Activity of pipistrelle bats (*Pipistrellus pipistrellus*) and Natterer's bats (*Myotis nattereri*) over lowland heathland

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Summary

Bats and lowland heathland are two subjects of high conservation priority in Britain. However, the interaction of the two i.e. the value of lowland heathland to bats is poorly understood. This study was an attempt to quantify the importance of lowland heathland in the English Midlands to two common vespertilionid bat species, the pipistrelle (*Pipistrellus pipistrellus*) and the Natterer's bat (*Myotis nattereri*). A bat detector survey was conducted over a series of nights during the summer of 1998 by walking transects on a remnant heathland in north-west Leicestershire.

The data obtained suggest that lowland heathland is of lower value to bats than woodland interior, woodland edge and open water environments. Only 9% of total bat passes were detected over heathland. *P. pipistrellus* was found to favour open rides within the woodland whilst *M. nattereri* exhibited a preference for both woodland and open water environments.

Where heathlands are being restored and have conifer plantations or regenerating scrub, there may be a particular conflict. In areas with known bat roosts the possibly detrimental effects of plantation removal as part of heathland re-creation and scrub clearance as part of heathland management should be considered by environmental managers. These practices could result in the loss of foraging habitat and commuting routes.

Introduction

Several of the resident species of bat in Britain have undergone significant population declines in recent times with one species, the greater mouse-eared bat (*Myotis myotis*), now declared extinct (Harris *et al.*, 1995). Human disturbance and changes in the landscape have been deemed largely responsible for these declines. The use of pesticides and wood preservatives has made potential roost sites within buildings too hazardous to utilise, whilst traditional roosts and feeding habitats in the countryside have been lost to woodland clearance and agricultural intensification *etc.* (Stebbings and Jeffries, 1986).

Legal protection is given to all resident bat species in Britain and their roost sites by the *Wildlife and Countryside Act* (1981). However, foraging sites remain largely unprotected by legislation. Little has been published in the UK pertaining to the feeding habitat requirements of different bat species (e.g. Vaughan, Jones and Harris, 1997). In addition a lack of standard survey methodologies has prevented direct comparison of data from different studies (Walsh, Harris and Hutson, 1995).

The National Bats and Habitats Survey (Walsh, Harris and Hutson, 1995; Walsh and Harris, 1996a,b) was conducted across the UK in the summers of 1990-92. This survey sought to produce base-line abundance data against which future surveys and land-use changes could be compared. General habitat preferences for broad-leaved woodland and open water were found; as was an avoidance of arable land, moorland (including lowland heathland) and improved grassland. These findings concur with earlier studies on foraging habitats (e.g. Racey and Swift, 1985). Avoidance of open environments is thought to be due to the lack of landscape structures by which bats can navigate, whilst intensively managed land is likely to be avoided due to low insect densities (all British bats species being insectivorous).

However, Emms (1995) studying activity of vespertilionid bats over lowland heathland in the south of England, found that a wide variety of bats species was present. There were eight out of the twelve resident vespertilionid species including the smaller species (e.g. pipistrelle (*Pipistrellus pipistrellus*)) that are thought to find it difficult to navigate over open landscapes due to their weaker echolocation calls. Emms suggested that the variety of species of bat detected on the Dorset heathland was due to the high invertebrate densities associated with this environment which might be drawing bats away from more typical feeding habitats. Possible navigation by subtle landscape features not apparent to humans was also suggested. As already indicated, lowland heathland had previously been thought a low value habitat for bats, but no specific studies of bat activity had been conducted.

Lowland heathland itself has a high conservation priority in Britain being the subject of a Habitat Action Plan and there are targets to re-create approximately 6000ha of the habitat-type across England and Wales by 2005. As land-use change has been identified as a factor in bat population declines, this study sought to determine the relative importance of lowland heathland in the English Midlands as foraging habitat for bats. The primary objective was to quantify the bat activity on a lowland heathland site in the region and compare this with activity measured in adjacent habitat-types. The possible effects on bat populations that lowland heathland re-creation in the Midlands and heathland management in general may have, are then discussed with regards to bat conservation.

Materials and Methods

Survey site and survey species

The survey work was carried out at **Charnwood Lodge** in northwest Leicestershire (National Grid SK 467 163 Figure 1.), a nature reserve of approximately 227ha most of which has **Site of Special Scientific Interest** (SSSI) status. It is managed by the Leicestershire and Rutland Wildlife Trust and contains some of the best examples of lowland heathland in the East Midlands, in addition to wetland and woodland areas. The site is one of the last remnants of the Charnwood Forest 'wastes' which once covered this area of the country.

The largest area of woodland on the site is Gisborne's Gorse which is composed mainly of oak (*Quercus* sp.), pine (*Pinus* sp.), sycamore (*Acer pseudoplatanus*) and spruce (*Picea* sp.). The woodland contains a network of wide rides in addition to more enclosed paths. The open area of the site consists of rough heathland and acid grassland, much of which is covered by bracken. Dry heath occurs on the hillsides around rock outcrops with areas of heather (*Calluna vulgaris*) and less frequently bilberry (*Vaccinium myrtillus*) amongst the wavy hair-grass (*Deschampsia flexuosa*). In a few lower lying areas a wet heath community occurs where purple moor-grass (*Molinia caerulea*) is the dominant species with patches of crossed-leaved heath (*Erica tetralix*). Colony Reservoir is a small area of open water located within a separate closed woodland.

Photograph 1. Woodland environments: Interior of Gisborne's Gorse with bluebells

Photograph 2. Heathland environments: A mosaic of heather and wavy hair-grass

Two roost sites in the north of Gisborne's Gorse are known to contain colonies of pipistrelles, Natterer's bats (*Myotis nattereri*) and brown long-eared bats (*Plecotus auritus*). These species are all relatively common and widespread in Britain, although even the commonest species, the pipistrelle, has reportedly declined by over 60% since 1978 (Stebbings, 1995). Natterer's bats are not common outside the United Kingdom and the national population may be of international importance (Hutson, 1993). The colony size of Natterer's bats on the study site varies yearly between thirty and forty-five individuals while the colony of brown long-eared bats numbers around ten to eleven. The size of the pipistrelle colony, which is believed to be of the 45kHz phonic type, is not recorded.

photograph 3. Open water environment: View across Colony Reservoir

Survey methodology

Bats produce a series of ultrasonic clicks when echo-locating. A series of clicks heard through a bat detector between a bat coming into range and going out of range is termed a 'bat pass'. The use of bat detectors cannot ascertain the number of bats heard but the level of bat activity in a certain area can be measured. In addition, foraging behaviour can be detected: as a bat homes in on a prey item, the rate of echo-location clicks accelerates to a characteristic 'terminal feeding buzz' (Vaughan, Jones and Harris, 1997). As different species have different call frequencies and structures, species identification is also possible.

Fieldwork was conducted over a series of nights between July and September 1998. The site had been visited during daylight and a navigable and repeatable circular transect devised (see Fig.1a). Nights of severe weather (heavy rain and strong winds) were avoided as these are known to severely reduce bat activity (Walsh, Harris and Hutson, 1995). Dense fog caused one field night to be abandoned. The air temperature at waist height was recorded with a digital thermometer before surveying started and again at its conclusion (Vaughan, Jones and Harris 1997). The circular transect around the study site (approximately 3.6km in distance) was walked twice a night, the

Figure 1. Location of the Charnwood Forest area in the English Midlands, with the study site (Charnwood Lodge) as inset.

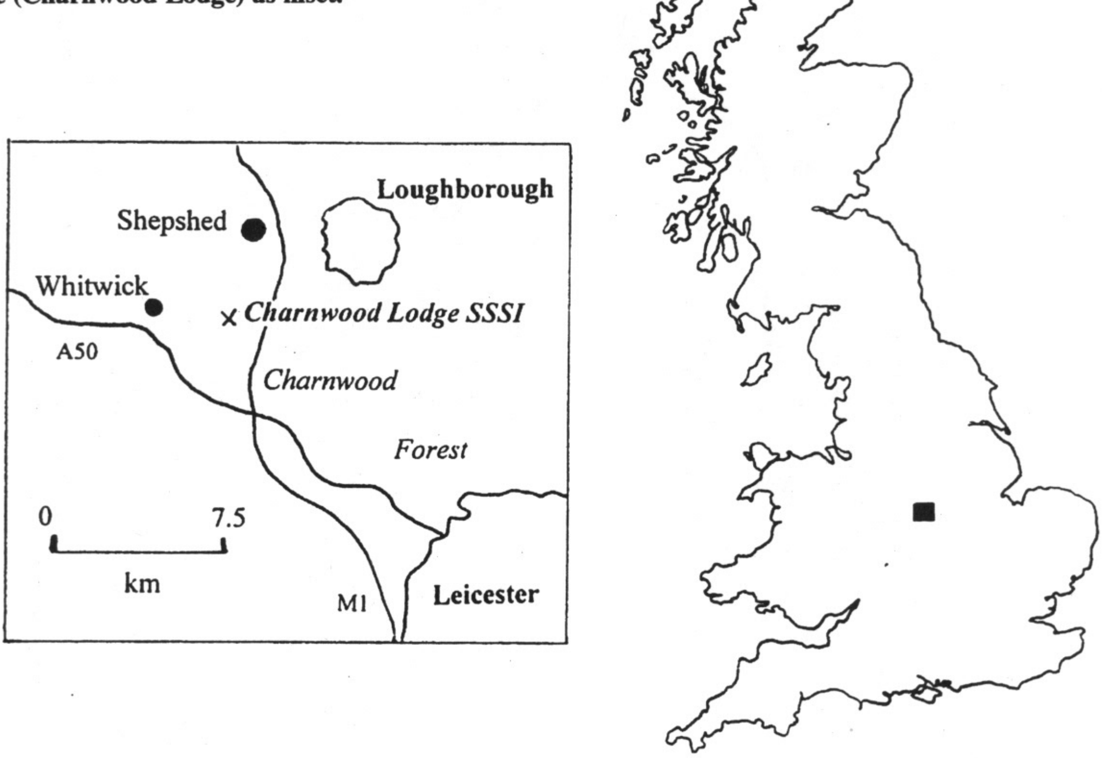
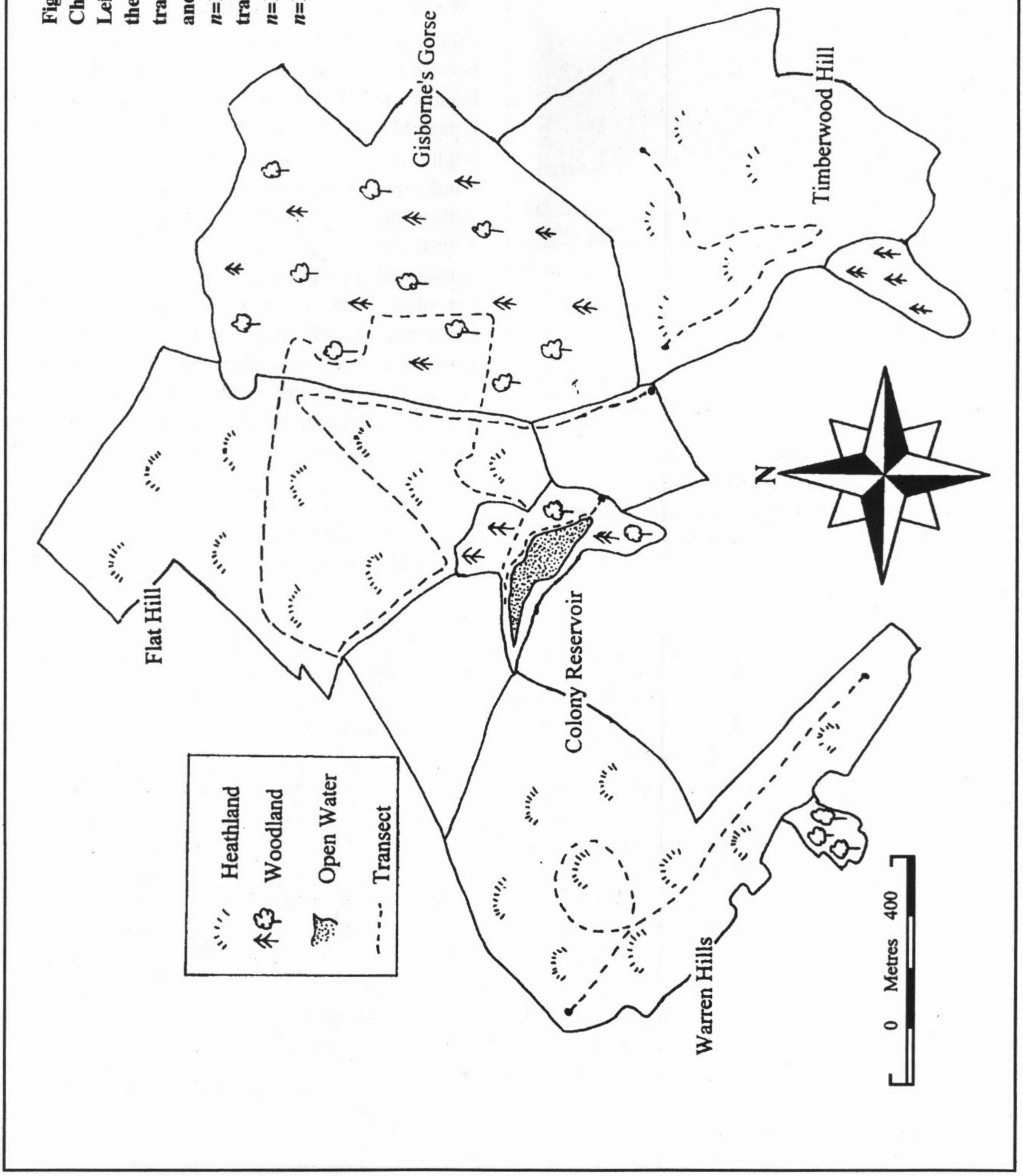


Figure 1a. The study site at Charnwood Lodge SSSI, Leicestershire, indicating the route of the main transect (Gisborne's Gorse and Colony Reservoir, *n*=16) and the two shorter transects(Warren Hills, *n*=1, and Timberwood Hill, *n*=1).



first walk commencing 30 minutes after sunset and the second commencing 30 minutes after the first was completed. Walking rate is known to affect detection rates (Walsh, Harris and Hutson, 1995) so effort was made to keep this constant. A **Mini-III Bat Detector** (Ultra Sound Advice, London) tuned to 45 kHz was used to detect echolocation passes along the transect, the detector being held at chest height. A frequency of 45 kHz was used as it is near the strongest part of the echolocation calls given by P. pipistrellus and M. nattereri and within the frequency range emitted by all other vespertilionid bats (Catto, 1994). Transect surveying was used in favour of point surveying (i.e. surveying at a fixed station for a set duration) as it reduces the chances of the same bat being detected more than once (G. Jones pers. comm.). The start point of the transect was rotated each night to minimize the effects of time of night on the data collected. (P. Racey pers. comm.; Walsh, Harris and Hutson, 1995). In addition two shorter, linear transects were walked on other areas of heathland on the site on different nights using the same methodology.

The main transect was divided into five stages, the end of each stage occurring with a change in habitat-type. Four basic habitat-type classes were identified: woodland, woodland edge, open water (one stage each) and heathland (two stages). The transect thus sampled each of the main habitat-types found on the site. The time spent surveying each stage was recorded. Bat passes were identified as *P. pipistrellus* or *M. nattereri* where reasonable confidence existed and noted down under the appropriate habitat as was the appendage of a terminal feeding buzz. Within the woodland an additional note was made if the pass was detected on a narrow path (<2m wide) or an open ride (>2m wide). Where species identification could not be made with reasonable confidence, an echo-location pass was assigned to an 'unidentified' category. These contacts were from unclear pipistrelle or Natterer's passes (too short, too faint *etc.*), signals from brown long-eared bats or from other unidentified species. Brown long-eared bats were not given a separate category. Their very quiet echo-location calls makes consistent detection of them very difficult (Catto, 1994). Coupled with the anticipated low numbers, separate study of brown long-eareds was not thought viable. Similarly the anticipated low numbers of other species did not justify separate categories.

Data analysis

Due to the differing lengths of transect stages, raw bat pass data was standardized using transect survey time. An index of bat activity (BA) was calculated where BA equals the number of bats that would be detected in an hour of surveying at the rate of detection observed. BA values were calculated for total bat passes (*P. pipistrellus* plus *M. nattereri* plus unidentified) in each habitat-type and for each species category separately in each habitat-type.

Mean air temperature for each survey night was calculated and relationships investigated using linear regression analysis. One-way analysis of variance (ANOVA) was used to analyse BA for significant differences. Mann Whitney U-tests were used to analyse path/ride preferences.

Results

Summary of the survey

In total 62km of transects (n=16) were walked. 825 bat passes and 97 terminal feeding buzzes were detected. Feeding buzzes thus occurred in 12% of total bat passes.

Pipistrelles were the species most often detected, accounting for 66% of all bat passes. Woodland was the environment in which most bat passes (52%) were detected, with heathland exhibiting the lowest amounts of activity (9%). The number of feeding buzzes detected in each habitat-type was significantly correlated with the number of bat passes ($p<0.05$). Due to this relationship and the low numbers of feeding buzzes detected, bat passes were used in all analyses as a measure of bat activity (Walsh, Harris and Hutson, 1995).

Analysis of bat activity and mean air temperature

Linear regression analysis found no significant correlation between mean air temperature and total bat passes per transect ($p>0.05$). It was thought that on colder nights bat activity may be concentrated more in the shelter of the woodland with less activity exhibited on the heathland. However, the correlation of total number of woodland passes per transect and mean air temperature, was again not significant ($p>0.05$). A similar result was obtained for heathland data ($p>0.05$).

Fig. 2. Mean BA per transect for all bats species. Values represented by histogram bars with different letters are statistically significantly different ($p<0.05$, Tukey test).

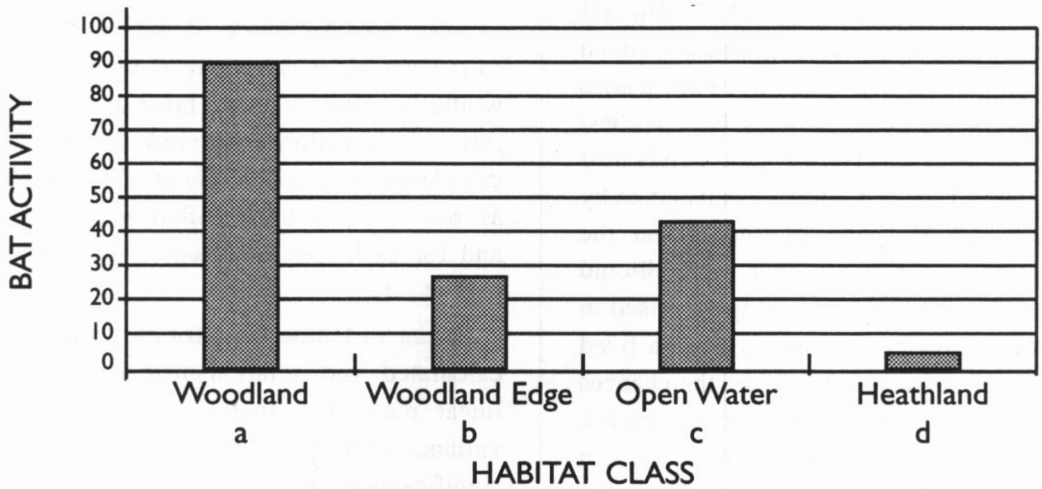


Fig. 3. Mean number of bat passes per transect for all bat species in woodland habitat subclasses

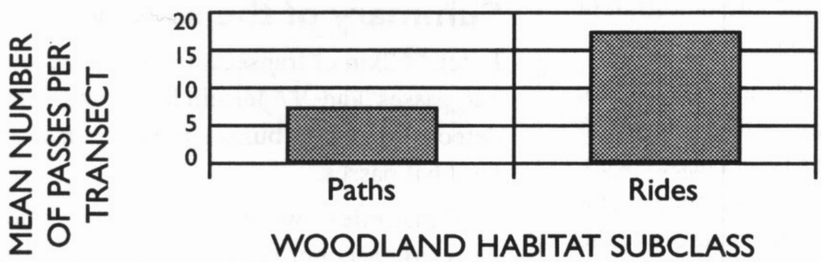


Fig. 4. Mean BA per transect for each bat species category. Within each species category values represented by histogram bars with different letters are statistically significantly different ($p<0.05$, Tukey test).

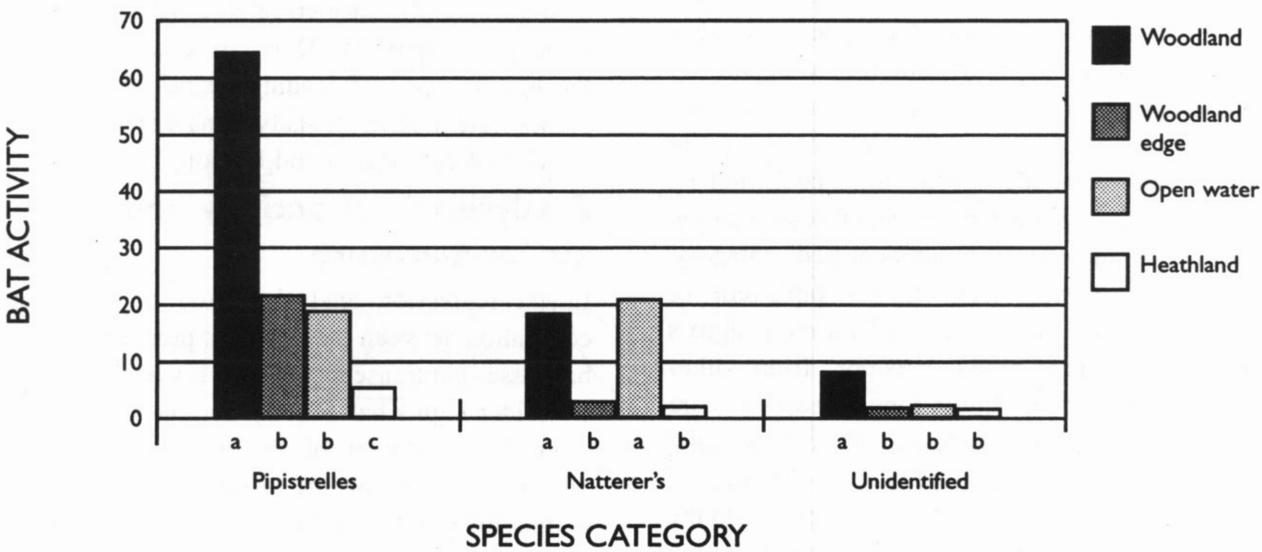
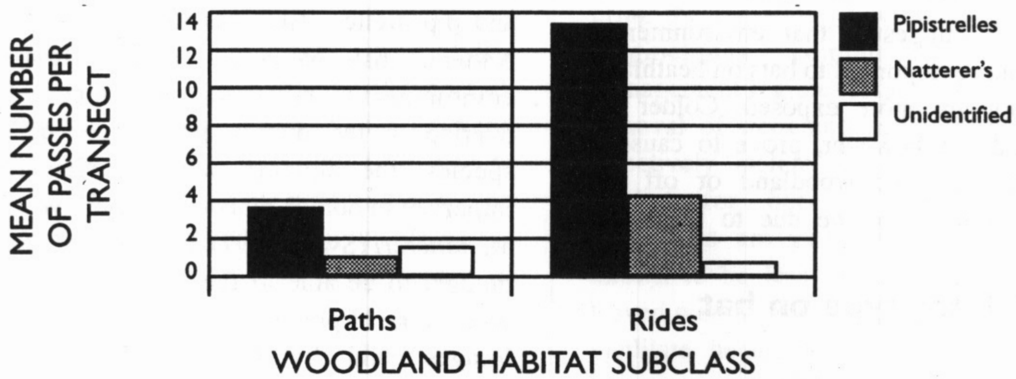


Fig. 5. Mean number of bat passes per transect for each category in woodland habitat subclasses.



Analysis of differences in overall bat activity between habitat classes

Fig. 2 shows the marked difference in average BA per transect between habitat-type classes. Analysis showed that woodland was the most used environment with heathland the least. Woodland edge and open water were of intermediate importance. Fig. 3 shows the average number of total passes per transect for the closed environment of narrow woodland paths and the more open habitat of the wide woodland rides. As the length of each of these habitat subclasses was approximately equal, data were not time adjusted. Analysis showed that there is a significant difference in these results with bats showing a preference for wide rides ($p<0.05$, U-test).

Analysis of differences in utilisation of habitat by species categories

The activity pattern of the pipistrelle (Fig. 4), as one would expect of the most common bat in the study, mirrors that of overall bat activity (Fig. 2). Woodland is the most used habitat, heathland the least used, and the other two habitat-type classes being intermediate. Natterer's bats however showed a significantly different pattern of activity (Fig. 4), with open water being as important a habitat as woodland. Within the unidentified category woodland was the most important habitat-type.

Fig. 5 shows the differential utilisation of the paths and rides within the woodland by different species. The more open environment of the rides was favoured by both pipistrelles (80% of passes, $p<0.05$, U-test) and Natterer's bats (82%, $p<0.05$, U-test). However, within the unidentified category more activity was detected on the paths (75%, $p<0.05$, U-test).

Discussion

Effects of mean air temperature

No significant relationship was detected between air temperature and the total number of bat passes per night. A similar result was obtained by Seal (1998) working at the same site. Since it is widely accepted that bat activity is generally higher under warmer conditions these results are surprising. This expected pattern of use is due to insect (prey) abundance being reduced on colder nights combined with the high rates of body heat loss that small bats experience. A positive correlation between bat activity and air temperature was found for example by Emms (1995), Walsh, Harris and Hutson (1995), and Vaughan, Jones and Harris (1997). It is unlikely that some other environmental parameter is responsible for the results obtained as it has been shown humidity, moon phase, cloud cover or (moderate) wind speed do not have a significant effect on bat activity (Emms, 1995; Vaughan, Jones and Harris, 1997). The result may be due to the lower number of samples in this study and the small range of temperatures experienced.

Importantly for analysis of the present data however, since mean air temperature was not seen to have an effect on total bat activity, it was not necessary to adjust data for this factor.

Emms (1995) suggested that environmental factors may be more important to bats on heathland sites where they are more exposed. Colder air temperatures did not however, prove to cause a shift in activity into the woodland or off the heathland. Again this may be due to the small sample size.

Effect of habitat-type on bat activity

The overall pattern of habitat preference found in this study, of woodland being the most used environment and heathland the least used, with woodland edge and open water being of intermediate importance (Fig. 2) largely reflects the dominance within the dataset of *P. pipistrellus* (Fig. 4). High levels of activity in woodland and over rivers and lakes by 45 kHz pipistrelles were found by Vaughan, Jones and Harris (1997) whilst 55 kHz pipistrelles showed a strong dependence on just rivers and lakes, as was found by Oakeley and Jones (1998). As the phonic type of the pipistrelles known to be roosting at Charnwood Lodge is believed to be the 45 kHz type these findings correlate well with those of the present study. Woodland edge was used much less by pipistrelles than the woodland interior. These results are perhaps surprising as woodland edges, being ecotones are likely to support high insect abundance (Seal, 1998). The national survey (Walsh, Harris and Hutson, 1995) found woodland edge to be an optimally selected habitat-type. Vaughan, Jones and Harris (1997) found equally high activity in woodland interiors and along woodland edges, but there was selection for more sheltered areas. As the woodland edge surveyed in this study was along a single side of a wood, the lower activity levels detected may be due to the exposed nature of this transect stage.

The pattern of habitat utilisation by Natterer's bats is markedly different to that exhibited by pipistrelles (Fig. 4). Activity in woodland and along the woodland edge is lower whilst activity over the open water of Colony Reservoir is higher, although woodland interior is still an important foraging habitat for this species. Seal (1998) in a study on the same site proposed that the high abundance of pipistrelles in the woodland was resulting in interspecific competition between Natterer's bats and pipistrelles. This was limiting the number of Natterer's bats that could effectively forage in this environment. This theory is supported by an overlap in the dietary preferences of the two species; the dipteran suborder Nematocera is important to both *P. pipistrellus* (Barlow, 1997) and *M. nattereri* (Swift, 1997). However, *M. nattereri* is thought to be able to feed opportunistically on a wide range of prey (Swift, 1997). *M. nattereri* also forages mainly by gleaning prey from vegetation surfaces (Shiel, McAney and Fairley, 1991), whilst *P. pipistrellus* feeds mainly by aerial hawking (catching insects in flight) (Catto, 1994). It may be that a greater preference of *M. nattereri* for open water environment and not niche overlap is responsible for the difference in habitat utilisation. Analysis of thirty-two other Natterer's bat roosts by Seal (1998) found that proximity to water bodies was an important factor in roost selection. Waters in forests and those lined with trees and shrubs were found to be more attractive to bats than those without surrounding high vegetation by Zahn and Maier (1997). Colony Reservoir is situated in a small wood and this may increase its foraging value to bats.

An avoidance of the open heathland environment by all bats is evident from the results. Small bats, like pipistrelles and Natterer's bats, which have only short-range sonar, tend to avoid open environments as they must keep close to landscape structures for orientation. Larger species with long-range sonar, like the noctule (*Nyctaclus noctula*) and the serotine (*Eptesicus serotinus*) have been observed as active over open habitat-types (Verboom and Huitema, 1997). Another possible reason for avoidance of open areas by small, slow-flying bats is that flying in such environments increases the risk of predation by birds (e.g. tawny, barn and long-eared owls) (Swift, 1997). Racey and Swift (1985) found that linear landscape elements such as hedgerows and tree lines were habitually used by pipistrelles as commuting routes between colony and foraging areas. This probably accounts for the activity of bats in the area of heath between Gisborne's Gorse and the Colony Reservoir wood that are linked by an avenue of birch trees. Seal (1998) concluded that this tree line was being used as a commuting route by Natterer's bats. Over the rest of the heathland, which is largely devoid of linear landscape features, detected bat activity may have been due to disorientated bats. Emms (1995) suggested that bats may use individual landmark features, such as lone trees, as orientation cues and navigate across heathland by flying from one to another. Casual (unquantified) observation during the present study noted that many of the bat passes detected on heathland stages were in the vicinity of lone trees, bushes, rocky outcrops *etc*. However, the low levels of activity over the heathland do support the suggestion that it is a relatively unimportant foraging habitat for bats.

Both pipistrelles and Natterer's bats were more active along the rides than the narrower paths (Fig. 5). This was possibly due to differences in insect abundance but the structural complexity of a habitat also has an influence on activity levels. Brigham *et al.* (1997) showed that increased amounts of structural clutter negatively affected foraging activity in small bats (*Myotis* spp.), suggesting that increased difficulties in flight and echolocation make foraging in a complex environment more costly than in relatively open areas. The rides probably provide commuting lanes between the roost and feeding areas.

Unidentified bat passes were more often detected on narrow paths. The high pulse rate and pitch casually noted in many of these passes, especially in the area surrounding the roost sites suggests that many were long-eared bats which may favour foraging in this environment. Other unidentified passes in this area may have been pipistrelles and Natterer's bats modifying their signals in the closed habitat conditions.

Management implications

This study suggests that lowland heathland in the English Midlands is of limited foraging value to bats but may be commuted across. This has implications concerning heathland re-creation and management. An important factor in the decline of lowland heathland in Britain has been neglect and lack of management which has led to many heathlands being invaded by scrub and bracken. The wildlife value of heathlands is lost under these conditions as the associated increase in soil nutrient concentrations is unsuitable for heathland species (Mitchell *et al.*, 1997; De Graaf *et al.*, 1998). The National Lowland Heathland Programme seeks to bring the remaining lowland heathland, a classic plagioclimax community, under effective management regimes (Anon., 1993). However, the removal of trees and scrub from heathland may effectively isolate suitable patches of foraging habitat for bats. Similarly, whilst conifer plantations are generally poor for wildlife and known to be less important to bats than broad-leaved woodland (de Jong, 1995), their removal to facilitate heathland creation or restoration may have detrimental effects on bat foraging.

Conclusions

This study presents the first quantified investigation of the activity of bats over lowland heathland on a case study site in the English Midlands. It does not support the suggestion by Emms (1995) that heathland may be of unsuspected importance to bats. This low level of importance found in the study was possibly due to lack of orientation cues and an increased predation risk. *P. pipistrellus* utilises a variety of habitat-types, but on the study site favoured the wide open rides within mixed woodland. *M. nattereri* also utilised the mixed woodland but foraging over open water was especially important for this species. In the light of current schemes for lowland heathland re-creation and probably expansion in this habitat-type in the future, the low value of open heathland to bats is a factor that we suggest environmental managers should consider. This is especially so where the removal of encroaching scrub or plantations is involved, and perhaps particularly if it is in areas where important bat communities are known.

Further study of bat activity on lowland heathland is needed to elucidate these relationships and to facilitate comparisons with other habitat-types/environments such as farmland. The present study involved a relatively small sample size and a limited geographic spread. Despite this, it does raise important issues. Similar case study work on heaths and moors in different situations and in other geographic locations is required. The activity of other bat species on heathland, particularly the larger species that may be better able to exploit heathland environment, should also be investigated.

Finally, this work does raise the potential detrimental impact of some heathland management on bat communities. There is therefore an urgent need to investigate appropriate mitigation and remedial techniques to help minimise this effect.

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References

Anon. (1993) *English Nature's National Lowland Heathland Programme*. English Nature, Peterborough.

Barlow, K. (1997) The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain, *Journal of Zoology*, **243**, 597-609.

Brigham, R.M., Grindal, S.D., Firman, M.C. and Morissette, J.L. (1997) The influence of structural clutter on activity patterns of insectivorous bats. *Canadian Journal of Zoology*, **75**, 131-136.

Catto, C. (1994) *The bat detector manual*. Bat Conservation Trust, London.

de Graaf, M.C.C., Verbeek, P.J.M., Bobbink, R. and Roelofs, J.G.M. (1998) Restoration of species-rich dry heaths: the importance of appropriate soil conditions. *Acta Botanica Neerlandica*, **47**, 89-111.

de Jong, J. (1995) Habitat use and species richness in a patchy landscape. *Acta Theriologica*, **40**, 237-248.

Emms, C. (1995) The nocturnal activity of bats of the family Vespertilionidae on lowland heathland and associated habitats in Dorset, England. Unpublished MSc thesis, Department of Biological Sciences, University of Warwick.

Harris, S., Morris, P., Wray, S. and Yalden, D. (1995) *A review of British mammals: population estimates and conservation status of British mammals other than cetaceans*. Joint Nature Conservation Committee, Peterborough.

Hutson, A.M. (1993) *Action plan for the conservation of bats in the United Kingdom*. Bat Conservation Trust, London.

Mitchell, R.J., Marrs, R.H., le Duc, M.G. and Auld, M.H.D. (1997) A study of succession on lowland heaths in Dorset, southern England: changes in vegetation and soil nutrient properties,. *Journal of Applied Ecology*, **34**, 1426-1444.

Oakeley, S.F. and Jones, G. (1998) Habitat around maternity roosts of the 55kHz phonic type of pipistrelle bats (*Pipistrellus pipistrellus*). *Communications from the Mammal Society* **No. 76**, *Journal of Zoology*, **245**, 222-228.

Racey, P. and Swift, S. (1985) Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *Journal of Animal Ecology*, **54**, 205-215.

Seal, H. (1998) The habitat use and foraging behaviour of Natterer's bats (*Myotis nattereri*) at Charnwood Lodge SSSI and implications for future conservation management. Unpublished BSc Dissertation, University of East Anglia.

Shiel, C.B., McAney, C.M. and Fairley, J.S. (1991) Analysis of the diet of Natterer's bat *Myotis nattereri* and the common long-eared bat *Plecotus auritus* in the West of Ireland. *Journal of Zoology*, **223**, 299-305.

Stebbings, R.E. (1995) Why should bats be protected? A challenge for conservation. *Biological Journal of the Linnean Society*, **56** (Suppl. A), 103-118.

Stebbings, R.E. and Jeffries, D.J. (1986) *Focus on bats: their conservation and the law*. Nature Conservancy Council, London.

Swift, S. (1997) Roosting and foraging behaviour of Natterer's bats (*Myotis nattereri*) close to the northern border of their distribution. *Communications from the Mammal Society*, **No. 74**, *Journal of Zoology*, **242**, 375-384.

Vaughan, N., Jones, G. & Harris, S. (1997) Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *Journal of Applied Ecology*, **34**, 716-730.

Verboom, B. and Huitema, H. (1997) The importance of landscape elements for the pipistrelle *Pipistrellus pipistrellus* and serotine bat *Eptesicus serotinus*. *Landscape Ecology*, **12**, 117-125.

Walsh, A.L. and Harris, S. (1996a) Foraging habitat preferences of vespertilionid bats in Britain. *Journal of Applied Ecology*, **33**, 508-518.

Walsh, A.L. and Harris, S. (1996b) Factors determining the abundance of vespertilionid bats in Britain: geographical, land class and local habitat relationships. *Journal of Applied Ecology*, **33**, 519-529.

Walsh, A.L., Harris, S. and Hutson, A.M. (1995) Abundance and habitat selection of foraging vespertilionidae bats in Britain: a landscape-scale approach. *Symposia of the Zoological Society of London*, **67**, 325-344.

Zahn, A and Maier, S. (1997) Hunting of bats at streams. *Zeitschrift fuer Sauegetierkunde*, **62**, 1-11.