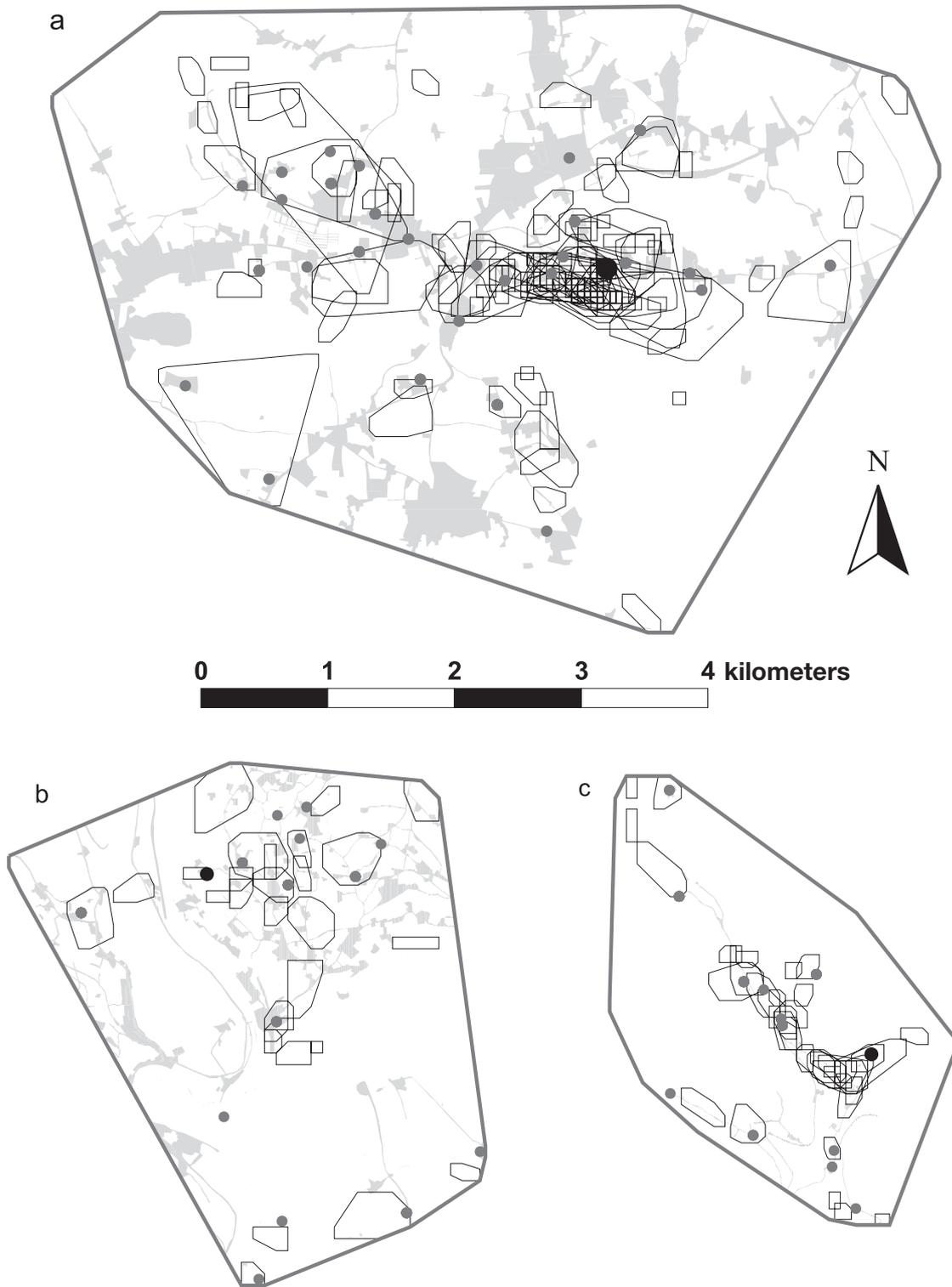
Fig. 1. *Rhinolophus hipposideros*. Distribution of maternity colonies (●) and night roosts (●) in relation to settlement habitat type (light grey lines and areas) in the (a) lowland, (b) high quality and (c) upland landscapes in southern Britain. Colony home range is delimited by a 100% minimum convex polygon (thick line) of fixes from all bats radio-tracked from the maternity roost during 2003 to 2005. The distribution of the active core nuclei (small areas bounded by thin lines) is also shown. In all cases the maternity sites also functioned as night roosts

roost) and the home range (100 % MCP) ($r_S = 0.40$, p < 0.01; $r_S = 0.42$, p < 0.01, respectively). There was also a positive correlation between the number of night roosts used (excluding and including the maternity roost) and the total size of the active cores ($r_S = 0.32$, p < 0.05; $r_S = 0.41$, p < 0.01, respectively).

The distribution of the night roosts in the 3 landscape types in relation to the active core nuclei (Fig. 1) shows that, overall, night roosts were contained predominantly within the active cores of all bats. On only 2 occasions did bats use night roosts (outside core areas) as transit roosts between the maternity roost and distant core foraging areas. In both instances the roosts were used when heavy rain curtailed commuting activity. Three night roosts within the lowland landscape were situated between 2 different foraging areas and could therefore have been acting as transit roosts. All other night roosts were either contained within, or were adjacent to the core foraging area(s). Individually, 86, 64 and 67 % of night roosts were contained within active cores within the lowland, high quality and upland landscape, respectively. The distances of the nearest active core nuclei from night roosts are provided in Table 2. The minimum distance between the night roosts and nearest nuclei did not vary among landscapes ($F_{2,36} = 0.53$, ns) and was not affected by reproductive status ($F_{5,36} = 0.93$, ns). The minimum distance of the active core nuclei from night roosts is significantly smaller than the minimum distance of the active core nuclei from the maternity roost (Wilcoxon signed-rank test = 572.50, p < 0.05).

The bats showed multimodal phases of activity during the night. There were between 1 and 8 night-roosting bouts (mean range 2.1 to 4.5, depending on landscape and reproductive status). Night-roosting bouts lasted on average 76 to 81 min (Table 3). In general,

Table 2. *Rhinolophus hipposideros.* Distance of edge of nearest nuclei in active core areas from night roosts for radio-tracked individuals in 3 different landscapes in Britain during 2003 to 2005. Values are means ± 1 SD; blanks indicate no data available

| | Distance of night roost from nearest nucleus (m) | | |
	Lowland	High quality	Upland
Adult female			
Early pregnancy	42 ± 65.2		
Late pregnancy	254 ± 308.4	13 ± 23.1	173 ± 193.3
Lactation	81 ± 83.7	50 ± 0.0	190 ± 94.3
Post-lactation	119 ± 199.4	91 ± 116.7	3 ± 5.8
Nulliparous female	28 ± 28.4		
Juvenile	15 ± 26.0		
Overall			
(adults only)	115 ± 179.7	52 ± 78.9	105 ± 129.8

Table 3. *Rhinolophus hipposideros.* Length of average night roosting bout (min) recorded for radio-tracked individuals from maternity roosts in 3 different landscapes in Britain during 2003 to 2005. Values are means ± 1 SD; blanks indicate no data available

| | Average night roosting bout (min) | | |
	Lowland	High quality	Upland
Adult female			
Early pregnancy	100 ± 34.9		
Late pregnancy	69 ± 33.6	107 ± 52.7	107 ± 102.2
Lactation	84 ± 56.6	58 ± 23.4	47 ± 9.6
Post-lactation	71 ± 30.9	64 ± 30.0	73 ± 31.4
Nulliparous female	102 ± 69.4		
Juvenile	85 ± 53.3		
Overall			
(adults only)	81 ± 39.6	76 ± 40.0	76 ± 59.7

bats emerged from the night roost before dawn for the final flying bout, except for 9 % of cases in which they remained in the night roost through to dawn. The number of night roosting bouts did not vary among landscapes ($F_{2,45} = 2.10$, ns) but was affected by reproductive status ($F_{5,45} = 2.46$, p < 0.05). Multiple comparisons for status indicated that the number of night roosting bouts was significantly shorter in early and late pregnancy compared with post-lactation, probably a reflection of varying night length. Average wind speed significantly affected number of bouts ($F_{1,45} = 7.71$, p < 0.01), with stronger winds associated with more bouts. Minimum temperature, average rainfall and all interaction terms were removed during model simplification.

Length of the average night roosting bout (log-transformed) did not vary among landscapes ($F_{2,43} = 0.48$, ns) and was not affected by reproductive status ($F_{5,43} = 1.75$, ns) or minimum air temperature ($F_{1,43} = 3.82$, p = 0.057). It was affected by rainfall (inverse-transformed) ($F_{1,43} = 9.69$, p < 0.01) and wind speed ($F_{1,43} = 9.79$, p < 0.01), with shorter night roosting bouts associated with increased rainfall and stronger winds. Interaction terms were removed during model simplification.

DISCUSSION

Night roosts were typically found within core home range areas, supporting the hypothesis that roost switching during the night allows minimisation of distance to feeding sites. Feeding habitat has been shown to be important for selection of maternity roosts in buildings, for example in *Plecotus auritus* (Entwistle et al. 1997), *Pipistrellus* sp. (Oakeley & Jones 1998), and *Rhinolophus hipposideros* (Reiter 2004). Therefore it is likely that feeding habitat may also be important for selection of night roosts. Conversely, however, we sug-

gest that given the proximity of night roosts to the core areas, feeding habitat may equally be constrained by availability of night roosts. The number of night roosts was significantly correlated with home range parameters (home range and core area). Therefore it can be postulated that a reduction in availability of night roosts could result in a corresponding reduction in home range. Availability of suitable maternity roosts may represent a primary constraint on the population size and distribution of different bat species (Humphrey 1975); further work is required to determine if this is also the case for night roosts.

The bats showed multimodal phases of activity throughout the reproductive season, with significantly more bouts occurring during post-lactation. Several hypotheses have been used to explain night roosting in bats, including thermoregulation (Anthony et al. 1981), information exchange (Wilkinson 1992), a reduction in prey availability (Anthony et al. 1981) and digestion (Barclay 1982). Anthony et al. (1981) observed that night roosting decreased with increasing temperature and postulated that night roosts are used for thermoregulation. However, we found that sub-optimal foraging conditions of stronger winds and increased rainfall reflected reduced time spent night roosting. Therefore it seems unlikely that night roosts serve primarily in a thermoregulatory capacity for *Rhinolophus hipposideros*. As regards the second hypothesis, since internal checks on night roosts were avoided in the study to avoid disturbance and disruption of activity patterns, it is not possible to comment on the potential social function of these roosts. However, roosts are likely to be communal, as they were used by more than 1 ind. from the same colony during successive tracking sessions. When exploring kin-biased behaviour in *R. ferrumequinum*, Rossiter et al. (2002) found that female bats and their adult daughters often shared night roosts, sometimes over several years, and no cases were recorded of non-relatives using the same night roost. Night roosts may therefore be important centres for information transfer among relatives, and this should be considered in conservation.

Reduction of prey availability explains unimodal or bimodal behaviour, as peaks of activity coincide with overnight peaks in insect numbers at dusk and, to a lesser extent, dawn (Taylor 1963). *Rhinolophus hipposideros* take mostly crepuscular Diptera by aerial hawking (Vaughan 1997, Knight 2006) and many of the families of Nematocera found in the diet of *R. hipposideros* together with Trichoptera and Sphaeroceridae are known to exhibit swarming behaviour. However moths, which are active all night with a peak activity occurring around midnight (Rydell et al. 1996), and non-volant prey are also present in the diet. The broad diet of the species may therefore allow it to feed throughout the night, for example feeding predominantly on swarming insects at dusk and dawn, and mainly on moths and non-volant prey during the intervening period, hence resulting in multimodal activity patterns.

Given periodic feeding throughout the night and the presence of faecal pellets within night roosts, it is likely that night roosts are used for digestion of food. We have shown that night roosts are in close proximity to the core foraging areas, and their use allows minimisation of distance to feeding sites. We suggest that minimisation of distance to feeding sites may be the primary function of the night roosts, which are used for resting and digestion between foraging bouts, with a secondary use for communal behaviour. As such, we postulate that night roosts are integral to the core foraging areas.

CONCLUSIONS AND PERSPECTIVES

This study has highlighted the importance of rural settlements for *Rhinolophus hipposideros*. However, the fact that night roosts are typically in buildings may lead to conflict. Many of the barns and outbuildings utilised are of period construction and the potential for conversion to dwellings is high. However, bats often fail to return to traditional roosts in barns after conversion for residential use, even if mitigation is in place (Briggs 2004). The multimodal nature of activity and frequent use of night roosts and alternative day roosts is a significant aspect of *R. hipposideros* behaviour, and should be considered carefully by conservation planners when designing management strategies to conserve the species. Although bat roosts are protected by law (e.g. the EC Habitats Directive 1992), current attention has largely focussed on day roosts. We have shown that night roosts are integral to core foraging areas and believe their protection is required to help maintain bat populations near human settlements. The usefulness of night roosts to lesser horseshoe bats will depend critically on their availability close to important foraging sites. Studies on potential availability of night roosts will therefore be valuable. Given that many of the sites used — especially old barns and outbuildings — are often renovated and made inaccessible to bats, we expect that the limited availability of night roosts may influence the selection of foraging patches in some cases. Ultimately, an experimental approach that removes access to some night roosts and explores consequences may be revealing, though this approach may be inappropriate if there are likely detrimental consequences for the bats. We recommend that the protection of night roosts should also be given a high priority until further research has been undertaken into the potential implications of their loss.

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