



# Improving the biodiversity benefits of hedgerows: How physical characteristics and the proximity of foraging habitat affect the use of linear features by bats

Katherine L. Boughey<sup>a,\*</sup>, Iain R. Lake<sup>a</sup>, Karen A. Haysom<sup>b</sup>, Paul M. Dolman<sup>a</sup>

<sup>a</sup> School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK

<sup>b</sup> Bat Conservation Trust, 15 Cloisters House, 8 Battersea Park Road, London SW8 4BG, UK

## ARTICLE INFO

### Article history:

Received 14 May 2010

Received in revised form 2 February 2011

Accepted 13 February 2011

Available online 12 April 2011

### Keywords:

Hedgerow management

Habitat associations

Pipistrelle

Noctule

Serotine

Multi-model inference with interactions

## ABSTRACT

Within agricultural landscapes, linear features such as hedgerows and tree-lines provide valuable habitat for many species. We use data from 315 transects, completed as part of a national acoustic survey of bat distribution, to examine the incidence of four bat species adjacent to linear features in rural areas. The use of linear features was assessed in relation to hedgerow width, tree density, the presence of water and woodland proximity. To examine the effect of tree density, linear features were classified as either hedgerows without trees, hedgerows with sparse trees (comprising <50% tree canopy) or tree-lines (>50% tree canopy). The use of linear features by *Pipistrellus pipistrellus* was not affected by tree density; linear features of all types were associated with a similar increase in *P. pipistrellus* incidence. The use of linear features by *Pipistrellus pygmaeus* was dependent on both tree density and the proximity of woodland; only linear features containing trees provided an increase in *P. pygmaeus* incidence regardless of woodland proximity. *P. pipistrellus* and *P. pygmaeus* incidence was not affected by hedgerow width or the presence of water. Incidence of *Nyctalus noctula* and *Eptesicus serotinus* was unaffected by the density of linear features of any type. Many agri-environment schemes offer financial incentives for the creation and management of hedgerows. Optimising the biodiversity gain provided by linear features will maximise the effectiveness of these schemes. Agri-environment measures that encourage the provision and retention of hedgerow trees will benefit bats in agricultural landscapes.

© 2011 Elsevier Ltd. All rights reserved.

## 1. Introduction

Hedgerows and tree-lines are a common feature of agricultural landscapes worldwide and play a key role in sustaining rural biodiversity. They enhance structural heterogeneity, landscape connectivity and botanical diversity, and provide breeding habitat and food resources for many species of birds, small mammals and invertebrates (Burel, 1996; Dover and Sparks, 2000; Hannon, 2009; Hinsley and Bellamy, 2000; Tattersall et al., 2002; Whittingham et al., 2009), including a suite of farmland species that have undergone widespread population declines across Europe (Robinson and Sutherland, 2002).

Agricultural intensification over the last half-century has resulted in the widespread removal of hedgerows in many regions. Losses of up to 71% of hedgerow length since 1950 have been reported in the American Midwest, Eastern Europe and the UK (Baltensperger, 1987; Robinson, 1997; Sklenicka et al., 2009). Remaining hedgerows are also threatened by a lack of appropriate management. In the UK, the length of managed hedgerows de-

clined by 6.2% between 1998 and 2007 (Carey et al., 2008), and half of all hedgerows are in poor condition as a result of nutrient enrichment, severe trimming, or excessive gaps (Wolton, 2010). In recognition of their ecological importance and vulnerable conservation status, many agri-environment schemes provide financial support for environmentally sensitive hedgerow management. The effectiveness of such initiatives, both in terms of cost and biodiversity gain, can be improved by an understanding of how the benefits provided by hedgerows are affected by factors such as physical structure and landscape context.

Many European bat species are closely associated with linear features such as hedgerows and tree-lines (Downs and Racey, 2006; Entwistle et al., 1996; Limpens and Kapteyn, 1991; Robinson and Stebbings, 1997; Walsh and Harris, 1996). Insect prey abundance is greater adjacent to linear features than in adjoining open habitat (Lewis, 1969), and these features may also provide a commuting route between foraging patches that is sheltered from predators and the elements (Limpens and Kapteyn, 1991; Verboom and Spoelstra, 1999). However, little is known about how the characteristics of linear features affect their use by bats. In a nationwide study of bat-habitat associations in the UK, Walsh and Harris (1996) found bat activity (of predominantly *Pipistrellus* spe-

\* Corresponding author. Tel.: +44 7800723320.

E-mail address: [katherineboughey@hotmail.com](mailto:katherineboughey@hotmail.com) (K.L. Boughey).

cies) was positively associated with hedgerows in all pastoral land classes, but in only one of three arable classes, suggesting landscape context may influence the use of linear features. At a smaller scale, isolation of the linear feature, represented by the distance from the linear fragment to the nearest other linear fragment, had no effect on common pipistrelle (*Pipistrellus pipistrellus*) activity (Verboom and Huitema, 1997). Studies that make a distinction between hedgerows and tree-lines find positive associations with tree-lines more often than with hedgerows (Downs and Racey, 2006; Russ and Montgomery, 2002; Walsh and Harris, 1996), although the effect of emergent trees within hedgerows is not known.

In this study, we examine how physical structure and the proximity of foraging habitat affect the use of linear features by bats in rural areas. Specifically, we use data from a national acoustic survey of bat distribution to test whether (i) the incidence of bats along hedgerows is affected by hedgerow width, (ii) the presence of linear features has a differing effect on bat incidence depending on the density of trees in the feature, and (iii) there is an interactive effect between linear features and either the presence of water or the proximity of woodland, and whether the strength of this interaction differs depending on the density of trees in the feature. Woodland is an important foraging habitat for European bat species (Racey and Entwistle, 2003). If linear features function primarily as commuting routes, the use of linear features by bats (measured relative to open areas) should increase closer to woodland. However, if linear features also provide foraging habitat, use will either be unaffected by woodland proximity, or will be greater in locations further from woodland.

## 2. Methods

### 2.1. Study species

The National Bat Monitoring Programme (NBMP) uses a national network of field transects to monitor UK populations of four bat species: common pipistrelle (*P. pipistrellus*), soprano pipistrelle (*Pipistrellus pygmaeus*), noctule bat (*Nyctalus noctula*) and serotine bat (*Eptesicus serotinus*) (Walsh et al., 2001). *P. pipistrellus* and *P. pygmaeus* are the smallest bats found in the UK, with a wingspan of between 180–240 mm (Schober and Grimmberger, 1997). They are common and widespread in the UK, with a nationwide range (Richardson, 2000). *N. noctula* and *E. serotinus* are among the larger European bats, with wingspans of 320–400 mm and 315–381 mm respectively (Schober and Grimmberger, 1997). *N. noctula* is found throughout England and Wales, up to southern Scotland. *E. serotinus* is restricted to southern England and South Wales (Richardson, 2000). As a result of recent population declines, *P. pygmaeus* and *N. noctula* are priority species in the UK Biodiversity Action Plan (Joint Nature Conservation Committee, 2007).

### 2.2. Survey methodology and sample construction

Incidence data were available from 315 field transects distributed across the UK, surveyed between 1998–2007. Trained volunteer surveyors were each assigned a 1 km grid square, selected using a stratified-random sample design proportional to the extent of the 40 UK national land classes (as defined by the Institute of Terrestrial Ecology Bunce et al., 1996; Howard et al., 1999; Walsh et al., 2001). Within each square a transect of around 3 km in length was mapped, following as closely as possible a triangular route. Transects were split into twelve approximately equal sections. Beginning 20 min after sunset, surveyors walked the transect with a heterodyne detector tuned to 25 kHz, noting the number of *N. noctula* and *E. serotinus* ‘passes’ heard along each section. A pass

was defined as a sequence of two or more echolocation calls made as a bat flew past the detector (Thomas and West, 1989). At the end of each section a two minute point count was made with the detector tuned to 50 kHz, and the number of *P. pipistrellus* and *P. pygmaeus* passes noted. Species were distinguished using the tonal quality, rhythm, repetition rate and peak frequency of their echolocation calls (*N. noctula* <21 kHz, *E. serotinus* 25–32 kHz, *P. pipistrellus* 44–48 kHz, *P. pygmaeus* >52 kHz) and where possible using visual clues such as size and flight pattern. To minimise identification error, passes that showed the characteristics of a species of interest, but could not be attributed with confidence, were noted as ‘unsure’. Transects were surveyed twice during July, and surveys were repeated annually. During the study period each transect was visited on an average of 4.7 ( $\pm 3.9$  SD) occasions.

The presence or absence of each species at each point count location or transect section was established by combining data from all surveys undertaken between 1998 and 2007. To reduce false absences those point counts or transect sections where a species was not recorded, but where unidentified bat passes were noted, were excluded from the analysis of that species.

Transects were selected for analysis from within the UK range of each study species. To delimit species range, minimum convex polygons were constructed using observations of *N. noctula* and *E. serotinus* from the present survey combined with UK National Biodiversity Network records from 1958 onwards. All sites were assumed to fall within the range of *P. pipistrellus* and *P. pygmaeus*.

This study focuses on the use of linear features by bats in rural areas, defined as all land cover types apart from urban and suburban areas. Point counts that fell within rural areas, or transect sections with greater than 75% of their length within a rural area, were included in the analysis. Land cover data were derived from the Landcover Map 2000 (LCM2000), a 25 × 25 m raster grid of 16 broad habitat types classified using spectral reflectance parameters from satellite images. A concurrent field survey of 569 1 km squares suggests LCM2000 identifies broad land cover types with an accuracy of c. 85% (Fuller et al., 2002). Satellite data were collected between 1998–2001, while the incidence data used in this study were collected between 1998–2007. From 1998 to 2007 the change in UK land mass under the most extensive land cover types was considered small enough for LCM2000 data to be applied across the entire study period (arable 1.9% decline, improved grassland 1.1% increase, broadleaved/mixed woodland 0.3% increase, coniferous woodland 0.2% decline; Carey et al., 2008).

### 2.3. Habitat data

A bat heard on a detector may be located some distance from the observer. Habitat data were therefore sampled from within the ‘detection radius’ of each point count or transect section. Typical detection radii for each species in the field were established using a Batbox Duet (Batbox Ltd., Sussex UK), one of the most frequently used detectors in the NBMP field survey (Supplementary material 1). The detection radii used for each species were: *P. pipistrellus* 20 m, *P. pygmaeus* 20 m, *E. serotinus* 35 m and *N. noctula* 75 m. This resulted in sample areas of 0.13 ha for *Pipistrellus* species, surveyed using point counts, and approximately 56.7 ha for *N. noctula* and 22.2 ha for *E. serotinus*, based on the average transect section length of 262 m.

Linear features were digitised from GoogleEarth orthorectified and georeferenced aerial photographs with a resolution of 50 cm per pixel or better, taken between 1999 and 2008. To assess the spatial accuracy of the imagery, a sample of 20 landscape features were digitised within GoogleEarth, and their co-ordinates compared to those derived from Ordnance Survey MasterMap data, which is accurate to within 0.4–3.5 m. Locations differed by on average 2.0 m, and by no more 3.8 m.

All linear features comprising shrubs or trees, no more than 30 m wide and located within 75 m of a transect were digitised. An upper width limit of 30 m was selected to encompass all features from narrow hedgerows up to a double row of mature trees. The features digitised were assumed to represent a random sample of linear features in the UK, as transect routes were distributed relative to the extent of national land classes and were equally likely to sample linear features of all types. Each feature was classified according to the 'gappiness' of the feature, the density of trees and, where present, the width of the shrub component (Table 1). Category definitions were based on observed variation in width, tree density and 'gappiness' determined by a visual inspection of aerial photographs from across the UK. However, there was insufficient variation in 'gappiness' across the UK to include this as an explanatory predictor in the analysis. Therefore only continuous or near continuous features were considered. Trees were distinguished from shrubs by their open grown canopy extending beyond that of the shrub component of the feature. Linear features were classified according to the dominant characteristics of the feature between intersections, or over lengths separated from other linear features by gaps greater than 20 m.

Within the detection radius of each point count, the presence of linear features of each type was determined. However, bats flying at the edge of the detection radius may be utilising linear features located immediately outside this area. In particular, this unexplained variation has the potential to mask the negative consequences of an absence of linear features within the detection radius. To reduce the likelihood of this occurring points counts that did not contain linear features within the detection radius, but did have linear features present immediately outside the detection radius (20–40 m), were excluded from analysis.

Transect sections sampled a far greater area than point counts, so rather than presence/absence, the density of linear features ( $\text{km}/\text{km}^2$ ) within the detection radius was calculated.

The proximity of woodland was measured from Ordnance Survey MasterMap data, which defines woodland as an area in which individual trees are no more than 30 m apart. Broadleaved, mixed and coniferous woodland all have the potential to provide foraging habitat for bats (Mortimer, 2006; Walsh and Harris, 1996), so dis-

tance to the nearest patch of any woodland type was used. Patch sizes ranged from  $26 \text{ km}^2$  to less than  $10 \text{ m}^2$  (mean  $0.02 \text{ km}^2$ ), representing all woodlands from relatively continuous blocks to highly fragmented small farm woodlands. Distances (m) were measured from the point count or mid point of the transect section and were square root transformed for analysis. Easting and northing (m, with reference to OSGB 36) were measured at the point count or mid point of the transect section. Additional explanatory predictors included only in the analysis of point count data included the presence of water and the width of hedgerows present within the detection radius, the former determined from OS MasterMap data. It was not considered appropriate to use records pooled along transect sections to test the effect of small scale variation in hedgerow width or the distribution of water features on bat incidence. Differences in survey effort were controlled by including the number of separate surveys at each point location or transect section, and section length for *N. noctula* and *E. serotinus*. Not all sites were surveyed in every year, so population change over the study period could result in a differing encounter rate between transects surveyed over different subsets of years. This was controlled by including a mean population index, calculated using the smoothed population trends estimated from NBMP field survey data (Bat Conservation Trust, 2009). For each transect the mean national population index for each species was calculated over the years that transect was surveyed. Previous studies of bat-habitat relationships have identified broadleaved woodland (Russ and Montgomery, 2002; Walsh and Harris, 1996) and pasture (Mackie and Racey, 2007; Robinson and Stebbings, 1997; Vaughan et al., 1997) as important foraging habitats for the species assessed in this study. Therefore, the proportion of broadleaved woodland and improved grassland within 1.5 km of each transect, calculated from LCM2000, was included to control for effects of landscape composition on bat incidence. The habitat classification scheme used by LCM2000 defines improved grassland as having a sward dominated by productive grass species, managed by reseeding, fertilizer treatment and/or weed control (Jackson, 2000). Ninety-seven percent of grassland classified as improved in the UK is agriculturally productive (Fuller et al., 2002). Of that, 43% is used for cattle pasture and 32% for sheep pasture, with the remaining area is used for hay or silage production (Carey et al., 2008). Improved grassland was therefore used as a proxy for pasture in this study. All predictors demonstrated acceptable levels of collinearity (squared Spearman correlation coefficients  $<0.5$ , Freckleton, 2002). Spatial data processing was carried out using ArcGIS 9.2 (ESRI, Redlands, CA).

## 2.4. Statistical analysis

Associations between bat incidence and the characteristics of linear features were modelled using mixed effects logistic regression. To control for increased similarity among samples located along the same transect, transect ID was fitted as a random effect (Rabe-Hesketh and Skrondal, 2008).

To assess the effect of hedgerow width on bat incidence, data from the subset of point counts that contained hedgerows within the detection radius was used. A null model was constructed containing the variables easting, northing, number of surveys, mean population index, proportion of broadleaved woodland and proportion of improved grassland within 1.5 km of the transect. The fit of the null model was compared to a second model that in addition included the explanatory predictors medium hedgerows and wide hedgerows (effect estimated relative to narrow hedgerows). The importance of predictors describing hedgerow width was assessed firstly by comparing the AIC<sub>c</sub> score of the two models, and secondly by whether the 95% confidence intervals of the coefficient estimates overlapped zero.

**Table 1**  
Criteria used to classify linear features according to hedgerow width, 'gappiness' and tree density, and the percentage of point counts containing features of each type within the 20 m detection radius.

| Category                      | Description                                                 | Sample size (%) |
|-------------------------------|-------------------------------------------------------------|-----------------|
| <i>Hedgerow width</i>         |                                                             |                 |
| Narrow                        | Shrub component of linear feature <2 m wide                 | 47 <sup>a</sup> |
| Medium                        | Shrub component of linear feature 2–5 m wide                | 67 <sup>a</sup> |
| Wide                          | Shrub component of linear feature >5 m wide                 | 32 <sup>a</sup> |
| <i>Feature 'gappiness'</i>    |                                                             |                 |
| Sparse                        | Gaps >20 m, or >50% of the feature by length                | 5 <sup>b</sup>  |
| Near-continuous or continuous | Gaps <20 m wide and <50% of the feature by length           | 95 <sup>b</sup> |
| <i>Tree density</i>           |                                                             |                 |
| Hedgerow without trees        | Shrubs but no trees                                         | 34 <sup>b</sup> |
| Hedgerow with sparse trees    | Shrubs and trees, with tree canopy covering <50% of length  | 10 <sup>b</sup> |
| Tree-line                     | Tree canopy covering >50% of length, with or without shrubs | 30 <sup>b</sup> |

<sup>a</sup> Of point counts that contain hedgerows within the detection radius.

<sup>b</sup> Of all point counts.

The effect of tree density, woodland proximity and water on the use of linear features by bats was evaluated using AIC-based model selection on the full dataset, with the following explanatory predictors: The presence of hedgerows without trees, hedgerows with sparse trees and tree-lines were included to assess how the association between bats and linear features differs depending on the density of trees within the feature. The effects of woodland proximity and water on linear feature use, and the extent to which

these associations are affected by tree density, were modelled by including the interactions between these predictors and the presence of linear features in each of the three tree density categories. In addition, variation in the effect of tree density on linear feature use across the UK was assessed by modelling the interaction between the presence of linear features in each tree density category and easting and northing. Where necessary, predictors were centred by subtracting the mean value from each observation to reduce collinearity between main effects and interaction terms.

An initial candidate set of models was constructed in which predictors describing the presence/density of linear features were constrained to appear together and interaction terms did not appear without their corresponding main effects; within these constraints every allowable combination of explanatory predictors and interactions was fitted (Supplementary material 2). Initial candidate sets consisted of 39 models for *Pipistrellus* species and 13 models for *N. noctula* and *E. serotinus*. Model weights were calculated using the methods described by Burnham and Anderson (2002). The relative importance of each predictor can be assessed by summing the Akaike weight of each candidate model in which that predictor appears. This produces a selection probability ( $\Sigma w_i$ ); the estimated probability that, of all predictors considered, the predictor in question appears in the best approximating model (Whittingham et al., 2005). The calculation of relative importance requires that each predictor appears with a similar frequency within the candidate set of models. This can be a problem when the candidate set contains models both with and without interactions, as the main effects will appear in a greater number of models than the interaction terms. To create a balanced candidate set, support for the inclusion of interactions terms was first assessed over the initial full candidate set of models. An interaction term was deemed to be supported if it appeared within the subset of sub-

**Table 2**

Parameter estimates for the logistic regression model relating bat incidence to the presence of hedgerows of different widths. The effects of medium and wide hedgerows are measured relative to narrow hedgerows.

| Predictor                        | $\beta$ | SE      | 95% CI   |         |
|----------------------------------|---------|---------|----------|---------|
|                                  |         |         | Lower    | Upper   |
| <i>P. pipistrellus</i> (N = 758) |         |         |          |         |
| Medium hedgerows                 | −0.170  | 0.263   | −0.685   | 0.345   |
| Wide hedgerows                   | 0.046   | 0.318   | −0.576   | 0.669   |
| Easting                          | 3.57E−6 | 1.76E−6 | 1.10E−6  | 7.02E−6 |
| Northing                         | 6.56E−8 | 9.37E−7 | −1.77E−6 | 1.90E−6 |
| Number of surveys                | 0.265   | 0.045   | 0.177    | 0.352   |
| Mean population index            | 0.035   | 0.009   | 0.017    | 0.053   |
| Broadleaved woodland             | 0.049   | 0.026   | −0.001   | 0.099   |
| Improved grassland               | 0.020   | 0.011   | −0.001   | 0.041   |
| <i>P. pygmaeus</i> (N = 757)     |         |         |          |         |
| Medium hedgerows                 | 0.077   | 0.321   | −0.552   | 0.707   |
| Wide hedgerows                   | −0.164  | 0.378   | −0.906   | 0.578   |
| Easting                          | 3.72E−6 | 2.43E−6 | −1.05E−6 | 8.48E−6 |
| Northing                         | 2.16E−6 | 1.26E−6 | −3.12E−7 | 4.63E−6 |
| Number of surveys                | 0.106   | 0.047   | 0.014    | 0.198   |
| Mean population index            | 0.123   | 0.077   | −0.028   | 0.274   |
| Broadleaved woodland             | 0.062   | 0.032   | −0.001   | 0.126   |
| Improved grassland               | 0.017   | 0.015   | −0.011   | 0.046   |

**Table 3**

Results of AIC-based model selection across a candidate set of models predicting bat species incidence. Candidate sets were defined after assessing the importance of interaction terms (Supplementary material 2). Candidate sets also include the 'null' model, which contains only predictors common to all models<sup>a</sup>. For each model the number of estimable parameters ( $K$ ), AIC score corrected for small sample size ( $AIC_c$ ), Akaike difference from the best model ( $\Delta_i$ ) and Akaike weight ( $w_i$ ) are presented.

| Rank                   | Model <sup>a</sup>                                 | $K$ | $AIC_c$ | $\Delta_i$ | $w_i$    |
|------------------------|----------------------------------------------------|-----|---------|------------|----------|
| <i>P. pipistrellus</i> |                                                    |     |         |            |          |
| 1                      | HNT + HST + tree + distwood + water                | 13  | 2368.51 | 0.000      | 0.556    |
| 2                      | HNT + HST + tree + distwood                        | 12  | 2368.98 | 0.464      | 0.441    |
| 3                      | HNT + HST + tree + water                           | 12  | 2380.57 | 12.059     | 0.001    |
| 4                      | HNT + HST + tree                                   | 11  | 2381.56 | 13.042     | 0.001    |
| 5                      | Distwood + water                                   | 10  | 2402.64 | 34.125     | 2.16E−8  |
| 6                      | Distwood                                           | 9   | 2408.04 | 39.526     | 1.45E−9  |
| 7                      | Water                                              | 9   | 2426.24 | 57.724     | 1.63E−13 |
| 8                      | Null model                                         | 8   | 2434.18 | 65.665     | 3.06E−15 |
| <i>P. pygmaeus</i>     |                                                    |     |         |            |          |
| 1                      | HNT + HST + tree + distwood + HNT*distwood         | 13  | 1807.79 | 0.000      | 0.696    |
| 2                      | HNT + HST + tree + distwood + HNT*distwood + water | 14  | 1809.45 | 1.661      | 0.304    |
| 3                      | Water                                              | 9   | 1834.91 | 27.114     | 9.02E−7  |
| 4                      | Null model                                         | 8   | 1835.59 | 27.798     | 6.40E−7  |
| <i>N. noctula</i>      |                                                    |     |         |            |          |
| 1                      | Distwood                                           | 10  | 1818.00 | 0.000      | 0.655    |
| 2                      | Null model                                         | 9   | 1820.31 | 2.309      | 0.207    |
| 3                      | dHNT + dHST + dTree + distwood                     | 13  | 1821.70 | 3.702      | 0.103    |
| 4                      | dHNT + dHST + dTree                                | 12  | 1823.83 | 5.832      | 0.035    |
| <i>E. serotinus</i>    |                                                    |     |         |            |          |
| 1                      | Distwood                                           | 10  | 846.42  | 0.000      | 0.899    |
| 2                      | dHNT + dHST + dTree + distwood                     | 13  | 851.04  | 4.625      | 0.089    |
| 3                      | Null model                                         | 9   | 855.50  | 9.082      | 0.010    |
| 4                      | dHNT + dHST + dTree                                | 12  | 858.39  | 11.964     | 0.002    |

<sup>a</sup> Note that all models include transect ID fitted as a random effect, and also easting, northing, number of surveys, mean population index, proportion of broadleaved woodland and proportion of improved grassland within 1.5 km. *N. noctula* and *E. serotinus* models also contained section length. Predictor descriptions: HNT = presence of hedgerows without trees; HST = presence of hedgerows with sparse trees; tree = presence of tree-lines; dHNT = density of hedgerows without trees; dHST = density of hedgerows with sparse trees; dTree = density of tree-lines; distwood = distance to the nearest woodland patch; water = presence of water.

stantially supported models ( $\Delta_i < 2$ , Burnham and Anderson, 2002), and the 95% confidence interval of the averaged coefficient estimate did not overlap zero. Where the inclusion of an interaction term was supported, all models in which the main effects appeared without the associated interaction term were removed from the candidate set. Where there was little support for the interaction term, all models containing the interaction term were removed from the candidate set. Averaged parameter estimates and the relative importance of the predictors were recalculated over this new reduced candidate set. All analyses were performed using STATA 10 (StataCorp, TX).

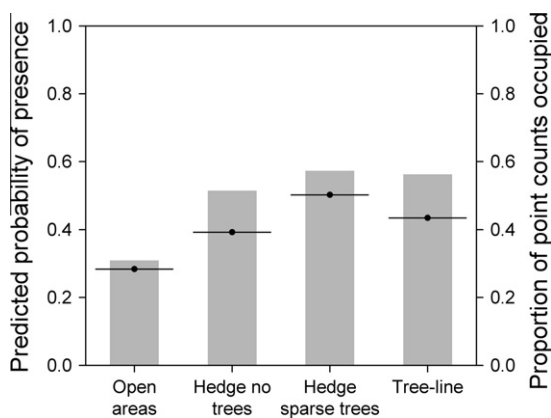


**Fig. 1.** The predicted probability of encountering *P. pipistrellus* adjacent to linear features with differing densities of trees (lines), with the predicted probability of encountering *P. pipistrellus* in open areas shown for reference. Also shown is the proportion of point counts adjacent to each feature type at which *P. pipistrellus* was present (bars).

### 3. Results

#### 3.1. Bat species incidence

*P. pipistrellus* was the most commonly encountered of the two *Pipistrellus* species, being present at 44% of point count locations, while *P. pygmaeus* was present at 19% of point count locations. Of the two larger bat species *N. noctula* was the more commonly occurring species. Within the national range of each species *N. noctula* was present along 21% of transect sections and *E. serotinus* was present along 10% of transect sections.

#### 3.2. UK linear features

In total 891 km of linear features were mapped. Of the total length of mapped features 95% were continuous or near continuous, of which 43% were hedgerows without trees, 11% were hedgerows with sparse trees and 46% were tree-lines. Thirty-eight percent of hedgerows were less than 2 m wide, 42% were between 2 m and 5 m wide, and 20% were greater than 5 m wide.

#### 3.3. The use of linear features by *P. pipistrellus* and *P. pygmaeus*

The incidence of *P. pipistrellus* and *P. pygmaeus* along hedgerows was not affected by hedgerow width. Adding the effect of medium and wide hedgerows (estimated relative to narrow hedgerows) to the null model resulted in an AIC<sub>c</sub> increase for both species (*P. pipistrellus*: AIC<sub>cNULL</sub> = 815, K = 8, AIC<sub>cWIDTH</sub> = 819, K = 10,  $\Delta_i = 3$ . *P. pygmaeus*: AIC<sub>cNULL</sub> = 659, K = 8, AIC<sub>cWIDTH</sub> = 663, K = 10,  $\Delta_i = 4$ ), indicating that the inclusion of hedgerow width did not improve explanatory power. The fitted coefficients of medium and wide hedgerows (estimated relative to narrow hedgerows) had 95% confidence intervals that overlapped zero for both species (Table 2), suggesting they had a similar effect on bat incidence as narrow

**Table 4**

Averaged coefficient estimates, unconditional standard errors, relative importance ( $\Sigma w_i$ ) and 95% confidence intervals of the averaged coefficients calculated for *P. pipistrellus* and *P. pygmaeus* over all models retained in the final candidate set after the importance of interaction terms had been assessed.

| Predictor                                    | $\beta$  | SE      | $\Sigma w_i$        | 95% CI   |         |
|----------------------------------------------|----------|---------|---------------------|----------|---------|
|                                              |          |         |                     | Lower    | Upper   |
| <i>P. pipistrellus</i> (N = 2357)            |          |         |                     |          |         |
| Hedgerow without trees                       | 0.489    | 0.138   | >0.999 <sup>a</sup> | 0.219    | 0.760   |
| Hedgerow with sparse trees                   | 0.937    | 0.212   | >0.999 <sup>a</sup> | 0.521    | 1.353   |
| Tree-line                                    | 0.664    | 0.147   | >0.999 <sup>a</sup> | 0.376    | 0.952   |
| Distance to woodland                         | -0.040   | 0.011   | 0.998               | -0.062   | -0.018  |
| Water                                        | 0.146    | 0.113   | 0.558               | -0.075   | 0.367   |
| Easting                                      | 1.83E-6  | 1.17E-6 |                     | -4.60E-7 | 4.13E-6 |
| Northing                                     | -1.17E-6 | 6.20E-6 |                     | -1.30E-5 | 1.10E-5 |
| Number of surveys                            | 0.228    | 0.027   |                     | 0.175    | 0.281   |
| Mean population index                        | 0.037    | 0.005   |                     | 0.027    | 0.047   |
| Broadleaved woodland                         | 0.013    | 0.016   |                     | -0.018   | 0.044   |
| Improved grassland                           | 0.014    | 0.007   |                     | 2.80E-4  | 0.028   |
| <i>P. pygmaeus</i> (N = 2354)                |          |         |                     |          |         |
| Hedgerow without trees                       | 0.280    | 0.166   | >0.999 <sup>b</sup> | -0.046   | 0.606   |
| Hedgerow with sparse trees                   | 0.572    | 0.231   | >0.999 <sup>b</sup> | 0.119    | 1.025   |
| Tree-line                                    | 0.511    | 0.171   | >0.999 <sup>b</sup> | 0.176    | 0.846   |
| Distance to woodland                         | -0.060   | 0.016   | >0.999 <sup>b</sup> | -0.091   | -0.029  |
| Hedgerow without trees* distance to woodland | 0.068    | 0.023   | >0.999 <sup>b</sup> | 0.022    | 0.113   |
| Water                                        | 0.036    | 0.064   | 0.304               | -0.090   | 0.162   |
| Number of surveys                            | 0.163    | 0.031   |                     | 0.104    | 0.223   |
| Mean population index                        | 0.069    | 0.050   |                     | -0.029   | 0.168   |
| Easting                                      | 1.98E-6  | 1.56E-6 |                     | -1.07E-6 | 5.03E-6 |
| Northing                                     | 8.46E-7  | 8.08E-7 |                     | -7.38E-7 | 2.43E-6 |
| Broadleaved woodland                         | 0.056    | 0.021   |                     | 0.015    | 0.096   |
| Improved grassland                           | 0.014    | 0.010   |                     | -0.005   | 0.033   |

<sup>a,b</sup> These predictors were constrained to appear as a group in the final candidate set of models, as such this value represents the relative importance of the group of predictors, rather than of the individual predictors themselves.

hedgerows. It is therefore unlikely that *P. pipistrellus* or *P. pygmaeus* discriminate between hedgerows of different widths.

For *P. pipistrellus* there was little support for the inclusion of interactions between the presence of linear features of any type and any other explanatory predictor, indicating that the association between *P. pipistrellus* and linear features is not affected by the presence of water, woodland proximity or geographical location. Within the initial candidate set of models, no substantially supported model ( $\Delta_i < 2$ , Burnham and Anderson, 2002) contained an interaction term, and the 95% confidence intervals of all interaction coefficients overlapped zero (Tables S1 and S2, Supplementary material 2). Models containing interactions were therefore removed from the candidate set and Akaike weights were recalculated over the remaining seven models (Table 3).

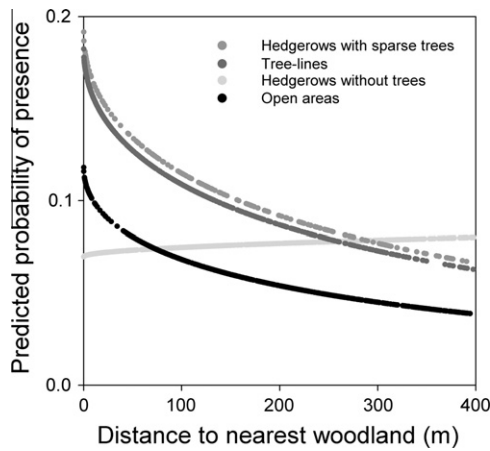


Fig. 2. The effect of woodland proximity on the predicted probability of encountering *P. pygmaeus* adjacent to linear features with differing densities of trees, and in areas without linear features (open areas).

*P. pipistrellus* incidence was greater at point counts adjacent to linear features than in areas without linear features (Fig. 1), and the density of trees within the feature had little effect on this association. The coefficients of hedgerows without trees, hedgerows with sparse trees and tree-lines had 95% confidence intervals that overlapped substantially (Table 4), suggesting a similar strength of association between *P. pipistrellus* and all three types of linear feature. This group of three predictors had high relative importance ( $\Sigma w_i > 0.999$  over all models in which they appeared), indicating very strong support for the effect of linear features on *P. pipistrellus* incidence. The probability of encountering *P. pipistrellus* was greater for point counts closer to woodland, with strong support for this effect ( $\Sigma w_i = 0.998$ ). The weak positive association between the presence of water and *P. pipistrellus* incidence had a low relative importance (0.558) and the 95% confidence interval of the coefficient estimate overlapped zero (Table 4), indicating very little support for this relationship.

For *P. pygmaeus*, an interaction between woodland proximity and the presence of hedgerows without trees was supported. This interaction appeared in the best performing model in the initial candidate set, and the 95% confidence interval of the coefficient estimate did not include zero (Tables S1 and S2, Supplementary material 2). No other interaction terms were supported. A new candidate set was constructed in which woodland proximity and the presence of hedgerows without trees were constrained to appear alongside their interaction, and the remaining interaction terms were omitted (Table 3). Averaged coefficients and the relative importance of the predictors were recalculated over this new candidate set (Table 4).

*P. pygmaeus* incidence declined as distance to the nearest woodland patch increased. However, *P. pygmaeus* incidence adjacent to hedgerows with sparse trees and tree-lines was always higher than in areas without linear features, regardless of woodland proximity (Fig. 2). In contrast, the association between *P. pygmaeus* and hedgerows without trees was entirely dependent on the proximity

Table 5

Averaged coefficient estimates, unconditional standard errors, relative importance ( $\Sigma w_i$ ) and 95% confidence intervals of the averaged coefficients calculated for *N. noctula* and *E. serotinus* over all models retained in the final candidate set after the importance of interaction terms had been assessed.

| Predictor                              | $\beta$  | SE      | $\Sigma w_i$       | 95% CI   |          |
|----------------------------------------|----------|---------|--------------------|----------|----------|
|                                        |          |         |                    | Lower    | Upper    |
| <i>N. noctula</i> ( <i>N</i> = 2170)   |          |         |                    |          |          |
| Hedgerow without trees                 | −0.002   | 0.003   | 0.174 <sup>a</sup> | −0.009   | 0.005    |
| Hedgerow with sparse trees             | 0.008    | 0.009   | 0.174 <sup>a</sup> | −0.009   | 0.025    |
| Tree-line                              | −0.001   | 0.003   | 0.174 <sup>a</sup> | −0.007   | 0.005    |
| Distance to woodland                   | −0.024   | 0.011   | 0.955              | −0.046   | −0.001   |
| Number of surveys                      | −3.42E−7 | 1.60E−6 |                    | −3.47E−6 | 2.79E−6  |
| Section length                         | −1.77E−6 | 9.94E−7 |                    | −3.72E−6 | 1.82E−7  |
| Mean population index                  | 0.167    | 0.030   |                    | 0.108    | 0.226    |
| Easting                                | 2.66E−4  | 6.16E−4 |                    | −9.41E−4 | 1.47E−3  |
| Northing                               | −1.47E−3 | 1.63E−2 |                    | −0.033   | 0.030    |
| Broadleaved woodland                   | 0.016    | 0.019   |                    | −0.022   | 0.054    |
| Improved grassland                     | 0.011    | 0.010   |                    | −0.009   | 0.032    |
| <i>E. serotinus</i> ( <i>N</i> = 1607) |          |         |                    |          |          |
| Hedgerow without trees                 | 6.26E−5  | 1.98E−3 | 0.092 <sup>b</sup> | −3.81E−3 | 3.93E−3  |
| Hedgerow with sparse trees             | 0.001    | 0.004   | 0.092 <sup>b</sup> | −0.006   | 0.008    |
| Tree-line                              | 0.002    | 0.002   | 0.092 <sup>b</sup> | −0.003   | 0.007    |
| Distance to woodland                   | −0.066   | 0.020   | 0.998              | −0.106   | −0.026   |
| Number of surveys                      | 1.09E−5  | 2.52E−6 |                    | 5.94E−6  | 1.58E−5  |
| Section length                         | −9.99E−6 | 3.12E−6 |                    | −1.61E−5 | −3.88E−6 |
| Mean population index                  | 0.043    | 0.038   |                    | −0.031   | 0.117    |
| Easting                                | 1.75E−3  | 8.25E−4 |                    | 1.29E−4  | 3.36E−3  |
| Northing                               | 0.045    | 0.027   |                    | −0.008   | 0.098    |
| Broadleaved woodland                   | −0.002   | 0.025   |                    | −0.050   | 0.046    |
| Improved grassland                     | 0.031    | 0.018   |                    | −0.004   | 0.066    |

<sup>a,b</sup> These predictors were constrained to appear as a group in the final candidate set of models, as such this value represents the relative importance of the group of predictors, rather than of the individual predictors themselves.

of woodland. In close proximity to woodland, *P. pygmaeus* incidence adjacent to hedgerows without trees was no higher than in open areas. A marginal increase in incidence relative to open areas was seen at distances beginning 100 m from woodland, while beyond 300 m from woodland the effect of hedgerows without trees became comparable to linear features containing trees (Fig. 2). As a comparison, 79% of the area within 5 km of the transects used in this study fell within 300 m of a woodland patch.

Incidence of *P. pygmaeus* was not related to the presence of water ( $\Sigma w_i = 0.288$ ). Furthermore, the lack of support for an interaction between the presence of linear features and either water, easting or northing indicates that the use of linear features by *P. pygmaeus* is not affected by the presence of water or by geographical location.

#### 3.4. The use of linear features by *N. noctula* and *E. serotinus*

No model containing interaction terms appeared within  $\Delta_i < 2$  of the best model in the initial candidate sets of either *N. noctula* and *E. serotinus*, and the 95% confidence interval of all interaction coefficients overlapped zero (Tables S1 and S3, Supplementary material 1). Interaction terms were therefore removed from the candidate sets and model weights were recalculated over the three remaining models (Table 3).

Incidence of both species was lower where the distance from the transect section to the nearest woodland was greater (Table 5). The large Akaike weight of the model containing the single predictor 'distance to nearest woodland patch' lends strong support to it being the best model within the candidate set for *E. serotinus* ( $w_i = 0.899$  for, Table 3), however this model provided only a marginal improvement over the null model for *N. noctula* ( $\Delta_i = 2.309$ , Table 3). Woodland proximity was strongly supported within the averaged model for both species ( $\Sigma w_i > 0.900$ ). Incidence of *N. noctula* and *E. serotinus* was not affected by the local density of linear features, regardless of the density of trees within the feature. The group of three predictors describing linear feature density had a low relative importance for both species ( $\Sigma w_i < 0.2$ ) and the 95% confidence interval of the individual coefficients overlapped zero (Table 5).

## 4. Discussion

#### 4.1. Associations with linear features

Hedgerows and tree-lines are widely assumed to be beneficial to bats. This study demonstrates that the strength of association between bats and linear features varies among species. *P. pipistrellus* and *P. pygmaeus* occurred more frequently adjacent to linear features than in open areas, while no evidence was found of an association between linear feature density and the incidence of either *N. noctula* or *E. serotinus*. Both *Pipistrellus* species are associated with structurally complex habitats such as woodland and woodland edge (Davidson-Watts et al., 2006; Nicholls and Racey, 2006), while *N. noctula* and *E. serotinus* are often observed foraging over open habitats such as pasture (Glendell and Vaughan, 2002; Vaughan et al., 1997), so they may be less dependent on linear features. However, it is possible that the lack of association between linear features and incidence of *N. noctula* and *E. serotinus* may be an artefact of the use of acoustic detectors as survey tools. Calls of *N. noctula* and *E. serotinus* carry further than those of smaller vespertilionid species, making it difficult to associate a bat pass heard on a detector with a specific habitat (Russ et al., 2003). Here, this problem was compounded by the pooling of records along transect sections, further increasing the area from which a bat pass may have originated. However, studies that use point counts to

compare activity levels in open areas to activity recorded adjacent to linear features also shown a negligible association between these species and linear features (Pocock and Jennings, 2008; Verboom and Huitema, 1997). If a strong association between the incidence of either *N. noctula* or *E. serotinus* and the extent of linear features in the landscape existed, it is likely that it would have been seen in this study.

#### 4.2. The use of linear features by *Pipistrellus* species

The use of linear features by *P. pipistrellus* was not affected by tree density within the feature; linear features of all types provided a similar increase in incidence relative to open areas. In contrast, the use of linear features by *P. pygmaeus* was affected both by the density of trees within the feature and by the distance of the feature from the nearest woodland patch. Only linear features containing trees were associated with an increase in *P. pygmaeus* incidence regardless of the proximity of woodland. Hedgerows without trees were associated with a similar increase in *P. pygmaeus* incidence when located further than 300 m from woodland, suggesting that hedgerows without trees are utilised only when other, higher quality habitats are unavailable. To put this in context, more than three quarters of the rural landscape randomly sampled by this study fell within 300 m of a patch of woodland, so linear features lacking trees may have limited benefits for *P. pygmaeus* in all but the most sparsely wooded rural landscapes. The differing responses of *P. pipistrellus* and *P. pygmaeus* to tree density suggests a possible mechanism by which habitat is partitioned between these two morphologically similar species.

Many European bat species utilise linear features (Downs and Racey, 2006; Entwistle et al., 1996; Limpens and Kapteyn, 1991). The density of hedgerow trees therefore has the potential to affect other bat species, particularly those that, like *P. pygmaeus*, are more strongly associated with structurally complex rather than open habitats. Hedgerow trees may benefit bats by providing increased shelter from predators and the elements (Limpens and Kapteyn, 1991; Verboom and Spoelstra, 1999). They also increase prey availability, as insect accumulation in the lee of hedgerows increases with increasing feature height (Lewis, 1967, 1969). In agricultural landscapes, hedgerow trees have been shown to increase the abundance and diversity of Lepidoptera (Merckx et al., 2009), which are found in the diet of most European bats and are the main prey item for species including the greater horseshoe bat (*Rhinolophus ferrumequinum*) and brown long-eared bat (*Plecotus auritus*). Hedgerow trees can also provide additional microhabitats, such as senescing and dead wood, that increase invertebrate abundance and diversity (DEFRA, 2010).

Both *P. pipistrellus* and *P. pygmaeus* were more likely to be encountered closer to areas of woodland, in agreement with previous studies that have found a positive association between these species and woodland habitats (Davidson-Watts et al., 2006; Nicholls and Racey, 2006; Russ and Montgomery, 2002; Walsh and Harris, 1996). However, the close proximity of woodland was not associated with an increased use of linear features (measured relative to open areas), as would be expected if linear features function primarily as commuting routes between foraging patches. Rather, the findings of this study suggest that linear features provide benefits to bats independent of their role as potential commuting corridors.

The remaining attributes tested, hedgerow width and the presence of water, did not affect the use of linear features by either *Pipistrellus* species. The absence of an effect of water on either bat incidence or the on use of linear features by bats is perhaps surprising given that both *Pipistrellus* species, and *P. pygmaeus* in particular, are associated with riparian habitats (Davidson-Watts et al., 2006; Nicholls and Racey, 2006). However, in this study

national data on the location of water features were taken from OS MasterMap data, which is dominated by small features such as field drains and ditches that have little surface area and are unlikely to be associated with significant riparian vegetation. Hedgerow width may fail to influence the use of linear features by bats if feature height, and not width, is of primary importance. Nationwide data describing feature height were not available to this study. Further research investigating the relationship between height and the use of linear features by bats is needed, in particular to assess the relative benefits of increasing hedge height in comparison to increasing the density of hedgerow trees.

#### 4.3. Conservation implications

Here we show that the presence of hedgerow trees affects the use of linear features by a bat species of conservation concern. Increasing the density of trees within hedgerows will benefit populations of *P. pygmaeus*, and may also benefit other bat species associated with structurally complex habitats, such as *P. auritus* and Natterer's bat (*Myotis nattereri*). This study was conducted using a national dataset and no evidence of regional variation in linear feature use was found, the results are therefore likely to be relevant across the UK and in other similarly fragmented rural landscapes across Europe.

The benefits of hedgerow trees to other taxa are linked to their use of or dependence on the tree canopy. Rodent species commonly found in hedgerows, such as wood mouse (*Apodemus sylvaticus*), yellow-necked mouse (*A. flavicollis*), and bank vole (*Myodes glareolus*) are generally unaffected by the density of hedgerow trees (Gelling et al., 2007; Kotzageorgis and Mason, 1997; Michel et al., 2007), as their arboreal activity is predominantly within a metre of the ground (Buesching et al., 2008). However, hedgerow trees increase both the abundance and diversity of larger moth species by providing increased shelter for less mobile species (Merckx et al., 2010). Trees also increase the abundance and diversity of birds in hedgerows (Hinsley and Bellamy, 2000; Walker et al., 2005), although negative impacts have been demonstrated for the shrub nesting species common whitethroat (*Sylvia communis*), and species occupying adjacent open habitats such as skylark (*Alauda arvensis*), red-legged partridge (*Alectoris rufa*) and meadow pipit (*Anthus pratensis*) (DEFRA, 2001; Green et al., 1994). The provision of hedgerow trees may therefore be broadly beneficial to rural biodiversity, however careful targeting is required to avoid negative impacts on species such as ground nesting birds.

The establishment of new emergent trees within hedgerows creates additional costs to land managers as they impede mechanical trimming and increase shading of adjacent crops. As a result populations of hedgerows trees are vulnerable to decline. Successive surveys have noted a 6.6% decline in the number of hedgerow trees in the UK over the last two decades (Carey et al., 2008; Haines-Young et al., 2000). Thirty percent of the hedgerow tree population remaining in the UK is now over 100 years old, while the number of newly established trees declined by 40% between 1990–1998 (DEFRA, 2010; Haines-Young et al., 2000). Specific conservation measures, such as those recently introduced into the English Entry Level Stewardship agri-environment scheme (Natural England, 2010), may be required to prevent similar declines elsewhere.

Linear features are a common characteristic of fragmented agricultural landscapes, and many agri-environment schemes include financial incentives for environmentally sensitive hedgerow management. This study shows that the biodiversity benefits of these schemes can be improved by considering the provision and retention of hedgerow trees. We recommend that future studies of linear features in rural landscapes consider the importance of hedgerow trees to rural biodiversity.

#### Acknowledgements

We thank all the National Bat Monitoring Programme (NBMP) volunteers who contributed data to this study, Kate Rickett and Beatriz Contreras for creating digital maps of linear features and Philip Briggs for assistance with NBMP data. The NBMP Field survey protocol was developed by Allyson Walsh, Colin Catto, Tony Hutson and Paul Racey. This study was funded by a Grant from the Natural Environment Research Council (Award No. NER/S/A/2005/13588) and by the Bat Conservation Trust. The NBMP is funded by the Joint Nature Conservation Committee in partnership with Bat Conservation Trust.

#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2011.02.017](https://doi.org/10.1016/j.biocon.2011.02.017).

#### References

- Baltensperger, B.H., 1987. Hedgerow distribution and removal in nonforested regions of the Midwest. *J. Soil Water Conserv.* 42, 60–64.
- Buesching, C.D., Newman, C., Twell, R., Macdonald, D.W., 2008. Reasons for arboreality in wood mice *Apodemus sylvaticus* and Bank voles *Myodes glareolus*. *Mamm. Biol.* 73, 318–324.
- Bunce, R.G.H., Barr, C.J., Clarke, R.T., Howard, D.C., Jane, A.M.L., 1996. ITE Merlewood land classification of Great Britain. *J. Biogeogr.* 23, 625–634.
- Burel, F., 1996. Hedgerows and their role in agricultural landscapes. *Crit. Rev. Plant Sci.* 15, 169–190.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*, first ed. Springer-Verlag, New York.
- Carey, P.D., Wallis, S., Chamberlain, P.M., Cooper, A., Emmett, B.A., Maskell, L.C., McCann, T., Murphy, J., Norton, L.R., Reynolds, B., Scott, W.A., Simpson, I.C., Smart, S.M., Ulliyett, J.M., 2008. Countryside Survey: UK Results from 2007. NERC/Centre for Ecology & Hydrology.
- Davidson-Watts, I., Walls, S., Jones, G., 2006. Differential habitat selection by *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* identifies distinct conservation needs for cryptic species of echolocating bats. *Biol. Conserv.* 133, 118–127.
- DEFRA, 2001. The Importance of Hedgerow Management for Wintering Farmland Birds. University of Bristol and the British Trust for Ornithology. Report to the UK Government Department for the Environment, Food and Rural Affairs, London.
- DEFRA, 2010. Trends, Long Term Survival and Ecological Values of Hedgerow Trees: Development of Populations Models to Inform Strategy. Forest Research, Forestry Commission. Report to the UK Government Department for the Environment, Food and Rural Affairs, London.
- Dover, J., Sparks, T., 2000. A review of the ecology of butterflies in British hedgerows. *J. Environ. Manage.* 60, 51–63.
- Downs, N.C., Racey, P.A., 2006. The use by bats of habitat features in mixed farmland in Scotland. *Acta Chiropterol.* 8, 169–185.
- Entwistle, A.C., Racey, P.A., Speakman, J.R., 1996. Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Philos. Trans. R. Soc. B Biol. Sci.* 351, 921–931.
- Freckleton, R.P., 2002. On the misuse of residuals in ecology: regression of residuals 584 vs. multiple regression. *J. Anim. Ecol.* 71, 542–545.
- Fuller, R.M., Smith, G.M., Sanderson, J.M., Hill, R.A., Thomson, A.G., Cox, R., Brown, N.J., Clarke, R.T., Rothery, P., Gerard, F.F., 2002. Countryside Survey 2000 Module 7: Land Cover Map 2000 Final Report. Centre for Ecology and Hydrology, UK.
- Gelling, M., Macdonald, D.W., Mathews, F., 2007. Are hedgerows the route to increased farmland small mammal density? Use of hedgerows in British pastoral habitats. *Landsc. Ecol.* 22, 1019–1032.
- Glendell, M., Vaughan, N., 2002. Foraging activity of bats in historic landscape parks in relation to habitat composition and park management. *Anim. Conserv.* 5, 309–316.
- Green, R.E., Osborne, J.L., Sears, E.J., 1994. The distribution of passerine birds in hedgerows during the breeding season in relation to characteristics of the hedgerow and adjacent farmland. *J. Appl. Ecol.* 31, 677–692.
- Haines-Young, R.H., Barr, C.J., Black, H.J.J., Briggs, D.J., Bunce, R.G.H., Clarke, R.T., Cooper, A., Dawson, F.H., Firbank, L.G., Fuller, R.M., Furse, M.T., Gillespie, M.K., Hill, R., Hornung, M., Howard, D.C., McCann, T., Morecroft, M.D., Petit, S., Sier, A.R.J., Smart, S.M., Smith, G.M., Stott, A.P., Stuart, R.C., Watkins, J.W., 2000. Accounting for Nature: Assessing Habitats in the UK Countryside. Department of the Environment, Transport and the Regions, London.
- Hannon, L.E., 2009. Hedgerows in an agri-natural landscape: potential habitat value for native bees. *Biol. Conserv.* 142, 2140–2154.
- Hinsley, S.A., Bellamy, P.E., 2000. The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. *J. Environ. Manage.* 60, 33–49.
- Howard, D.C., Barr, C.J., Bunce, R.G.H., Stark, G.J., 1999. Countryside Survey 2000: Selection of Environmental Zones for Reporting the Results of Countryside

- Survey 2000. Report to the Department of the Environment, Transport and the Regions, UK.
- Jackson, D.L., 2000. Guidance on the Interpretation of the Biodiversity Broad Habitat Classification (Terrestrial and Freshwater Types): Definitions and the Relationship 614 with other Classifications. Report 307, JNCC, UK.
- Joint Nature Conservation Committee, 2007. UK List of Priority Species and Habitats. <<http://www.ukbap.org.uk/NewPriorityList.aspx>> (accessed 15.01.10).
- Kotzageorgis, G.C., Mason, C.F., 1997. Small mammal populations in relation to hedgerow structure in an arable landscape. *J. Zool.* 242, 425–434.
- Lewis, T., 1967. The horizontal and vertical distribution of flying insects near artificial windbreaks. *Ann. Appl. Biol.* 60, 23–31.
- Lewis, T., 1969. The distribution of flying insects near a low hedgerow. *J. Appl. Ecol.* 6, 443–452.
- Limpens, H.J.G.A., Kapteyn, K., 1991. Bats, their behaviour and linear landscape elements. *Myotis* 29, 39–48.
- Mackie, L.J., Racey, P.A., 2007. Habitat use varies with reproductive state in noctule bats (*Nyctalus noctula*): implications for conservation. *Biol. Conserv.* 140, 70–77.
- Merckx, T., Feber, R.E., Riordan, P., Townsend, M.C., Bourn, N.A.D., Parsons, M.S., Macdonald, D.W., 2009. Optimizing the biodiversity gain from agri-environment schemes. *Agric. Ecosyst. Environ.* 130, 177–182.
- Merckx, T., Feber, R., McLaughlan, C., Bourn, N.A.D., Parsons, M.S., Townsend, M.C., Riordan, P., Macdonald, D.W., 2010. Shelter benefits less mobile moth species: the field-scale effect of hedgerow trees. *Agric. Ecosyst. Environ.* 138, 147–151.
- Michel, N., Burel, F., Legendre, P., Butet, A., 2007. Role of habitat and landscape in structuring small mammal assemblages in hedgerow networks of contrasted farming landscapes in Brittany. *France Landsc. Ecol.* 22, 1241–1253.
- Mortimer, G., 2006. Foraging, Roosting and Survival of Natterer's Bats, *Myotis nattereri*, in a Commercial Coniferous Plantation. PhD Thesis, University of St. Andrews.
- Natural England, 2010. Entry Level Stewardship: Environmental Stewardship Handbook, third ed. Natural England, UK.
- Nicholls, B., Racey, P.A., 2006. Habitat selection as a mechanism of resource partitioning in two cryptic bat species *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*. *Ecography* 29, 697–708.
- Pocock, M.J.O., Jennings, N., 2008. Testing biotic indicator taxa: the sensitivity of insectivorous mammals and their prey to the intensification of lowland agriculture. *J. Appl. Ecol.* 45, 151–160.
- Rabe-Hesketh, S., Skrondal, A., 2008. Multilevel and Longitudinal Modeling Using Stata, second ed. Stata Press, College Station, Texas.
- Racey, P.A., Entwistle, A., 2003. Conservation ecology of bats. In: Kunz, T.H., Fenton, M.B. (Eds.), *Bat Ecology*. University of Chicago Press, Chicago, pp. 680–743.
- Richardson, P., 2000. Distribution atlas of Bats in Britain and Ireland, 1980–1999. Bat Conservation Trust, London.
- Robinson, R.A., 1997. The Ecology and Conservation of Seed-eating Birds on Farmland. PhD Thesis, University of East Anglia, Norwich, UK.
- Robinson, M.F., Stebbings, R.E., 1997. Home range and habitat use by the serotine bat, *Eptesicus serotinus*, in England. *J. Zool.* 243, 117–136.
- Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.* 39, 157–176.
- Russ, J.M., Montgomery, W.I., 2002. Habitat associations of bats in Northern Ireland: implications for conservation. *Biol. Conserv.* 108, 49–58.
- Russ, J.M., Briffa, M., Montgomery, W.I., 2003. Seasonal patterns in activity and habitat use by bats (*Pipistrellus* spp. and *Nyctalus leisleri*) in Northern Ireland, determined using a driven transect. *J. Zool.* 259, 289–299.
- Schober, W., Grimmberger, E., 1997. The Bats of Europe and North America. T.F.H. Publications, Neptune, New Jersey.
- Sklenicka, P., Molnarova, K., Brabec, E., Kumble, P., Pittnerova, B., Pixova, K., Salek, M., 2009. Remnants of medieval field patterns in the Czech Republic: analysis of driving forces behind their disappearance with special attention to the role of hedgerows. *Agric. Ecosyst. Environ.* 129, 465–473.
- Tattersall, F.H., Macdonald, D.W., Hart, B.J., Johnson, P., Manley, W., Feber, R., 2002. Is habitat linearity important for small mammal communities on farmland? *J. Appl. Ecol.* 39, 643–652.
- Thomas, D.W., West, S.D., 1989. Sampling methods for bats. In: Ruggiero, L.F., Carey, A.B. (Eds.), *Wildlife-habitat Relationships: Sampling Procedures for Pacific Northwest Vertebrates*. United States Forest Service General Technical Report PNW-GTR-243, Portland, Oregon.
- Bat Conservation Trust, 2009. The National Bat Monitoring Program Annual Report 2009. Bat Conservation Trust, London.
- Vaughan, N., Jones, G., Harris, S., 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *J. Appl. Ecol.* 34, 716–730.
- Verboom, B., Huitema, H., 1997. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landsc. Ecol.* 12, 117–125.
- Verboom, B., Spoelstra, K., 1999. Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. *Can. J. Zool.* 77, 1393–1401.
- Walker, M.P., Dover, J.W., Hinsley, S.A., Sparks, T.H., 2005. Birds and green lanes: breeding season bird abundance, territories and species richness. *Biol. Conserv.* 126, 540–547.
- Walsh, A.L., Harris, S., 1996. Foraging habitat preferences of vespertilionid bats in Britain. *J. Appl. Ecol.* 33, 508–518.
- Walsh, A.L., Catto, C.M.C., Hutson, A.M., Racey, P.A., Richardson, P.W., Langton, S.D., 2001. The UK's National Bat Monitoring Programme, Final Report 2001. The Bat Conservation Trust, London.
- Whittingham, M.J., Swetnam, R.D., Wilson, J.D., Chamberlain, D.E., Freckleton, R.P., 2005. Habitat selection by yellowhammers *Emberiza citrinella* on lowland farmland at two spatial scales: Implications for conservation management. *J. Appl. Ecol.* 42, 270–280.
- Whittingham, M.J., Krebs, J.R., Swetnam, R.D., Thewlis, R.M., Wilson, J.D., Freckleton, R.P., 2009. Habitat associations of British breeding farmland birds. *Bird Study* 56, 43–52.
- Wolton, R., 2010. Local Hedgerow Survey Review 2006–2008. UK Hedgerow Habitat Action Plan Steering Group. <<http://hedgelink.org.uk/hedgelink/hedgerow-research-and-surveys.htm>> (accessed 13.03.10).