A national assessment of bat-habitat relationships in the UK

Katherine L. R. Boughey

Thesis submitted for the degree of Doctor of Philosophy
School of Environmental Sciences
University of East Anglia, UK

Submitted January 2010

Abstract

Effective biodiversity conservation requires an understanding of how land management choices effect the distribution of species. However, the response of bats to changes in landscape composition and configuration in temperate regions is not well understood. This thesis presents a national investigation of the habitat associations of seven UK bat species. Data from the National Bat Monitoring Programme are used to relate roost selection and foraging incidence to measures of landscape composition, configuration and linear habitat character. The availability of broadleaved woodland affected both roost selection and foraging incidence of every bat species assessed. In general, bats were more likely to roost and forage in landscapes with a greater proportion of broadleaved woodland. Roost location was not affected by the size of the nearest woodland patch, nor was there clear evidence of a negative effect of woodland disaggregation on foraging incidence. However, both roost selection and foraging incidence were affected by woodland proximity. Bats roosted closer to broadleaved woodland than would be expected by chance, and all species for which data were available were encountered more frequently as the distance to the nearest woodland patch decreased. The majority of species demonstrated a positive association with the proportion of improved grassland. Foraging incidence was higher in landscapes with more dispersed grassland patches, suggesting that grassland boundary features may influence landscape quality for bats. The use of linear features by four bat species was examined. *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* incidence was positively associated with the presence of hedgerows and tree-lines, however, only linear features that contained trees were consistently beneficial to *P. pygmaeus*. *Nyctalus noctula* and *Eptesicus serotinus* were not affected by the density of linear features in the landscape. Associations between roost location, foraging incidence and landscape structure was assessed at multiple spatial scales. No single scale captured all habitat associations demonstrated by each species. Increasing the provision of broadleaved woodland and hedgerow trees should form the focus of bat conservation strategies at a landscape scale. To benefit the bat species assessed in this thesis, woodland creation schemes should aim to maximise woodland extent, particularly in landscapes with limited woodland cover, and reduce patch isolation. Agri-environment options should be amended to include financial compensation for the provision and retention of hedgerow trees.

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Acknowledgements

I am extremely grateful to my two supervisors, Iain Lake and Paul Dolman. Thank you for your guidance, dedication and enthusiasm for this project.

This thesis would not have been possible without the support of the Bat Conservation Trust. I thank Karen Haysom, my supervisor at the BCT, for her advice and support throughout this project. I also thank Katie Parsons and Esther Collis, who provided valuable guidance during the development of this project and Steve Langton for statistical advice. I am extremely grateful to Philip Briggs for taking the time to guide me through the NBMP data, and for his quick response to many queries. Thank you for the many hours spent gathering information from volunteers, tracking down data and collating records on my behalf. Thanks also to the interns at the BCT for the assistance they provided.

I am extremely thankful to the huge number of volunteers who have taken part in the National Bat Monitoring Program, whose dedication to bat conservation has produced such a unique and valuable dataset. NBMP protocols were developed by Colin Catto, Allyson Walsh, Tony Hutson and Paul Racey. I also thank Jean Mathews at the Countryside Council for Wales for providing access to the Welsh Lesser horseshoe colony count data.

I thank Kate Rickett and Beatriz Contreras for their help digitising huge numbers of landscape features, and Rob Martin, Alex Lees, James Gilroy and Jessa Battersby for providing comments on the manuscripts.

Thank you to my family and friends for all their encouragement and support.

Finally, I thank my husband Rob for his love and support throughout this study, for all the nights spent with me in the field, and for helping in a myriad other ways too numerous to mention.

This study was supported by a grant from the Natural Environment Research Council (award no. NER/S/A/2005/13588) and by the Bat Conservation Trust. The National Bat Monitoring Programme is funded by the Joint Nature Conservation Committee in partnership with Bat Conservation Trust.

Chapter 1

Introduction

1.1. Understanding species distribution

One of the fundamental requirements of effective biodiversity conservation is an understanding of the environmental factors that determine the distribution of species (Rushton et al. 2004). Species distribution models (SDMs), statistical models that link the incidence or abundance of organisms to environmental measures, are the most widely used tool for the quantitative assessment of species-habitat relationships (Elith and Leathwick 2009). SDMs encompass a huge variety of approaches, with ever increasing sophistication. They are used to provide ecological insight, test hypotheses and, more recently, as a predictive tool of species distribution. A sizeable body of literature has developed concerning both methodological approaches and the application of SDMs. One of the most commonly identified issues is the choice of study scale (Rushton et al. 2004). The extent and resolution at which data are collected can affect both the performance and utility of the resulting model, and so require careful consideration when applying the results of SDMs to conservation problems.

1.1.1. Generality in species distribution modelling

The use of SDMs to inform conservation policy, and in particular as a means of predicting species' response to landscape change, can require the application of the model to sites beyond the geographic or environmental range originally sampled. This is termed extrapolation, and can have serious implications for model performance (Elith and Leathwick 2009; Whittingham et al. 2007). There are numerous reasons why an SDM may fail to accurately predict species distribution under novel conditions. If the relationship between species incidence and an environmental predictor is non-linear, its form may change considerably depending on the range sampled. Influential predictors may not display adequate variation within the original 'training' data to accurately model relationships. For example, hunting pressure may be negligible in some regions, as a result of protection measures or isolation from human populations, while in other regions it may exert a strong influence on species distribution (Gray et al. 2009). Species-habitat relationships may also be altered by interactions that result from novel combinations of environmental predictors, or by varying correlation between distal predictors and their underlying ecological drivers (Elith and Leathwick 2009). As an example of both these cases, the American Marten *Martes americana* displays a strong affinity with mature coniferous stands throughout its range, however this relationship is a poor predictor of Marten distribution in regions with extensive broadleaved cover. In such regions the availability of suitably structured forest is no longer correlated with the distribution of closed-canopy coniferous forest (Bissonette et al. 1997). Biotic interactions, both within and between species, operate alongside environmental predictors to determine species distribution (Wharton and Kriticos 2004). Biotic interactions have the potential to vary greatly in geographical space, but when measured in the field they can be hard to separate from abiotic effects (Guisan and Thuiller 2005). The presence of location-specific restrictions on dispersal, such as topographic barriers or historic population depression (Donohue et al. 2000), will also reduce the predictive ability of SDMs in novel situations. Given the potential pitfalls associated with extrapolation to unsampled locations, it is advantageous if the extent over which data are sampled matches the extent to which model insights or predictions are to be applied. As most conservation policy is enacted at a national level, this requires SDMs conducted across multi-regional or even national extents. With the proliferation of GIS technology and remote sensed environmental data, it is now feasible to collect and analyse data at such broad scales, and large scale modelling studies have been completed for many species (Corsi et al. 1999; Johnson et al. 2004; Sattler et al. 2007).

1.1.2. Data resolution

Species distribution can be influenced by factors acting across a range of scales (Levin 1992). Climatic factors will limit the global range of a species (Morin et al. 2007), while at the other extreme vegetation structure may determine the location of an individual within a habitat patch (Warren et al. 2000). Habitat selection can also be viewed as a hierarchy, in which the choice of foraging patch influences the selection of a home range, which in turn affects the species range (Elith and Leathwick 2009). To provide the closest fit to the data, the resolution of an environmental predictor, that is the size of the individual units of observation, should match the scale at which the predictor acts to influence distribution.

Although several methods have been developed to detect scales of pattern inherent in data (Beever et al. 2006; Cushman and McGarigal 2002), these are for the most part untested in species distribution modelling. The most widely used approach remains to select a scale or range of scales a priori, based on current ecological knowledge. New model algorithms are emerging that allow scale to be incorporated within model structure. For example, hierarchical regression, a type of generalized linear mixed model, allows data to be clustered in a hierarchy of scales, with cluster membership fitted as a random effect (Rabe-Hesketh and Skrondal 2008).

Just as extrapolating to novel extents carries an increased risk of prediction error, so does the use of species-habitat relationships modelled at one scale to predict habitat selection at different scales (Collingham et al. 2000). Species-habitat relationships should be assessed at a range of scales to provide a robust evidence base.

1.2. Distribution modelling of bats

1.2.1. Conservation status and threats to bat populations

There are currently 1,150 known species of bat worldwide, representing 20% of all mammalian biodiversity, second only to the Rodentia in terms of number of species. 15% of bat species are listed as vulnerable or endangered by the International Union for Conservation of Nature (IUCN 2008). Although population trends have proven hard to estimate due to a paucity of historical monitoring data, counts at hibernacula, documented range contractions and anecdotal evidence indicate a decline in a broad suite of species over the 20th century (Daan 1980; Harris et al. 1995; Hutson et al. 2001; Stebbings and Griffith 1986). Bat species with a restricted range, particularly those endemic to islands, are among the most threatened (IUCN 2008), however there have also been substantial declines in widespread and abundant species. *Rhinolophus hipposideros,* once found throughout Europe, is now critically endangered or extinct in a number of European countries, as a result of range contraction over the last 50 years

(Temple and Terry 2007). In Central and North America widespread declines in colony size of a number of cave roosting species have been reported since the 1950s. Losses of up to 99% of individuals at known *Tadarida brasiliensis* cave roosts were seen between 1950 and 1960 in the Southern United States, and colonies numbering hundreds of thousands of individuals in Mexico have disappeared completely (Hutson et al. 2001). Similar declines have also been reported for at *M. grisescens* and *Myotis sodalis* (Hutson et al. 2001). In the UK, monitoring data collected annually since 1995 indicate that *R. hipposideros* and *P. pipistrellus* populations are currently increasing (Bat Conservation Trust 2009), following respective historic declines of approximately 90% over the last 100 years, and 55% between 1978-83 (Stebbings 1988). Although the time span of data is not adequate to reveal reliable population trends for other UK bat species, there is no evidence of further marked declines.

Most threats to bats can be directly related to human activities. Over-hunting for food is known to have caused the extinction of a number of *Pteropus* species on islands throughout the tropics, and unregulated hunting of bats is widespread across Asia. Large scale persecution of fruit-eating bats in fruit producing regions is also common. In Australia it has been estimated that if the current rate of culling continues, the population of 2 million fruit bats will be reduced to 100,000 in 30 years (Richards and Hall 1998). Bats are also persecuted through fear of disease. A program to prevent the transmission of rabies from infected *Desmodus rotundus* to humans resulted in the destruction of 40,000 colonies in Venezuela (Hutson et al. 2001). An emerging threat to bats, which does not currently appear to be related to human activities, is White-nose syndrome. First observed in hibernating bats in the United States, it is characterised by white fungal growth on the skin, increased arousal and day flying during hibernation, emaciation, and mortality of up to 75% of individuals in infected colonies (Blehert et al. 2009; Gargas et al. 2009). To what extent the fungus is the cause of White-nose syndrome, or whether it is symptomatic of an underlying problem, has not yet been established.

The threats described above have strong regional effects, however at a global scale the primary cause of population declines is thought to be habitat loss (Hutson et al. 2001; Stebbings 1988). This includes the loss of both roosting and foraging habitat, and the fragmentation and degradation of remaining habitat patches. Habitat loss has principally been driven by the expansion and intensification of agriculture, and to a lesser extent by increasing urbanisation (Millennium Ecosystem Assessment 2005; Vitousek 1994). Agricultural intensification is also though to be responsible for a decline in insect abundance in rural landscapes (Conrad et al. 2006), a potential threat to the 70% of bat species that are insectivorous. Although the relationship between bat populations and habitat loss is poorly understood, habitat changes have occurred concurrently alongside most reported declines (Racey and Entwistle 2003). It is therefore essential for effective bat conservation that the links between bat distribution and habitat, and in particular the effects of habitat loss and fragmentation, are understood.

1.2.2. Methods used to survey bat distribution

The earliest surveys of bat distribution involved counts at maternity roosts or hibernacula (Bogdanowicz 1983), trapping (Meyer et al. 2004)**,** or observational records in the field, sometimes aided by the use of light tags or reflective markers (Racey and Swift 1985). Acoustic detectors were first used to establish bat-habitat relationships in the 1970s (Fenton 1970), and have become ubiquitous in bat research since, while perhaps the finest resolution distribution data are provided by radio-telemetry studies (e.g. Davidson-Watts et al. 2006). However, all methods contain inherent difficulties for the study of bat-habitat relationships. Visual observations of such highly mobile, nocturnal species are extremely error prone, and bats make minimal use of the surrounding landscape during hibernation, so neither of these methods are well suited to habitat association studies. The non-random selection of roost location has been used to infer habitat preferences (Entwistle et al. 1997; Oakeley and Jones 1998) but roosts, particularly of tree roosting species, are extremely difficult to locate without concurrent radio-tracking. As part of a roost survey validation exercise in the UK, an intensive search of 18 randomly selected 1km squares resulted in the location of just 2 previously unknown maternity roost locations, and in the majority of squares no roosts were located, despite previous reports of roosts within the square (Walsh et al. 2001). Both acoustic detector surveys and radio-tracking are extremely time and resource intensive, and the use of radio-telemetry for the study of bats has, until the recent development of miniature radio transmitters, been limited by guidance that transmitters should weigh no more than 5% of the body weight of the bat (Aldridge and Brigham 1988). The restrictions on sample size caused by these constraints have resulted in the majority of bat-habitat associations studies have been conducted at local or regional extents; large scale studies (e.g. Russ and Montgomery 2002; Walsh and Harris 1996) are rare. The extent to which local bat-habitat relationships can be successfully extrapolated to a national scale, and can therefore be used to inform national conservation policy, is untested.

1.2.3. Bat-habitat associations

It is estimated that between one third to one half of the terrestrial surface of the earth has been substantially altered by human activity (Turner et al. 1990; Vitousek 1994). In some landscapes, such as the New World Tropics, extensive habitat alteration is a relatively new phenomena (although the extent that habitat has been altered by the indigenous people of these regions is not yet fully understood, Williams 2000). However, in Europe, substantial habitat alteration took place over a millennia ago, creating a landscape of fragmented semi-natural habitat within a predominantly agricultural matrix. Over this time, European biodiversity may have adapted to habitat fragmentation, and as a result habitat associations described in more recently altered landscapes may not be directly transferable to Europe. As this thesis considers bat-habitat associations within a UK context, this review will focus primarily on the habitat associations of European bats.

Bat-habitat associations have been studied with respect to both roost location and the occurrence or abundance of foraging bats. Roost location is determined by the availability of suitable roosting structures (Baker and Lacki 2006; Miles et al. 2006), the prevailing climate (Bihari 2004; Briggler and Prather 2003) and the distribution of suitable foraging habitat. Associations between roost location and landscape structure have been demonstrated in previous studies. For example *Pipistrellus pipistrellus*, *Plecotus auritus*, and *Rhinolophus hipposideros*, species which roost primarily in man-made structures, all select roosts that are closer to broadleaved woodland, and are located in landscapes containing a greater proportion of broadleaved woodland, than would be expected if roost selection was random (Entwistle et al. 1997; Jenkins et al. 1998; Reiter 2004).

All bat species found on mainland Europe are insectivorous, and as such the selection of foraging habitat is strongly influenced by insect abundance (Fukui et al. 2006; Wickramasinghe et al. 2004). Elevated insect density is thought to be responsible for the positive association of many European bat species with bodies of water (Glendell and Vaughan 2002; Vaughan et al. 1997; Walsh and Harris 1996) and cattle pasture (Catto et al. 1996; McAney and Fairley 1988). Bats are also found a wide variety of other habitats, including woodland, scrub, arable farmland, wetlands and urban areas (Avila-Flores and Fenton 2005; Flaquer et al. 2006; Mackie and Racey 2007; Menzel et al. 2005; Russo and Jones 2003; Walsh and Harris 1996), however, broadleaved woodland is the habitat type favoured by the greatest range of European bat species (Racey and Entwistle 2003). In areas lacking broadleaved forest cover, bats make extensive use of linear woody habitats, such as hedgerows and tree-lines (Limpens et al. 1989; Limpens and Kapteyn 1991), as they are structurally similar to woodland edges and provide many of the same foraging opportunities (Kanuch et al. 2008; Kusch et al. 2004; Nicholls and Racey 2006). Linear features form an important component of the European landscape, and the management of linear habitat for biodiversity is a common conservation tool in rural areas. However, the benefit of such conservation actions for bats is restricted by a lack of knowledge of how the characteristics of linear features affect their use by bats.

The foraging associations of European bat species can be arranged approximately along a scale of increasing structural complexity (Schnitzler and Kalko 2001), from species that prefer to forage in open habitats, such as *N. noctula*, which forages at height over woodland and grassland (Kronwitter 1988), to species that prefer to forage in cluttered habitats, such as *Plecotus auritus*, which forages within the canopy of broadleaved woodland and around scattered trees (Schnitzler and Kalko 2001). This variation can be ascribed to differences in echolocation call and wing morphology (Russ 1999). Species that forage in open habitats typically echolocate at a near constant frequency (QCF). They concentrate the energy of the call within a narrow band of frequencies, so the call travels further, but the returning echo provides relatively little detail of their surroundings. Bats foraging in cluttered habitats typically produce a frequency modulated (FM) call, that spans a broader range of frequencies. The energy of the call is spread over a greater number of frequencies, so less energy is concentrated at each frequency. As a result an FM call cannot travel as far as a QCF call. It is therefore unsuitable for echolocating in very open areas, but it does provide greater detail of the surroundings when negotiating cluttered habitats. The response of bats to habitat complexity can also be related to wing morphology (Norberg and Rayner 1987). Species that forage in open habitats typically have long narrow wings that allow fast direct flight, while species that forage in cluttered habitats typically have broader wings that allow manoeuvrable flight, and are often able to hover briefly to glean insects from surfaces.

All European bat species take prey on the wing, and for the majority of species this is the only hunting technique employed (Dietz et al. 2009). However a minority of species have developed specialised hunting techniques that have resulting in specific habitat associations. For example, *Myotis daubentonii* and *Myotis dasycneme* specialise in taking insects from the surface of still water, and are therefore predominantly associated with water bodies and riparian vegetation (Dietz et al. 2006), while the large pinna of *P. auritus* allow it to hear insects moving across the surface of vegetation, so is often encountered foraging close to or within the tree canopy (Entwistle et al. 1996; Russ 1999).

An organism may respond to habitat changes at a variety of scales, so the scale of measurement can have a significant effect on the strength of observed habitat relationships (discussed further in section 1.1.2.). Studies of bat-habitat associations have considered the distribution of bats among different habitat patches (Russ and Montgomery 2002; Walsh and Harris 1996) and different landscapes (Sattler et al. 2007), and habitat associations at both scales correspond well. However, several studies have highlighted scale dependent associations between tropical forest bat species and landscape composition, related to differences in mobility and home-range size (Gorresen and Willig 2004; Gorresen et al. 2005; Klingbeil and Willig 2009). The extent to which scale dependent landscape associations are shown by other bat species is not well understood.

Habitat studies at a landscape scale are able to assess the response of bats to changing landscape configuration, and in particular the effect of habitat fragmentation on bat distribution. Habitat fragmentation can be characterised by three components; a reduction in the extent of the original habitat, decreasing patch size, and increasing patch isolation (Andrén 1994). It can impact biodiversity by reducing available habitat, impeding movement between patches, and reducing habitat quality as a result of edge effects such as increased light penetration, desiccation and predation. The effect of habitat fragmentation on bat distribution has been studied extensively in tropical regions, particularly the Neotropics, but is rarely studied in Europe.

Many studies have shown bat biodiversity is affected by the fragmentation of tropical forests, although the nature of the relationship is inconsistent. Meyer et al (Meyer and Kalko 2008) found Phyllostomid diversity on forested islands in Lake Gatún, Panama to be lower than diversity on the mainland, with islands furthest from the mainland having the lowest diversity. Phyllostomid abundance in Akumal, Mexico was significantly lower at sites where the forest had been fragmented by deforestation than in continuous forest (Fenton et al. 1992). Brosset et al. (1996) found bat species richness in a forested landscape in French Guiana to be negatively associated with deforestation, however bat abundance in deforested areas was over four times higher than in primary forest. Similarly, bat species diversity in a naturally fragmented savannah landscape in Bolivia was negatively associated with forest patch size, but abundance in forest islands was almost five times higher than in continuous forest (Loayza and Loiselle 2009). Other studies have found the greatest richness of bat species in moderately fragmented forest landscapes, as a result of the coexistence of both clutter adapted and open area adapted bat species (Estrada-Villegas et al.; Gorresen and Willig 2004; Klingbeil and Willig 2009).

When associations are considered at guild or species level, it becomes clear that characteristics such as diet and wing morphology play an important role in determining the response of bats to fragmentation (Gorresen and Willig 2004; Meyer and Kalko 2008). Frugivores that forage in the forest understorey, typically clutter adapted species with slow manoeuvrable flight, are more sensitive to forest loss than overstorey frugivores, which are typically strong, fast fliers able to cross larger areas between forest patches (Cosson et al. 1999). The latter species may actually benefit from fragmentation due to the proliferation of pioneer fruiting plants that colonise deforested areas (Ochoa 2000). Gleaning insectivores, which again are typically clutter adapted, are strongly negatively affected by fragmentation (Brosset et al. 1996; Fenton et al. 1992; Meyer and Kalko 2008; Ochoa 2000), while aerial insectivores of the family

Molossidae were positively association with forest loss (Ochoa 2000). Similar findings were reported by Estrada-Villegas et al. (2010), who found species richness of forest and forest edge specialist insectivores on islands in Lake Gatún was negatively affected by decreasing island size and increasing isolation from the mainland, while abundance of open area adapted insectivores was lower at mainland sites than on islands.

One of the few studies to address habitat fragmentation in a European landscape reported a similar pattern of species specific responses (Ekman and de Jong 1996). The occurrence of the forest specialists *P. auritus* and *Myotis brandti* (Dietz et al. 2009), on forested islands in lake Mälaren in Sweden was negatively impacted by the degree of isolation from similar habitat (Ekman and de Jong 1996), while *P. pipistrellus* and *Eptesicus nilssoni*, both species that could be characterised as edge specialists (Haupt et al. 2006; Nicholls and Racey 2006), were unaffected.

Evidence from field studies and simulations of landscape fragmentation suggest that in landscapes with a high proportion of original habitat, the effect of fragmentation on population size is primarily the result of declining habitat extent, and that the effect of patch disaggregation becomes more important as the proportion of suitable habitat decreases (Andrén 1994). Landscape scale measures of habitat fragmentation, such as mean patch size, mean nearest neighbour distance and edge density, tend to be correlated with habitat extent, and so untangling the independent effects of habitat extent and habitat disaggregation is difficult. This is rarely addressed in studies of bat habitat-associations. One of the most common methods used to correct for the confounding effect of habitat extent in fragmentation studies is the use of residual regression, employed by Gorresen et al (Gorresen and Willig 2004; Gorresen et al. 2005) in the study of Phyllostomid bats in the Atlantic forests of Paraguay. However, this technique has been shown to produce unreliable estimates of effect size (Freckleton 2002). No study of the effect of fragmentation on bats has employed metrics of fragmentation that are truly independent of habitat extent. The degree to which bats respond to changes in the spatial configuration of fragmented landscapes, as apposed to changes in habitat extent, is unknown.

The response of bats to fragmentation may also depend on the scale at which fragmentation is measured. Fragmentation is typically characterised as a series of discrete focal habitat patches imbedded within a matrix of less preferred habitat. However, this reductive representation of the landscape disguises the fact that as the size of the study landscape increases, so does patch complexity and internal heterogeneity. This can potentially affect the relationship between species distribution and landscape configuration (Kotliar and Wiens 1990). Studies of bats in tropical forests have shown scale dependent associations between a suite of species and metrics of fragmentation, (Gorresen et al. 2005; Klingbeil and Willig 2009), with no one scale able to capture the response of all species simultaneously (Gorresen et al. 2005).

1.2.4. The National Bat Monitoring Programme

The National Bat Monitoring Programme (NBMP) is a nationwide bat survey begun in 1995. Although designed primarily as a tool to monitor bat population trends, the records it has amassed offer an opportunity to address gaps in our understanding of bat-habitat associations, in particular the response of bats to habitat composition and configuration in a historically fragmented temperate landscape. It also provides the unique opportunity to investigate bat-habitat associations at a national scale, and evaluate the utility of small scale habitat association studies in national conservation planning. The Bat Conservation Trust, a UK non-governmental organisation, was commissioned to establish the NBMP by the Department of the Environment, Transport and the Regions in 1995 (Walsh et al. 2001). The program was conceived to provide an effective monitoring program for resident UK bat species, as required by The Agreement on the Conservation of Populations of European Bats (Bonn Convention/EUROBATS 1994) and the EC Habitats Directive (Council Directive 92/43/EEC). The program was designed to provide statistically robust estimates of population trends, updated distribution maps, and inform conservation policy development. The NBMP has run annually since 1997. Of the 18 bat species resident in the UK, 15 are currently monitored by the NBMP, and statistically significant population trends have been produced for 11 species. Surveys are carried out by a network of volunteers and local bat groups. In 2008, 1,018 volunteers completed surveys, and a total of 4,639 sites, covering England, Scotland, Wales and Northern Ireland, have been monitored since 1997 (Bat Conservation Trust 2008). The NBMP originally consisted of three multi-species survey components; colony counts, hibernation counts and field transect detector surveys, together with a waterway survey targeted towards *M. daubentonii*. It expanded in 2005 to include two further multi-species surveys, the bats and roadside mammals survey and the woodland survey. A survey targeted at *Myotis bechsteini* was launched in 2007, and a survey designed to locate *Pipistrellus nauthusi* was piloted in 2009. To provide the most widely applicable results, this thesis concentrates on multi-species survey data collected during the breeding season, when increased energetic demands mean habitat quality is likely to be most important. Of the four summer multi-species surveys, the colony counts and field survey were chosen for analysis, as they have the largest sample size both in terms of national coverage and repeat visits. Although both surveys were designed to monitor population trends, they also provide data suitable for habitat association modelling, as discussed in section 1.5.1. Three species of bat are monitored using both colony counts and field surveys. This will allow the cross validation of habitat associations modelled using different datasets.

Colony counts: Beginning in spring, female bats gather in maternity colonies, located most commonly in buildings or trees. The young, usually a single pup but exceptionally twins, are born in June and July. The adults leave the roost to forage at dusk. The NBMP monitors colony size using two counts of emerging bats, made on separate nights between late May and mid June. Roosts of six species are monitored: *Rhinolophus hipposideros, Pipistrellus pipistrellus*, *P. pygmaeus*, *Plecotus auritus*, *Myotis nattereri* and *Eptesicus serotinus* (Walsh et al. 2001).

Field survey: The field survey monitors numbers of foraging and commuting bats. A transect approximately 3km in length, contained within a 1km national grid square, is walked with a heterodyne detector twice during July. The number of *P. pipistrellus, P. pygmaeus*, *N. noctula* and *E. serotinus* passes heard along the transect are recorded (Walsh et al. 2001).

Each survey follows standardised monitoring protocols designed to reduce bias and maximise precision. These are described in greater detail in the relevant data chapters.

1.2.5. National digital datasets

The use of NBMP data to model habitat associations is made possible by the availability of high quality digital environmental datasets. Measures of habitat at a landscape scale can be derived from the Landcover Map 2000 (Fuller et al. 2002), a 25 x 25m raster grid of the UK classified into 16 broad habitat types (described further in chapter 2). However, digital data are now also available at much finer resolutions, allowing nationwide habitat metrics to be calculated at patch and even within-patch level. For this study, fine resolution data were derived from Ordnance Survey MasterMap, a digital topographic map of Britain providing the location of features such as buildings, woodland and water to within 0.4-3.5m, and from aerial imagery with a resolution of 50cm per pixel or better, available within GoogleEarth.

1.3 British Bats

This thesis uses data from NBMP colony counts and field surveys to investigate the habitat associations of seven British bat species. Their ecology and distribution are described below.

1.3.1. Pipistrellus pipistrellus
Common pipistrelle

Pipistrellus pipistrellus is the smallest bat in the UK, weighing between 3.5-8.5g (Schober and Grimmberger 1997). It is a fast flying, agile bat the forages close to vegetation, often around head height (Russ 1999). Its diet consists mainly of small Diptera, particularly Chironomidae, and small Lepidoptera (Arlettaz et al. 2000; Barlow 1997; Vaughan 1997).

Pipistrellus pipistrellus roosts are found predominantly in man-made structures (Jones et al. 1996), but also in tree cavities, rock crevices and bat boxes. They move between roosts throughout the year. In Germany, a colony of *P. pipistrellus* was reported to switch roosts every 11-12 days (Feyerabend and Simon 2000). Maternity colonies can number over 100 individuals, but are often smaller (Altringham 2003). During the winter *P. pipistrellus* hibernates in buildings (Racey 1973), caves (Nagy and Szanto 2003) and similar structures with a cool, stable microclimate.

Pipistrellus pipistrellus forages in a wide range of habitats (Davidson-Watts et al. 2006; Russ and Montgomery 2002; Vaughan et al. 1997), and is tolerant to deviations from optimal habitat (Sattler et al. 2007). It utilises broadleaved woodland, water bodies, grassland and human settlements (Davidson-Watts et al. 2006; Kusch et al. 2004; Sattler et al. 2007), and is also associated with linear habitats such as tree-lines, hedgerows and woodland edges (Downs and Racey 2006; Russ et al. 2003; Verboom and Huitema 1997). *Pipistrellus pipistrellus* occurs across Europe and North Africa (Nowak 1994). It is one of the most widespread and abundant bat species in Europe, and is common throughout the UK (Richardson 2000, fig 1.1a).

1.3.2. Pipistrellus pygmaeus

Soprano pipistrelle

Pipistrellus pygmaeus is morphologically similar to *P. pipistrellus* (Barlow et al. 1997; Häussler et al. 1999), and consumes a similar range of prey, but with a greater portion of aquatic diptera than *P. pipstrellus* (Vaughan 1997).

Roosts are found in predominantly man-made structures, with maternity roosts of between 500-700 individuals not uncommon. It demonstrates greater roost fidelity than *P. pipistrellus*, often using the same roost throughout the season and year after year (Altringham 2003; Schober and Grimmberger 1997). *Pipistrellus pygmaeus* is found in a similar range of habitats as *P. pipistrellus*, but shows a greater association with riparian habitats and water bodies (Davidson-Watts et al. 2006; Nicholls and Racey 2006; Russ and Montgomery 2002; Russo and Jones 2003).

Pipistrellus pygmaeus is found across Europe and North Africa, and overlaps that of *P. pipistrellus* (Mayer and Von Helversen 2001; Nowak 1994). However the relative abundance of the two species varies throughout their range. *Pipistrellus pygmaeus* is more abundant that *P. pipistrellus* in Sweden (Mayer and Von Helversen 2001) and in the Mediterranean region (Mayer and Von Helversen 2001). However, along over 20 road transects distributed throughout Switzerland, *P. pipistrellus* activity was over thirty times greater than *P. pygmaeus* (Sattler et al. 2007). *Pipistrellus pipistrellus* is the more abundant species generally across central Europe, however there is localised variation in relative abundance throughout this region (Mayer and Von Helversen 2001). In the UK, *P. pygmaeus* is common and widespread (Richardson 2000) with a nationwide range (fig. 1.1b). NBMP field survey data suggest that *P. pipistrellus* is generally the more abundant species, although there is localized variation across England and Wales, and *P. pygmaeus* is the more abundant of the two species in central Scotland (chapter 3, fig 3.2 and 3.3).

1.3.3. Rhinolophus hipposideros

Lesser horseshoe bat

Rhinolophus hipposideros is one of only two representatives of the Rhinolophid family in the UK (the other being the Greater Horseshoe bat, *Rhinolophus ferrumequinum*). It is a small bat (4-9g, Schober and Grimmberger 1997), with broad short wings allowing manoeuvrable flight in cluttered environments (Russ 1999). It has a distinctive nose-leaf, through which it produces echolocation vocalizations. Unlike Vespertilionid bats, *R. hipposideros* employs Doppler shift to echolocate. The diet of *R. hipposideros* includes Diptera and small Lepidoptera (Feldman et al. 2000; Vaughan 1997), and prey is taken in flight or gleaned from surfaces (Russ 1999).

Rhinolophus hipposideros roosts in man-made structures, caves, mines and tunnels. Individuals hang directly from the ceiling of the roost, and require a direct flight path to the roost position. Maternity roosts can number up to 300 individuals (Schober and Grimmberger 1997). Although individual bats may occasionally move between roosts, the majority of the colony will use a single roost throughout the summer (Knight 2006). Hibernacula are found in similar structures to those used during the summer, preferring locations with a cool and relatively stable microclimate (Zukal et al. 2005).

This species is associated with woodland and pasture (Bontadina et al. 2002; Reiter 2004; Wickramasinghe et al. 2003) and linear features such as hedgerows (Motte and Libois 2002). *Rhinolophus hipposideros* is found across Europe into central Asia and North Africa. In Europe it has undergone significant range contraction (Hutson et al.

2001). The species is at the northern limit of its distribution in the UK, where it is rare and restricted to South-west England and Wales (fig. 1.1c).

1.3.4. Plecotus auritus

Brown long-eared bat

Plecotus auritus is a medium sized bat (6-12 g, Schober and Grimmberger 1997) with short broad wings and a low wing aspect ratio, allowing slow manoeuvrable flight close to and within vegetation (Russ 1999). Its diet includes Lepidoptera (Vaughan 1997), Diptera and a wide range of arthropod prey gleaned from vegetation (Shiel et al. 1991).

Relative to *Pipistrellus* species, it forms small roosts (Furmankiewicz and Altringham 2007). Mean colony size of 12 intensively studied roosts in north-east Scotland was 16 individuals (Entwistle et al. 2000). A study of 34 roosts along the river Dee in Scotland found a mean roost size 16.8 individuals (Speakman et al. 1991). Individuals regularly change their position within the roost, but demonstrated a high degree of roost fidelity during the year (Entwistle et al. 2000). This species is associated with woodland habitat (Entwistle et al. 1996), areas with scattered trees (Fuhrmann and Seitz 1992) and makes use of linear features such as hedgerows as commuting routes (Entwistle et al. 1997). It is found across Europe and Asia, and is common and widespread throughout the UK (fig 1.1d)

1.3.5. Nyctalus noctula

Noctule

Nyctalus noctula is the largest bat in the UK, and one of the largest across Europe (19-40g, Schober and Grimmberger 1997). It has large, relatively narrow wings allowing fast straight flight (Russ 1999). *Nyctalus noctula* typically forages between 10-40m from the ground (Schober and Grimmberger 1997). Prey consists primarily of Diptera, but Coleoptera and Lepidoptera are also taken (Vaughan 1997).

It roosts in tree cavities (Boonman 2000), particularly old woodpecker holes (Ruczynski and Bogdanowicz 2005), and to a lesser extent in bat boxes and buildings. Maternity roosts typically number between 20-60 individuals. Hibernation occurs in thick walled tree cavities and crevices in buildings, caves and cliffs (Dietz et al. 2009). *Nyctalus noctula* forages in a wide range of habitats including pasture, parkland and suburban areas (Gaisler et al. 1998; Glendell and Vaughan 2002; Mackie and Racey 2007), but is particularly associated with water bodies (Rachwald 1992) , open canopy woodland and woodland edge (Kanuch et al. 2008; Mackie and Racey 2007). *Nyctalus noctula* is found across Europe and most of temperate Asia, and patchily in Indonesia and Algeria. In the UK it is fairly common throughout England and Wales, and is occasionally recorded in southern and central Scotland (fig 1.1e).

1.3.6. Eptesicus serotinus

Serotine

Eptesicus serotinus is a large bat (15-35g, Schober and Grimmberger 1997) with broad wings and a relatively slow flight speed. It forages up to heights of 5-10m (Russ 1999). The diet consists mainly of Coleoptera, but a wide range of other prey items including Diptera and Lepidoptera are also consumed (Catto et al. 1994; Vaughan 1997), including prey gleaned from the ground (Catto et al. 1996).

Maternity roosts are found predominantly in buildings, but this species is also occasionally found in bat boxes and tree cavities. Colonies number up to 30 individuals, and bats are strongly philopatric to their roost when reproductively active (Catto et al. 1996). *Eptesicus serotinus* forages in a wide range of habitats including woodland, suburban habitats, water bodies, unimproved grassland, parkland and pasture, especially where dung from livestock is present (Bartonicka and Zukal 2003; Catto et al. 1996; Glendell and Vaughan 2002; Robinson and Stebbings 1997; Vaughan et al. 1997). It is found throughout western and central Europe, and in Asia to Korea. In the UK is restricted to southern England and South Wales (fig 1.1f), where it is widespread and fairly common (Richardson 2000).

1.3.7. Myotis nattereri

Natterer’s bat

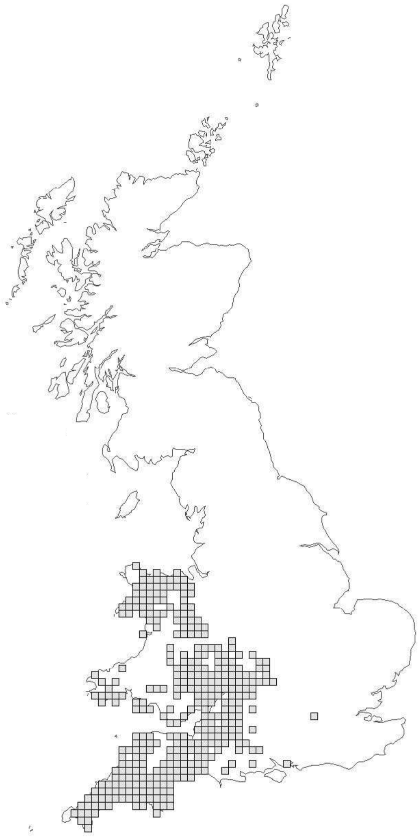
Myotis nattereri is a medium sized bat (6-12g, Schober and Grimmberger 1997) with broad wings that allow it to forage close to vegetation and low over water (Russ 1999;

Siemers and Schnitzler 2000). It takes insects on the wing and also gleans prey from surfaces The diet consists of medium sized arthopods 5-15mm long, including Opiliones and small numbers of Lepidoptera, Diptera, Coleoptera, Trichoptera, Neuroptera and Araneae (Swift 1997; Swift and Racey 2002; Vaughan 1997). Up to 42% of prey is gleaned (Shiel et al. 1991).

Roosts are found in tree cavities (Kanuch 2005; Smith and Racey 2005), buildings (Swift 1997) and bat boxes. Maternity roosts number up to 200 individuals, including up to 25% males (Swift 1997). *Myotis nattereri* frequently moves between roosts during the summer. A study of a *M. nattereri* population inhabiting bat boxes in a Scottish coniferous plantation found that they switched roosts on average every 2.5 days (Mortimer 2006). Roosts are located within a ‘core’ area of approximately 2km^2(Smith and Racey 2005). *Myotis nattereri* is associated with coniferous and broadleaved woodland, grassland, parkland and water bodies (Mortimer 2006; Parsons and Jones 2003; Smith and Racey 2008; Swift 1997). It is found across Europe, North Africa and the Middle East and is widespread and fairly common throughout the UK (fig 1.1g).

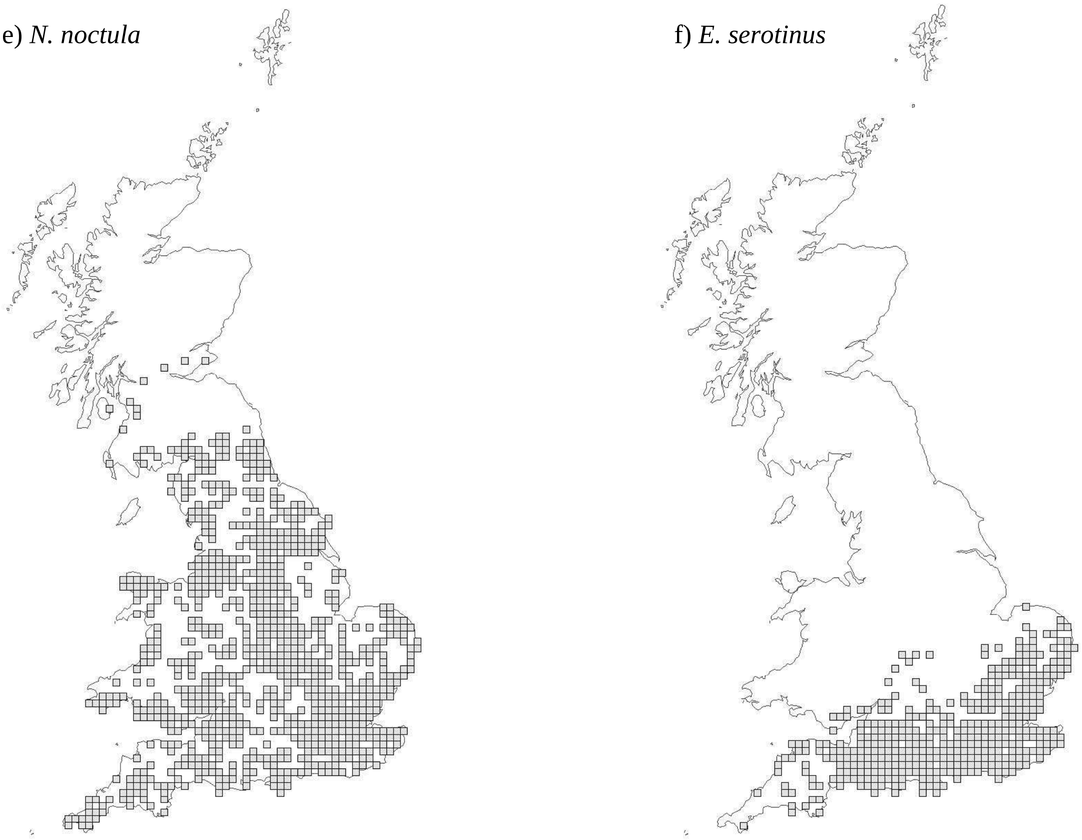
a) *P. pipistrellus*

b) *P. pygmaeus*



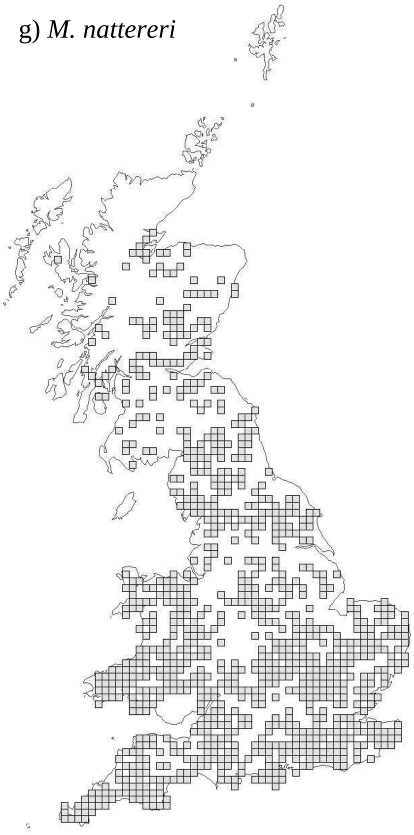
c) *R. hipposideros*

d) *P. auritus*



e) *N. noctula*

f) *E. serotinus*



g) *M. nattereri*

Figure 1.1 Distribution maps of the bat species monitored by the National Bat Monitoring Program colony counts and field survey. Maps reproduced with permission from the *Second Report by the UK under Article 17 on the implementation of the Habitats Directive from January 2001 to December 2006* (Joint Nature Conservation Committee 2007).

1.4. Thesis aims

The aim of this thesis is to examine the relationship between the distribution of seven UK bat species and habitat at a national scale. Specifically, I address two aspects of habitat use that are poorly understood within a European context: the response of bats to habitat configuration, and the use of linear habitat features in rural landscapes. This thesis uses data from the NBMP colony counts and field survey to model habitat associations simultaneously for a suite of UK bat species. The results will be used to evaluate the utility of NBMP data in the study of bat-habitat associations and, through partnership with the Bat Conservation Trust, help inform effective bat conservation.

1.5. Model construction and selection

1.5.1. Selection of model algorithm

There are a vast array of statistical techniques currently used to model species distribution. One of the most basic distinctions is between techniques that model distribution in terms of presence/absence, and those that use a measure of abundance. NBMP survey data offer the opportunity to model presence/absence and abundance, in the form of colony size and the number of bat passes recorded along field transects (termed activity). Measures of abundance can provide a more sensitive measure of habitat suitability, however both colony counts and activity present problems in the investigation of habitat associations. Colony counts provide a relative measure of the number of bats occupying a particular roost, but the link between colony size and population size is untested. The population of bats utilising a particular landscape may occupy one large roost, or several smaller roosts. As a result, the relationship between colony size and landscape suitability is likely to be highly variable. The link between roost location and the surrounding landscape is expected to be more robust, and so was employed in this study.

The field survey provides a relative measure of bat activity along a transect. Of the four species monitored, *N. noctula* and *E. serotinus* are comparatively rare, resulting in a high proportion of zero counts. Statistical distributions used to model count data, such as the Poisson or negative binomial distribution, performed poorly for these species. A high proportion of zero counts can sometimes be addressed by fitting a zero-inflated generalized linear model, which distinguishes between factors that affect presence/absence and those that affect the abundance of individuals at occupied sites (Hall 2000). However, performance remained poor using both zero-inflated Poisson and zero-inflated negative binomial models. Presence/absence, fitted using logistic regression, was a more robust measure of *N. noctula* and *E. serotinus* incidence along field transects, and was therefore used to model the distribution of these two species.

1.5.2. Model selection and inference

The use of information theoretic criteria to select among and draw inferences from multiple models is now common-place in the ecological literature, and is used in this thesis. The modelling techniques advocated by Burnham and Anderson (2002) have been followed, with the exception of two areas in which the nature of the investigation required an alternative approach.

Burnham and Anderson recommend the use of a small set of discrete candidate models, each designed to test a separate, carefully conceived hypothesis (Burnham and Anderson 2002). They caution against the use of every possible combination of explanatory predictors as a form of data dredging. However, there are problems with this recommendation in practice. Having identified predictors with a plausible causal relationship with the dependent variable, there is often no ecological evidence to support one combination of predictors being any more or less valid than any other. Making an a priori judgement as to which candidate models to test also risks introducing bias, and limits the scope of the investigation. Using a candidate set of all possible subsets negates these issues. It also balances the frequency with which each predictor appears within the candidate set, a requirement when model averaging techniques are used (Burnham and Anderson 2002). For these reasons, all possible combinations of predictors were used to generate candidate model sets.

Secondly, Burnham and Anderson oppose the use of arbitrary levels of significance to distinguish between important and unimportant predictors. However, in practice it is useful to be able to distinguish between predictors that have a well supported association with the dependent variable, and those unlikely to have an effect. Any such method must also account for the probability that a given level of importance could have arisen by chance, whether this is implicit in the method, or explicit, as with the use of significance levels. Burnham and Anderson themselves suggest several ways of distinguishing between models, and by extension the predictors they contain: Models that vary by less than two units of Akaike's Information Criterion (AIC) from the best model are deemed to have substantial support, while those that vary by more than 10 have essentially no support (Burnham and Anderson 2002). They also describe the use of a confidence set of supported models, constructed by summing the Akaike weight of each model from largest to smallest, until it equals or exceeds 0.95. Thus the confidence set is the group of models with a 95% probability of including the best approximating model. Here, I use the concept of a null interval to distinguish between important predictors and those with an effect no better than a random variable. This concept has been developed in this thesis from an approach used by Whittingham et al. (2005). The relative importance of a predictor can be assessed by summing the Akaike weight of all models in which that predictor appears. This value can be interpreted as a selection probability, the estimated probability that, of all predictors considered, the predictor in question is in the best approximating model (Whittingham et al. 2005). The null interval represents the distribution of selection probabilities achieved by 1000 randomly generated variables. Predictors with a selection probability exceeding the 950th value of this distribution, when ranked from highest to lowest, were considered well supported. This approach described in greater detail in chapters 2.

1.6. Thesis structure

The data chapters of this thesis are structured as intended for publication. The first two data chapters examine the associations between bats and measures of landscape composition and configuration. Chapter two uses data from the NBMP colony counts to relate roost selection by six bat species to the structure of the landscape surrounding the roost. In particular, I consider the association between roost location and the spatial arrangement of woodland patches. Models are produced at two spatial scales to contrast habitat associations within the 'core' foraging radius of the roost to those measured across the home range of the colony. Chapter three relates the incidence of four bat species along field transects to the structure of the landscape surrounding the transect, using data from the NBMP field survey. Associations with a suite of habitat classes are modelled at a landscape scale. An index of fragmentation that is independent of habitat extent is used to evaluate the independent effects of habitat extent and habitat disaggregation of two focal habitat types: broadleaved woodland and improved grassland. Models are fitted at three spatial scales to examine patterns of scale dependency in the observed relationships. Chapter four examines the use of linear features, such as hedgerows and tree-lines, by four bat species in rural landscapes. Data from the NBMP field survey is used to investigate how bat incidence adjacent to linear features is affected by hedgerow width, tree density, association with water and proximity of woodland. The final chapter summarises and evaluates the findings of the previous chapters in respect to the aims of the thesis, provides conservation recommendations, and presents directions for further work.

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Chapter 2

The effect of landscape scale measures of broadleaved woodland extent and configuration on roost selection by UK bats

Abstract

European landscapes have been transformed by centuries of deforestation and the remaining forest cover is highly fragmented. Broadleaved woodland is an important habitat for European bat species, therefore woodland creation schemes have potential as bat conservation tools. However, the benefits of such schemes are limited by a lack of knowledge of how bats respond to changes in woodland extent and to the spatial arrangement of woodland patches. I use data from a national bat survey to relate roost selection by six UK bat species to the composition and configuration of the landscape surrounding the roost. In particular I examine the association between roost location, woodland proximity and the size of the nearest broadleaved woodland patch. Landscape metrics are measured at two spatial scales selected to approximate the ‘core’ foraging area and the home range of the colony, derived from radio-telemetry studies. For the majority of species, models fitted using metrics of the core foraging area performed better than models fitted using metrics of the home range, although this difference was only significant for *Pipistrellus pipistrellus*. In contrast, roost selection by *Myotis nattereri* was better explained using metrics of the home range. Roost selection by all species was positively associated with either the extent or proximity of broadleaved woodland. Where a positive association existed, the greatest effect of increasing woodland extent was seen between 0-20% woodland cover. *Pipistrellus pipistrellus, Pipistrellus pygmaeus, Rhinolophus hipposideros, Eptesicus serotinus* and *M. nattereri* all roosted closer to broadleaved woodland than would be expected by chance. Across all species 90% of roosts were located within 440m of broadleaved woodland. Roost selection by bats was not affected by the size of the nearest broadleaved patch. These findings suggest that the bat species assessed by this study will benefit from the creation of an extensive network of woodland patches, including small patches, in landscapes with little existing woodland cover.

2.1. Introduction

Habitat destruction and degradation are the primary drivers of biodiversity loss in terrestrial ecosystems (Millennium Ecosystem Assessment 2005; Tilman et al. 1994; Vitousek 1994). Deforestation is one of the principal causes of habitat destruction globally, and has been largely responsible for the transformation of the European landscape (Williams 2000). In the UK, deforestation began with early settlement around 6500 years ago, and extensive forest loss had already occurred by the end of the 15th century. Today forests and woodland cover 12% of the UK, compared to a Europe-wide average of 37%, and the remaining habitat is highly fragmented. However forest cover in the UK is currently increasing, after reaching a low of 5% at the beginning of the 20th century (Forestry Commission 2009). The conservation of forests and the promotion of sustainable forestry are now subject to a number of international agreements (Convention on Biological Diversity 1992, Ministerial Conferences on the Protection of Forests in Europe), and continued reforestation and the promotion of the non-market benefits of woodland, such as biodiversity conservation and amenity use, are UK government policies (Forestry Commission 2004).

The primary policy mechanism for promoting the conservation of woodland in the UK is the provision of grants for woodland creation and management (Forestry Commission 2004). These grants are funded by the EU and UK Department of the Environment, Food and Rural Affairs, as set out in regional Rural Development Programmes. Grants are awarded to woodland managers through national agri-environment schemes and the Forestry Commission’s Woodland Grant Scheme. To satisfy funding, grant applications must meet the priorities set out by the UK Forestry Standard (Forestry Commission 2004). Funding is provided for the creation of woodland totalling 0.25ha or more, with priority given to the creation of larger woodlands or those which buffer or connect existing patches. The use of native species is encouraged.

The biodiversity benefits provided by new woodland creation schemes depend not only on the characteristics of the woodland, such as species composition, stand age, and structural complexity, but also on landscape scale factors such as woodland extent and the spatial arrangement of woodland patches. Almost all European bat species utilise woodland as foraging habitat (Bontadina et al. 2002; Davidson-Watts et al. 2006; Glendell and Vaughan 2002; Kanuch et al. 2008; Mackie and Racey 2007; Meschede and Heller 2000; Nicholls and Racey 2006b; Robinson and Stebbings 1997; Russ et al. 2003; Russ and Montgomery 2002; Vaughan et al. 1997; Walsh and Harris 1996). Woodland reforestation policy therefore has the potential to benefit bat conservation. However, the response of bats to increasing woodland extent has been studied only for a small range of species. Oakeley and Jones (1998) found a significantly greater proportion of deciduous woodland around *Pipistrellus pygmaeus* roosts than around random points, and Sattler et al. (2007) demonstrated that a series of factors describing *P. pygmaeus* incidence along driven transects were positively correlated with the extent of open woodland, although the form of the relationship was not described. There is also little knowledge regarding how bats are affected by the spatial distribution of woodland patches in European landscapes. The occurrence of *Plecotus auritus* and *Myotis brandti* on forested islands in Lake Mälaren in Sweden was negatively affected by the degree of isolation from similar habitat (Ekman and de Jong 1996), suggesting that increasing distances between woodland fragments in the agricultural matrix may have a similar effect. Patch size may also affect bat distribution. Bat species characterised as woodland specialists, which depend on woodland for both roosting and foraging habitat, are found to occur more frequently in larger woodland patches, however bat species that predominantly roost in man-made structures appear less affected by patch size (Lesinski et al. 2007).

In this study I use data from a nationwide bat survey to investigate roost selection by six UK bat species in relation to patterns of habitat configuration and landscape composition measured at different spatial scales. In particular I assess 1) the relationship between roost location and the proportion of broadleaved woodland in the landscape, the proximity of broadleaved woodland and the size of the nearest broadleaved patch, and discuss how these associations are reflected by current woodland reforestation policy, as underpinned by the UK Forest Standard, and 2) the scale at which associations between roost location and landscape composition are strongest. Radio-telemetry studies suggest that most bat species focus concentrate foraging effort close to the roost. It is therefore predicted that roost location will be better predicted by habitat composition measured within this ‘core’ foraging area than by the habitat composition of the home-range of the colony. Sample radii approximating the core and home-range areas of the species in this study were derived from previous radio-telemetry studies of bat distribution.

2.2. Methods

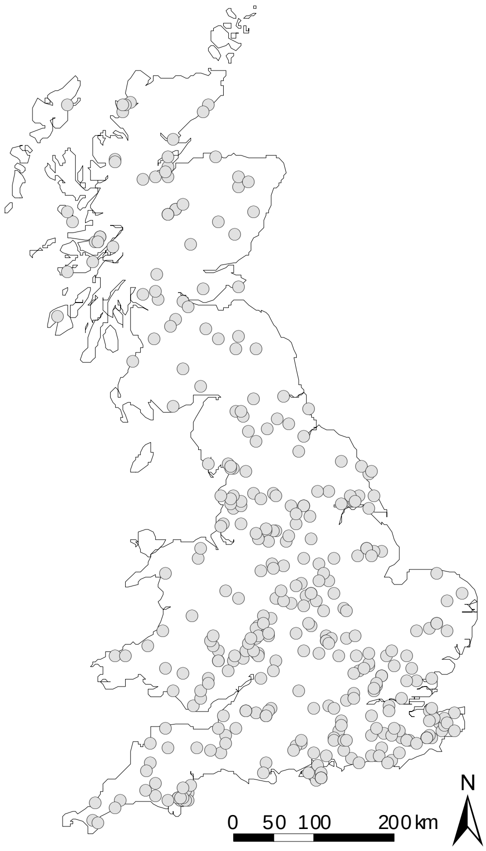
2.2.1. Study design

Data on the location of bats roosts was available from the National Bat Monitoring Programme (NBMP) Summer Colony Counts, part of a suite of surveys designed to monitor bat population trends in the UK (Walsh et al. 2001). Volunteer surveyors identify a roost and count emerging bats on two separate evenings between late May and early June. Surveys are carried out in early summer to coincide with the period of peak occupancy and are repeated annually. Data were available for six species: *Pipistrellus pipistrellus, P. pygmaeus, Rhinolophus hipposideros, P. auritus, Eptesicus serotinus* and *Myotis nattereri*. Four of these species (*P. pipistrellus, P. pygmaeus, P. auritus* and *M. nattereri*) have a nationwide distribution, while *R. hipposideros* is restricted to Wales and south-west England, and *E. serotinus* to southern and eastern England. Range maps and a description of the ecology of each species are presented in chapter one. NBMP Colony Counts began in 1995, with additional data for *R. hipposideros* available from a comparable survey begun in 1991. As of 2007, 2382 volunteers have taken part and 2050 roost locations have been recorded.

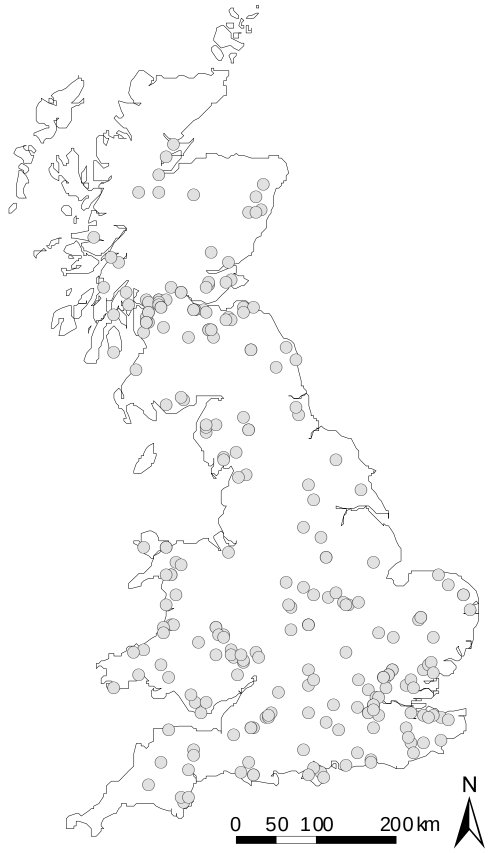
Roosts were selected for this study if they were occupied for at least one year during the period 1991-2007 (Fig. 2.1, *P. pipistrellus* n = 359, *P. pygmaeus* n = 246, *R. hipposideros* n = 235, *P. auritus* n = 129, *E. serotinus* n = 91, and *M. nattereri* n = 69). Roost location was determined by matching the roost address to a 12 figure grid reference using Ordnance Survey MasterMap data. As roosts were self-selected by volunteers they do not represent a random sample of bat roosts. All roosts were located in manmade structures, 73% being in private homes. Of the six study species, five are though to roost predominantly in man-made structures. However *M. nattereri* is also found commonly in tree cavities (Kanuch 2005; Smith and Racey 2005), and *P. pipistrellus, P. pygmaeus, P. auritus* and *E. serotinus* will make use of cavities in trees and rocks, especially in areas of low building densities. It is unlikely that the foraging preferences of bats roosting in man-made structures differ from those roosting in natural structures, so habitat associations demonstrated in this study are likely to be generally applicable to the species. However, the distribution of roosts followed patterns of building density (Fig. 2.1) so habitats that generally contain a low density of buildings, such as wetlands or upland heath, or which were rare within the species range, were underrepresented in this study. Such habitats, for which no association could be demonstrated, should not be considered unimportant to bats.

It is also possible that roosts reported as part of the NBMP Colony Counts are the larger and hence more readily noticed roosts. In general, female bats roost in larger numbers than males, which form smaller bachelor colonies or roost alone (Dietz et al. 2009), so the roosts sampled here are probably largely maternity roosts dominated by females. Previous studies suggest that the high energetic demands of pregnancy and lactation restrict reproductive females to optimal roosting and foraging locations, while non-reproductive females and males are able to forage at higher elevations and in marginal habitat (Cryan et al. 2000; Dietz et al. 2006; Mackie and Racey 2007; Senior et al. 2005). As such, the habitat associations demonstrated by female bats are likely to represent optimal habitat requirements for the species as a whole, but not the full range of habitats utilised by all individuals.

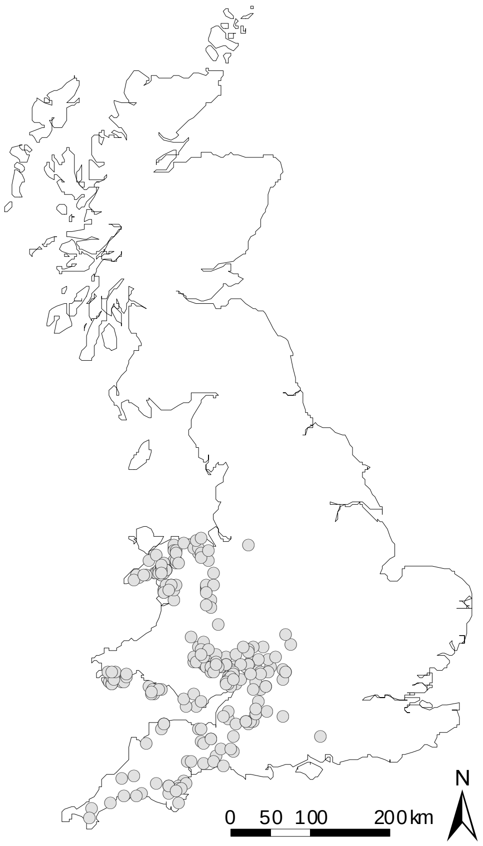
Pipistrellus pipistrellus



Pipistrellus pygmaeus



Rhinolophus hipposideros



Plecotus auritus

Eptesicus serotinus

Myotis nattereri

Figure 2.1 Distribution of roosts used in this study, reported by voluntary surveyors as part of the National Bat Monitoring Programme Summer Colony Counts between 1995-2007. Species range maps are presented in chapter 1.

This study employed a ‘used-available’ analysis design, which quantifies the degree to which habitat surrounding roosts deviates from that which is available (Manly et al. 2002). To ensure a valid comparison between roosts and the available landscape, the distribution of locations used to sample the available landscape must follow the same geographical distribution as the sample of roosts. This was achieved by pairing each roost with a building chosen at random from within a 40km radius of the roost. The 40km radius was chosen to encompass the largest possible area sharing similar climate parameters, as described by the CRU TS 2.1 climate grid (Mitchell and Jones 2005). Selecting either a random address or a random location would have biased the available sample towards high or low building densities, respectively. To avoid this, the UK was divided into six building density bands, constructed using the urban and suburban habitat classes defined by the CEH Landcover Map 2000 (see section 2.2.2.). The density band within which the roost fell was identified, and a random point was generated within the same density band, and within a 40km radius of the roost (using the Hawth's Tools extension for ArcGIS, Beyer 2004). The building closest to this point was identified using OS MasterMap, and used to form the sample of the available landscape.

2.2.2. Habitat data

Potential predictors of bat roost distribution were identified from previous studies of habitat associations (Glendell and Vaughan 2002; Kanuch et al. 2008; Russ and Montgomery 2002; Sattler et al. 2007; Vaughan et al. 1997; Walsh and Harris 1996), and reviewed with respect to the availability of nationwide datasets that described these predictors with sufficient resolution and accuracy.

Radiotracking studies demonstrate that many bat species concentrate their foraging activity within 'core areas' of their home range, usually within 1-2km of the roost (Bontadina et al. 2002; Entwistle et al. 1996; Fuhrmann and Seitz 1992; Harbusch 2003; Simon et al. 2004; Trappmann and Clemen 2001). To explore whether associations in this core area differ from those across the home range as a whole, data were extracted at two spatial scales: (i) from within 1km of each sample point and (ii) from an area equivalent to the home range of the species, defined by a radius corresponding to the greatest straight line distance a radio tracked bat has been recorded from its roost (table 2.1.). Models were fitted separately for each species, at each spatial scale.

Table 2.1. Maximum foraging radii, used as a proxy for home range in the analysis, and sample sizes across all studies consulted.

Species	Maximum foraging radius (km)	No. roosts where captures took place	Bats tracked
R. hipposideros	4 [1,2]	2	9
P. pipistrellus	4 [3,4,5]	5	45
P. pygmaeus	3 [3,5]	2	35
Plecotus auritus	3 [6,7]	8	24
E. serotinus	7 [8,9,10,11]	11	80
M. nattereri	4 [12,13]	6	21

1. Bontadina et al. 2002; 2. Holzhaider et al. 2002; 3. Davidson-Watts and Jones 2006; 4. Feyerabend and Simon 2000; 5. Nicholls and Racey 2006a; 6. Fuhrmann and Seitz 1992; 7. Entwistle et al. 1996; 8. Robinson and Stebbings 1997; 9. Catto et al. 1996. One observation of *E. serotinus* recorded 11.5km from it's roost was discarded as exceptional, being almost twice as far as the next greatest distance recorded in the study; 10. Harbusch 2003; 11. Simon et al. 2004; 12. Trappmann and Clemen 2001; 13. Meschede and Heller 2000.

Habitat data were derived from the Landcover Map 2000 (LCM2000), produced as part of the Countryside Survey 2000 (CS2000). LCM2000 classifies the entire UK into a 25 x 25m raster grid of 16 habitat classes, based on spectral reflectance parameters derived from satellite images (Fuller et al. 2002). Data for LCM2000 were collected between 1998 and 2001. 57% of roosts used in this study were confirmed to be active between 1998-2001. The remaining roosts may have been active during this period, but were not monitored. Between 1998 and 2007 the change in UK land mass under the most extensive land cover types was considered small enough for LCM2000 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, change in urban areas not reported, Carey et al. 2008). Comparison with the field survey element of CS2000, which surveyed 569 one-kilometre squares in detail, suggests that LCM2000 identifies habitat classes with an accuracy of *c*. 85% (Fuller et al. 2002). Of key habitats; broadleaved woodland, coniferous woodland, arable land and grassland were well classified, while the distinction between improved and semi-natural grassland was less robust due to difficulties defining a cut off point in an essentially continuous scale of improvement (Fuller et al. 2002). However, the marked ecological differences between improved and semi-natural grassland warranted considering them here as separate categories. At each spatial scale, the proportion of each LCM2000 habitat class was extracted, and for selected habitat classes (positively associated with roost location reported in previous studies), mean patch area, patch density, patch edge density, mean perimeter-area ratio and mean nearest neighbour distance were calculated using FRAGSTATS (McGarigal et al. 2002). Sea was excluded from calculations. Distance from the sample location to the nearest patch of broadleaved/mixed woodland (minimum patch size of one pixel = 625m^2), and the size of the nearest broadleaved/mixed woodland patch was calculated using ArcGIS 9.1 (ESRI, Redlands, CA). LCM2000 excludes features less than 50m in length or 0.5ha in area, making identification of small water bodies problematic. Distance from the sample location to the nearest water body was therefore measured using a vector layer extracted from OS Land-line.Plus, locating the position of all rivers, streams, drains, canals, lakes, reservoirs and ponds to within 0.4-3.5m. Elevation of the sample location was obtained from the OS Panorama digital terrain model. This provides elevation to the nearest metre with 50m x 50m resolution.

2.2.3. Statistical analysis

From the large number of predictors generated (table 2.5, Appendix I), predictors appearing in fewer than 10% of observations per species were excluded as having insufficient variation. Colinearity was evaluated among the remaining set. Pairs of predictors with squared correlation coefficients >0.5 were considered unacceptably correlated (Freckleton 2002). All landscape scale measures of habitat configuration (mean patch area, patch density, patch edge density, mean perimeter-area ratio and mean nearest neighbour distance) were strongly correlated with habitat extent. They were removed from the analysis in favour of the proportion of the habitat in landscape, which is most often a stronger predictor of species incidence than measures of landscape configuration (Fahrig 2003). Nine predictors were retained for modelling (table 2.2.).

Table 2.2. Explanatory predictors used to model bat roost distribution.

Predictor	Units	Description
Arable[1]	%	Proportion of cereals, horticulture, perennial crops or unknown arable crops. Also includes freshly ploughed land and rotational setaside
Broadleaved[1]	%	Proportion of broad-leaved woodland or mixed woodland with canopy cover greater than 20%, or scrub with cover greater than 30%.
Coniferous[1]	%	Proportion of coniferous woodland or plantation with canopy cover greater than 20%
Improved[1]	%	Proportion of improved grassland, including setaside grass
Semi-natural[1]	%	Proportion of rough, calcareous and acid semi-natural grasslands and bracken
Distbroad[1]	km	Euclidian distance from sample point to edge of nearest broadleaved/mixed woodland patch
Areabroad[1]	km^2	Area of the nearest broadleaved/mixed woodland patch
Distwater[2]	km	Euclidian distance from sample point to nearest water body
Elevation[3]	m	Elevation of sample point

1. LCM2000
2. OS Landline.Plus
3. OS Panorama DEM.

Conditional logistic regression was used to account for the paired nature of the data (Compton et al. 2002). The used-available design does not provide a truly binomial response variable, as bat roosts can be found in both the present and available sample. In this situation, logistic regression has been shown to produce valid parameter estimates, with the caveat that predicted probabilities of occurrence can not be directly interpreted, instead they represent a value that is proportional to the probability of occurrence (Johnson et al. 2006; Manly et al. 2002; Pearce and Boyce 2006).

Model evaluation and parameter estimation was performed using the multi-model inference techniques described by Burnham and Anderson (2002). All species, with the exception of *P. pipistrellus*, had a ratio of observations to predictors of approximately 40 or below (15.6-46.6), therefore AIC corrected for small sample size, AIC_c, was used in all modelling. All possible combinations of the nine predictors were modelled, creating a candidate set of 511 models. Regression coefficients and unconditional standard errors were weighted by the Akaike weight of each model, then averaged across the candidate set (Burnham and Anderson 2002).

The prediction accuracy of the averaged models was assessed using receiver operating characteristic (ROC) curves. Predictive power is represented by the area under the curve (AUC), with 1 equating to perfect classification and 0.5 representing prediction no better than chance. ROC curves may underestimate the accuracy of presence-available models, as the response variable is not truly binomial (Boyce et al. 2002). However, they are useful for comparing the predictive accuracy among models, and there is not yet a commonly adopted alternative (although see Johnson et al. 2006). AUC values were compared between models using a chi-square test of the hypothesis that $AUC_1=AUC_2$, adjusted for independent samples, as described by DeLong et al. (1988).

To assess the relative importance of each predictor to the model, the Akaike weight of all models in which that predictor appeared was summed across the candidate set. This produced a selection probability; the estimated probability that, of all predictors considered, the predictor in question is in the best approximating model (Whittingham et al. 2005). Poor predictors may not have selection probabilities close to zero. To identify predictors unlikely to be associated with the dependent variable, a random variable (range 0-1) was generated and added to the original set of predictors, following Whittingham et al. (2005). All possible combinations of predictors were modelled and the selection probability of the random variable calculated. This process was repeated 1000 times, creating a distribution of possible null selection probabilities specific to the dataset (for an example see Fig. 2.2.). A ‘95% null-interval’ was determined from this distribution. The lower bound of this distribution was defined by the smallest null selection probability and the upper limit (95% $\Sigma\, w_{null}$) was defined as the 950th value when ranked from lowest to highest. This interval represents the range which contained the selection probability of the random variable in 95% of model-averaging runs. Predictors with selection probabilities within the null interval were considered weakly supported. Statistical analysis was carried out using custom written routines in STATA 8 (StataCorp, TX).

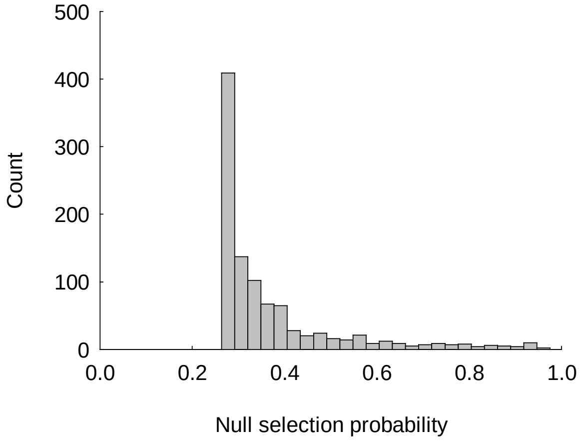


Figure 2.2. Frequency distribution of selection probabilities calculated for a randomly generated variable over 1000 model-averaging runs. The selection probability of the random variable was assessed within a candidate set of models relating *R. hipposideros* roost location to the landscape within 1km of the roost.

2.3 Results

The ability of the averaged models to correctly identify landscapes containing roosts varied between species (table 2.3). The strongest association between roost location and the surrounding landscape was shown by *R. hipposideros*, *P. pygmaeus*, *P. auritus* and *M. nattereri,* with AUC scores between 0.805-0.877, representing reasonable predictive accuracy (Swets 1988). Prediction accuracy of *E. serotinus* models was lower but still reasonable (AUC 0.784 and 0.744), while *P. pipistrellus* demonstrated the weakest association between roost location and the surrounding landscape, with model AUC scores of 0.708 and 0.670. All candidate models with cAIC < Δ_i 2 are shown in table 3.6, appendix II.

Table 2.3 AUC scores of models fitted using habitat predictors extracted from within 1km of the sample point, and from within a scale equivalent to the home-range of the species. Also reported are the results of a chi-square test of the equality of AUC scores at the two scales.

	1km sample radius		HR sample radius			
Species	AUC	SE	AUC	SE	χ^2	*p*
P. pipistrellus	0.708	0.019	0.670	0.200	6.66	0.010
P. pygmaeus	0.843	0.018	0.841	0.018	0.03	0.854
R. hipposideros	0.823	0.190	0.810	0.020	1.90	0.169
P. auritus	0.830	0.025	0.805	0.027	2.59	0.108
E. serotinus	0.784	0.033	0.744	0.036	2.20	0.138
M. nattereri	0.835	0.035	0.877	0.028	2.54	0.111

At least one broadleaved woodland metric was associated with roost location for all study species (table 2.4, fig. 2.3 and 2.4). *Plecotus auritus* roosts were more likely to be located in landscapes with a greater proportion of broadleaved woodland (Σw_{i1km} = 0.999, Σw_{iHR} = 0.986), while *E. serotinus* and *M. nattereri* selected roosts that were located closer to broadleaved woodland than would be expected given the availability of broadleaved patches in the landscape ($\Sigma w_i \geq 0.983$, fig. 2.3). *Pipistrellus pipistrellus, P. pygmaeus* and *R. hipposideros* roosts were positively associated with the extent of broadleaved woodland and were also located closer to broadleaved woodland than would be expected ($\Sigma w_i \geq 0.813$). The greatest effect of increasing broadleaved woodland extent within a radius of 1km on roost selection by *P. pipistrellus, P. auritus* and *R. hipposideros* occurred at proportions between 0% and approximately 20% broadleaved cover (fig. 2.4). For *P. pygmaeus* the effect of changing proportion of broadleaved woodland within 1km remained constant across the range of woodland extents tested. Across all species, roosts were located on average 183m ± 482 SD from the nearest patch of broadleaved woodland, whereas randomly selected building were located on average 354m ± 618 SD from broadleaved woodland. 90% of all roosts were within 440m of broadleaved woodland. There was little support for an association between roost location and the size of the nearest broadleaved woodland patch in any model. The selection probability of this predictor was low ($\Sigma w_i < 0.450$) and within the 95% null interval in every model. Of the five habitat types for which proportion measures were calculated, broadleaved woodland had the strongest association with roost location for *P. pipistrellus, P. pygmaeus, R. hipposideros* and *P. auritus.* No species demonstrated a strongly supported association with the extent of coniferous woodland, however a positive association between *P. auritus* and coniferous woodland received moderate support. The selection probability of coniferous woodland came close to exceeding the null interval when extracted from within 1km of the sample point (Σw_i = 0.638, 95% Σw_{null} = 0.689).

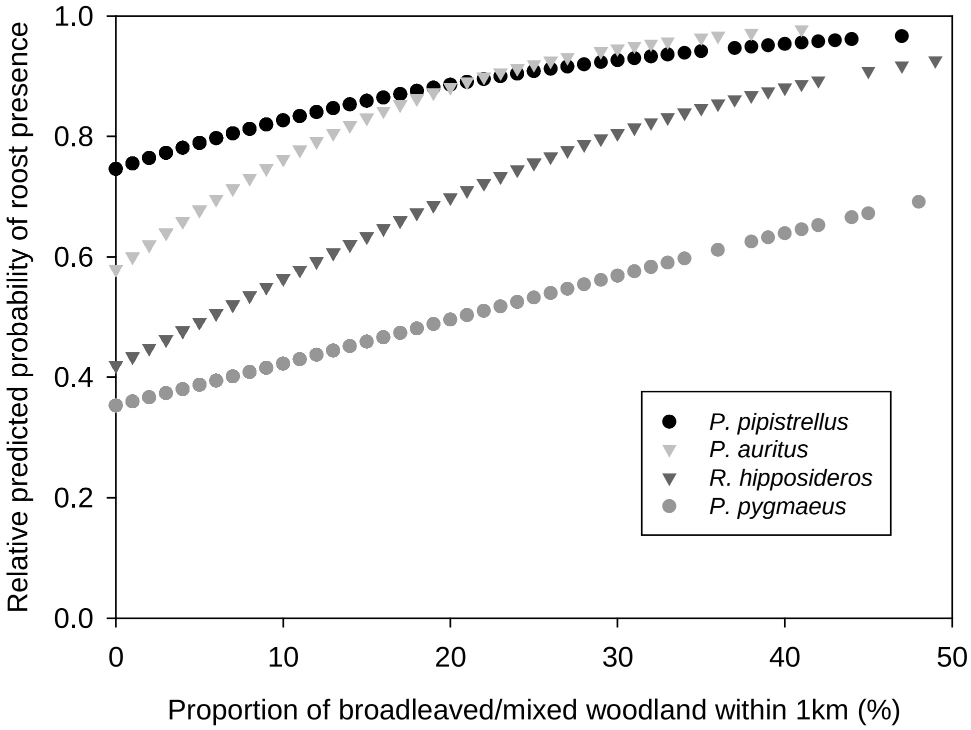


Figure 2.3 The relative probability of roost presence in relation to the proportion of broadleaved woodland within 1km of the sample point, shown for species that demonstrated a supported association with this predictor at the 1km spatial scale.

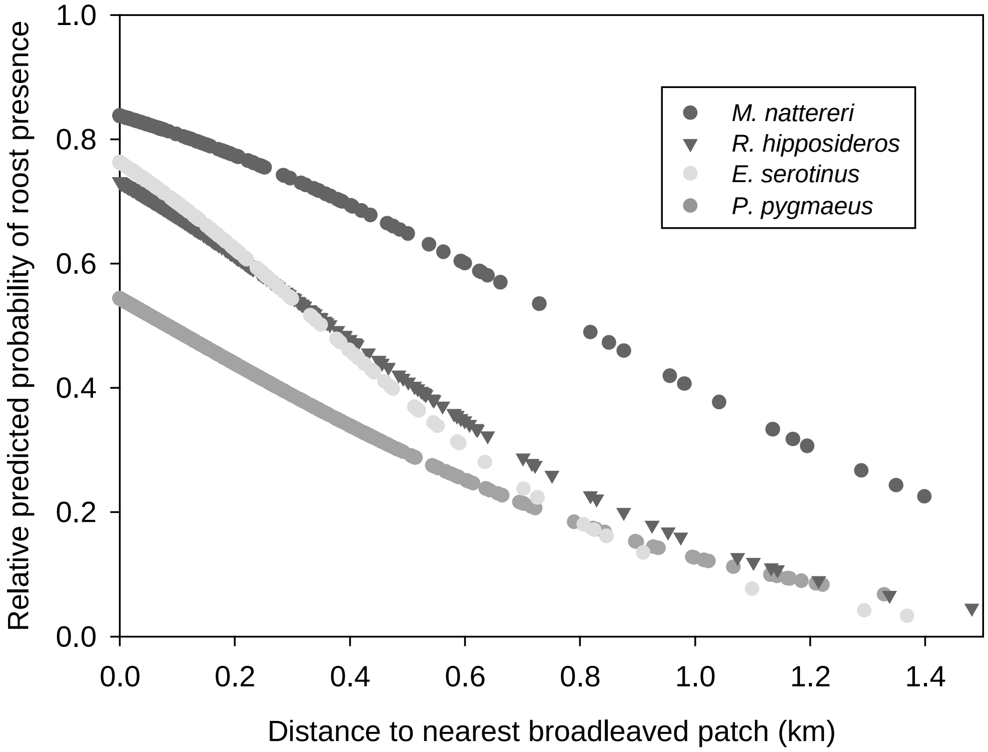


Figure 2.4 The relative probability of roost presence in relation to the distance to the nearest broadleaved woodland patch, shown for species that demonstrated a supported association for this predictor when modelled alongside landscape composition measured within 1km of the sample point.

All species except *R. hipposideros* selected roosts in landscapes with a greater proportion of improved grassland at one or both of the spatial scales tested ($\Sigma w_i \geq 0.781$ where predictor exceeded the null interval, fig 2.5). Increasing the proportion of improved grassland within 1km had the greatest effect on roost location between 0% and approximately 40% improved grassland cover for *P. pipistrellus, P. auritus* and *E. serotinus*. For *P. pygmaeus* the effect of increasing the proportion of improved grassland within 1km remained constant across the range of extents tested. Roost selection by *M. nattereri* was positively associated with the proportion of semi-natural grassland at the home-range scale ($\Sigma w_{iHR} = 0.994$), however support for an association between the remaining species and this habitat type was equivocal, as the selection probability of semi-natural grassland failed to exceed the null interval in all other models at either spatial scale. Two species, *P. pipistrellus* and *M. nattereri* were more likely to roost in landscapes with a greater proportion of arable land ($\Sigma w_i \geq 0.840$). At the spatial scales considered, no habitats were avoided.

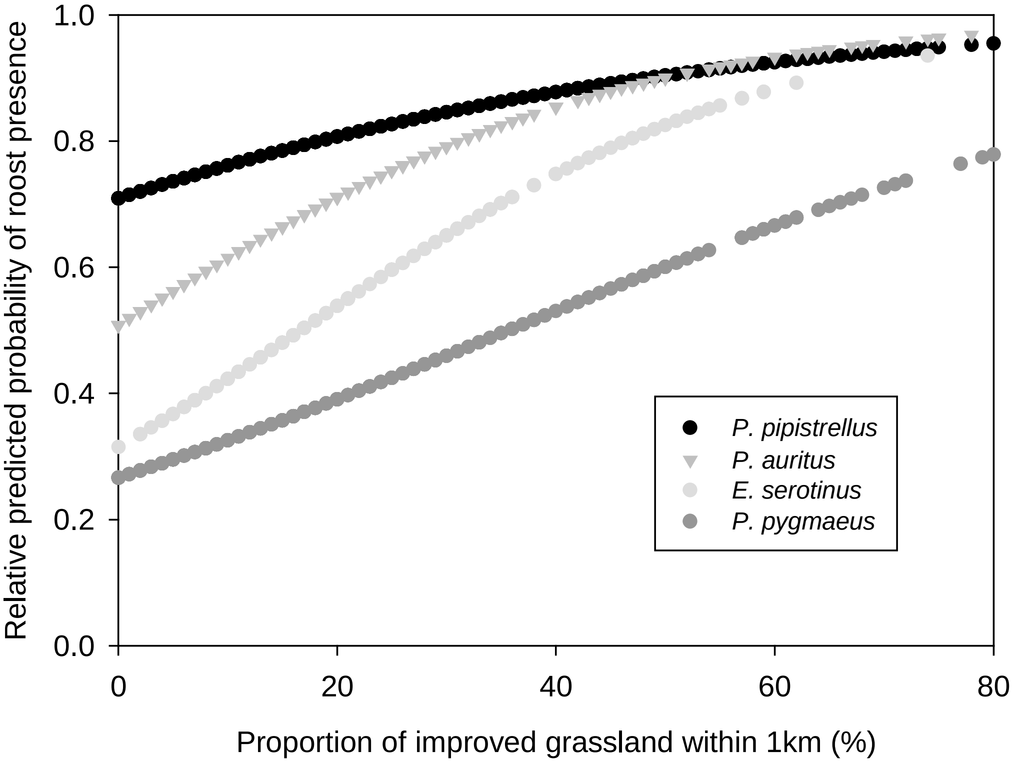


Figure 2.5 The relative probability of roost presence in relation to the proportion of broadleaved woodland within 1km of the sample point, shown for species that demonstrated a supported association with this predictor at the 1km spatial scale.

An association between *P. pygmaeus* roost location and the distribution of water features received strong support at both spatial scales. *Pipistrellus pygmaeus* was more likely to roost closer to water than would be expected given the availability of water features in the landscape (Σw_{i1km} = 0.930, Σw_{iHR} = 0.956). On average *P. pygmaeus* roosts were located 0.1km ± 0.1 SD from the nearest water feature, compared to an average distance of 0.15km ± 0.2 SD between randomly selected buildings and the nearest water. An association between distance to the nearest water features and *P. auritus* roost location received moderate support when tested alongside measures of habitat proportion extracted at the 1km scale, and strong support when tested alongside was measures of habitat proportion extracted at the home-range scale (Σw_{i1km} = 0.617, 95% $\Sigma w_{null\ 1km}$ = 0.687, Σw_{iHR} = 0.721, mean distance from roost to water feature 0.1km ± 0.12D, mean distance from randomly selected building to water feature 0.16km ± 0.20 SD). Both *P. pygmaeus* and *P. auritus* was also more likely to roost at lower elevations ($\Sigma w_i \geq 0.928$). The mean elevation of *P. pygmaeus* and *P. auritus* roosts was 69m ± 54 SD and 87m ± 73 SD above sea level, respectively, compared to the mean elevation of randomly selected buildings of 112m ± 107 SD for buildings paired with *P. pygmaeus* roosts, and 113m ± 104 SD for buildings paired with *P. auritus* roosts. All other associations between roost location and the explanatory predictors tested here received weak or no support.

Table 2.4 Averaged coefficient estimates, unconditional standard errors and selection probabilities ($\Sigma\ w_i$) calculated over a candidate set of models relating roost location to measures of landscape composition and configuration. For predictor definitions see table 2.2.

	1km sample radius			HR sample radius		
Predictor	ß	SE	$\Sigma\ w_i$	ß	SE	$\Sigma\ w_i$
P. pipistrellus						
Arable	0.015	0.006	0.944	0.013	0.006	0.840
Broadleaved	0.049	0.012	>0.999	0.043	0.016	0.948
Coniferous	0.008	0.007	0.488	0.005	0.006	0.340
Improved	0.027	0.007	0.999	0.014	0.007	0.808
Semi-natural	0.007	0.005	0.538	0.001	0.004	0.306
Distbroad	-0.080	0.083	0.443	-0.278	0.152	0.830
Areabroad	-0.010	0.017	0.307	-0.011	0.019	0.315
Distwater	-0.345	0.299	0.503	-0.561	0.366	0.663
Elevation	9.36E-05	1.39E-04	0.371	5.11E-05	1.17E-04	0.300
Mean $\Sigma\ w_{null}$			0.382			0.379
95% $\Sigma\ w_{null}$			0.746			0.749
P. pygmaeus						
Arable	0.005	0.005	0.443	0.001	0.003	0.297
Broadleaved	0.029	0.015	0.813	0.057	0.023	0.926
Coniferous	0.002	0.005	0.291	0.007	0.009	0.367
Improved	0.028	0.010	0.984	0.020	0.011	0.781
Semi-natural	0.010	0.008	0.525	0.015	0.011	0.616
Distbroad	-2.108	0.659	0.997	-2.177	0.580	>0.999
Areabroad	-0.004	0.033	0.277	-0.036	0.049	0.348
Distwater	-2.175	0.906	0.930	-2.213	0.864	0.956
Elevation	-0.010	0.002	>0.999	-0.011	0.003	>0.999
Mean $\Sigma\ w_{null}$			0.376			0.375
95% $\Sigma\ w_{null}$			0.720			0.733
R. hipposideros						
Arable	0.009	0.008	0.504	0.008	0.008	0.458
Broadleaved	0.058	0.019	0.993	0.049	0.023	0.837
Coniferous	-0.002	0.006	0.300	-0.005	0.009	0.316
Improved	0.007	0.006	0.509	0.010	0.008	0.606
Semi-natural	-0.012	0.009	0.623	-0.007	0.008	0.459
Distbroad	-2.729	0.885	0.994	-3.936	0.858	>0.999
Areabroad	-0.033	0.064	0.300	0.101	0.102	0.445
Distwater	-0.133	0.222	0.312	-0.225	0.270	0.372
Elevation	-2.88E-05	6.66E-05	0.281	-9.86E-06	6.03E-05	0.269
Mean $\Sigma\ w_{null}$			0.371			0.372
95% $\Sigma\ w_{null}$			0.722			0.701

Table 2.4 continued

	1km sample radius			HR sample radius		
Predictor	ß	SE	Σ w_i	ß	SE	Σ w_i
P. auritus						
Arable	-0.001	0.004	0.306	-0.005	0.006	0.405
Broadleaved	0.085	0.022	0.999	0.076	0.025	0.986
Coniferous	0.018	0.012	0.638	0.010	0.011	0.428
Improved	0.043	0.015	0.990	0.035	0.015	0.902
Semi-natural	0.013	0.011	0.542	0.014	0.012	0.509
Distbroad	-0.023	0.110	0.265	-0.160	0.181	0.392
Areabroad	-0.102	0.119	0.371	-0.030	0.076	0.279
Distwater	-1.197	0.853	0.617	-1.421	0.856	0.721
Elevation	-0.010	0.003	0.984	-0.007	0.003	0.928
Mean Σ w_{null}			0.370			0.366
95% Σ w_{null}			0.689			0.694
E. serotinus						
Arable	0.005	0.007	0.386	0.002	0.006	0.279
Broadleaved	-0.006	0.009	0.326	0.022	0.021	0.440
Coniferous	-0.064	0.053	0.543	-0.001	0.025	0.269
Improved	0.047	0.017	0.965	0.075	0.032	0.909
Semi-natural	-2.98E-04	0.007	0.264	0.013	0.017	0.334
Distbroad	-3.328	1.090	0.998	-2.933	1.008	0.995
Areabroad	0.017	0.038	0.287	-0.007	0.030	0.274
Distwater	0.083	0.225	0.277	-0.016	0.198	0.267
Elevation	-0.002	0.002	0.411	-0.003	0.002	0.516
Mean Σ w_{null}			0.370			0.376
95% Σ w_{null}			0.703			0.733
M. nattereri						
Arable	0.023	0.017	0.605	0.078	0.034	0.950
Broadleaved	0.016	0.021	0.399	-0.009	0.017	0.285
Coniferous	-0.002	0.011	0.274	0.008	0.017	0.293
Improved	0.027	0.020	0.639	0.142	0.061	0.994
Semi-natural	0.019	0.020	0.458	0.076	0.044	0.771
Distbroad	-2.059	0.801	0.983	-3.030	0.996	0.999
Areabroad	-0.233	0.250	0.449	-0.059	0.116	0.289
Distwater	-0.400	0.591	0.323	-0.258	0.525	0.287
Elevation	-0.002	0.002	0.410	0.002	0.002	0.349
Mean Σ w_{null}			0.375			0.379
95% Σ w_{null}			0.749			0.760

2.3.1. The effect of measurement scale on landscape scale habitat associations

The association between the location of *P. pipistrellus* roosts and measures of landscape composition and configuration was strongest within 1km of the roost (table 2.3). Landscapes containing *P. pipistrellus* roosts were identified with significantly better accuracy using data extracted from within 1km of the sample location than from within the home range (AUC_{1km} = 0.708 ± 0.019 SE, AUC_{HR} = 0.670 ± 0.200 SE, χ^2 = 6.66, *p* = 0.010), although associations at both spatial scales were relatively weak when compared to the other study species. The effect of all three strongly supported habitat associations (with arable, broadleaved woodland and improved grassland) weakened at the larger spatial scale (table 2.4). Landscapes containing roosts of *R. hipposideros, P. auritus* and *E. serotinus* were also identified more accurately using data extracted from within 1km, however the difference between the two spatial scales was not significant (table 2.3). The ability of the averaged model to identify landscapes containing *P. pygmaeus* roosts was virtually identical at both spatial scales (AUC_{1km} = 0.843± 0.018 SE, AUC_{HR} = 0.841± 0.018 SE, χ^2 = 0.03, *p* = 0.854). The effect of the proportion of broadleaved woodland on roost selection was weaker at the larger spatial scale, but the effect of improved grassland was slightly stronger. In contrast to the other species tested, landscapes containing *M. nattereri* roosts were identified more accurately using data from within the home-range of the roost. The difference was not significant (AUC_{1km} = 0.835 ± 0.035 SE, AUC_{HR} = 0.877 ± 0.028 SE, χ^2 = 2.54, *p* = 0.111), however associations with measures of landscape composition were only supported at the larger spatial scale. The effect of these habitats weakened considerably when using proportions calculated within 1km of the roost, and no measure of landscape composition exceeded the 95% null interval.

2.4 Discussion

2.4.1. Roost selection by UK bats

Roost selection by all six bat species considered in this study displayed a positive association with broadleaved woodland, and all but one species displayed a positive association with the proportion of improved grassland in the landscape. The proportion of arable and semi-natural grassland was associated with roost selection by fewer species (two species and a single species, respectively), and no species demonstrated a strongly supported association with the proportion of coniferous woodland.

The strength of association between roost location and landscape structure (both composition and configuration) at both the 1km and larger home-range scales was markedly weaker for *P. pipistrellus* than the other species tested. *Pipistrellus pipistrellus* is by far the most adaptable British bat, foraging in a wide range of habitats (Davidson-Watts et al. 2006; Russ and Montgomery 2002; Russo and Jones 2003) and tolerant to deviations from its optimal requirements (Sattler et al. 2007). Such flexible habitat requirements may explain the poor predictive accuracy of *P. pipistrellus* models.

2.4.2. Associations with the extent and spatial arrangement of broadleaved woodland

Either the extent or distribution of broadleaved woodland was associated with the location of roosts of all species tested in this study. This is in agreement with previous studies of bat habitat-associations, which suggest forest distribution is the most important determinate of bat distribution in temperate regions (Racey and Entwistle 2003), and corresponds with previous studies of roost selection by *P. pipistrellus, P. auritus*, and *R. hipposideros* which showed these species selected roosts closer to broadleaved woodland, and in areas with a greater proportion of broadleaved woodland, than would be expected if roost selection was random (Entwistle et al. 1997; Jenkins et al. 1998; Reiter 2004). Many species of bats roost in the cavities formed in mature and senescent broadleaved trees, so an association with broadleaved woodland may be explained by the availability of suitable roost structures. However, species that predominantly roost in man-made structures also show strong associations with the proportion of broadleaved woodland (Bontadina et al. 2002; Davidson-Watts et al. 2006; Nicholls and Racey 2006b; Vaughan et al. 1997). Broadleaved woodland provides a complex three dimensional habitat structure, and also has the capacity to act as a wind break in otherwise exposed environments. Both these characteristics increase insect abundance and diversity (Lewis and Dibley 1970; Merckx et al. 2010; Verboom and Huitema 1997; Verboom and Spoelstra 1999), and may therefore enhance landscape quality for bats. The habitat vertical of broadleaved woodland may also offer bats shelter from the elements and protection from aerial predators (Limpens et al. 1989; Verboom and Spoelstra 1999).

Five out of the six study species selected roosts that were closer to broadleaved woodland than would be expected by chance. This may be the result of a need to maximise foraging efficiency, or may reflect the increased vulnerability of bats to diurnal predators as they emerge at dusk (Avery 1986; Duvergé et al. 2000). *Plecotus* *auritus* was the only species for which roost location was not associated with the distance to the nearest woodland patch. However, an effect of woodland proximity was demonstrated in previous studies of both *P. auritus* roost selection (Entwistle et al. 1997) and foraging patch selection (Ekman and de Jong 1996). Given the strong association with woodland extent seen here (the greatest in terms of effect size of all species tested) it seems likely that the spatial distribution of woodland will have an effect on the distribution of *P. auritus*. 90% of all roosts were within 440m of broadleaved woodland, suggesting that bats are unwilling to travel further to reach suitable foraging habitat.

Despite strongly supported associations with woodland proximity, none of the species tested showed an association between roost location and the size of the nearest broadleaved woodland patch. Although the effect of patch size has been investigated extensively in tropical regions (Gorresen et al. 2005; Klingbeil and Willig 2009; Loayza and Loiselle 2009), relatively few studies have addresses the effect of patch size on bats in European landscapes. Lesinski et al (2007) found the effect of patch size on bat incidence within forest patch ‘islands’ in Poland differed among species, with species dependent on tree roosts most likely to be negatively affected by decreasing patch size. The six species tested in this study all roost in man-made structures, and additionally they can all be characterised as ‘edge specialists’ (Schnitzler and Kalko 2001), showing a greater association with woodland edge and open canopy woodland than closed canopy woodland interior (Kanuch et al. 2008; Kusch et al. 2004; Nicholls and Racey 2006b). Small woodland patches may therefore provide suitable foraging habitat for these species, and as such their distribution may be little affected by decreasing patch size. However, further research into the use of woodland patches in temperate agricultural landscapes is needed to confirm this expectation.

2.4.3 Associations with landscape composition

Improved grassland was positively associated with roost selection by all species except *R. hipposideros*. Studies that quantify bat incidence within discrete habitat patches have found *P. pygmaeus* and *P. pipistrellus* occur less frequently within improved grassland than would be expected by chance (Nicholls and Racey 2006b; Russ and Montgomery 2002; Sattler et al. 2007; Walsh and Harris 1996). In contrast *E. serotinus* is positively associated with grassland habitats, particularly improved cattle pasture where livestock dung is present (Catto et al. 1996; Robinson and Stebbings 1997; Vaughan et al. 1997). In this study, the preference for improved grassland seen across species may reflect the sampling of improved grassland at a landscape rather than patch scale, which will capture the association between improved grassland and other habitat types, particularly linear features such as hedgerows and trees. The species tested in this study, with exception of *E. serotinus,* all show a consistent association with linear features (Downs and Racey 2006; Limpens et al. 1989; Walsh and Harris 1996). Linear features occur at a greater density in grassland than in arable landscapes (Haines-Young et al. 2000). Insect density is also higher in grassland landscapes. Evans et al. (2007) found aerial insect abundance to be between two to seven times higher over grazed fields than cropped fields, even when livestock were absent. This was attributed to the regular input of dung, lack of mechanical tillage and reduced inputs of pesticides and fertilizers to grasslands. Linear features within an improved grassland matrix may therefore provide high quality foraging habitat for bats. Similarly, the occurrence of linear features in arable landscapes, although at a lower density than grassland landscapes, may explain the positive association between roost location and the proportion of arable land demonstrated by *P. pipistrellus* and *M. nattereri*, a habitat that is typically used less than expected by several bat species when use is assessed among patches (Vaughan et al. 1997).

An association between roost location and the proportion of semi-natural grassland was shown by only *M. nattereri,* which is perhaps surprising given the number of species positively associated with improved grassland in this study. Across all landscapes sampled, improved grassland made up on average 26% of the available habitat, whilst semi-natural grassland comprised 16% of available landscape. Semi-natural grassland appeared in over 90% of samples, however this was predominantly in the form of small isolated patches. Concentrations of semi-natural grassland large enough to impact landscape quality were concentrated in upland areas of Wales, northern England and Scotland, where the negative effect of increased elevation may mask habitat associations (Kanuch and Kristin 2006; Sattler et al. 2007). Higher elevations are generally associated with lower proportions of broadleaved woodland, and also cooler temperatures, which impede the development of young bats (Zahn 1999). Selection of roosts at lower elevations was shown by *P. pygmaeus* and *P. auritus* in this study.

Pipistrellus pygmaeus also selected roosts located closer to water than would be expected by chance, demonstrating that the strong association between *P. pygmaeus* and water features seen in studies of foraging associations (Davidson-Watts et al. 2006; Downs and Racey 2006; Nicholls and Racey 2006b; Sattler et al. 2007) extends to the selection of roost location.

2.4.4. Scale of response to landscape composition

For all species, with the exception of *M. nattereri,* there was a slight but in most cases insignificant improvement in model fit using landscape measures from within 1km of the roost as apposed to measures calculated over an area representing the maximal likely home-range of the colony. This is in accordance with observations that foraging activity of many bat is higher closer to the roost (Bontadina et al. 2002; Entwistle et al. 1996; Fuhrmann and Seitz 1992; Harbusch 2003; Simon et al. 2004; Trappmann and Clemen 2001), suggesting that the landscape composition closer to the roost may exert a greater influence on bats that the composition of their home range.

Myotis nattereri was the only species for which models performed better using landscape measures calculated at the home range scale. *Myotis nattereri* is a prolific roost switcher (Smith and Racey 2005). A study of *M. nattereri* inhabiting bat boxes in a coniferous plantation in Scotland found colonies moved between roosts on average every 2.5 days (Mortimer 2006). The better predictive ability of landscape composition measured across the home range as apposed to the habitat composition within 1km of one particular roost may result from the use of a number of roosts located throughout the home-range.

2.4.5. Study limitations

Roosts used in this study were located entirely in buildings, and therefore their national distribution followed patterns of population and building density. To account for this in the methodology the sample of the available landscape was constrained to follow the same distribution as the sample of roosts. However, landscape types with low population or building density, including upland, wetland and heath, were underrepresented in the sample, and as a result their association with bat distribution could not be assessed. Habitat associations may also be affected by the availability of suitable roosts. For example, many bat species are found at low density in coniferous plantations due in part to the paucity of suitable roost structures. However, bats will readily colonise bat boxes in coniferous forests, and in such instances are found to forage extensively in coniferous habitat (Mortimer 2006). This study controlled for roost availability by comparing the habitat around roosts to that surrounding randomly selected buildings located within the same strata of building density. The habitat associations demonstrated here are therefore likely to reflect foraging associations rather than differences in roost availability.

Finally, this study did not consider roost selection by any true woodland specialist bat species, such as *Barbastella barbastellus* or *M. bechsteini*, that roost and forage predominantly within broadleaved woodland (Dietz et al. 2009). Such species are likely to show a different response to woodland extent and spatial configuration than the edge specialist species considered here (Lesinski et al. 2007). Their needs should also be considered when designing conservation measures for bats.

2.4.6. Conservation implications

A broad suite of bat species are associated with broadleaved woodland, so the creation and management of woodlands has great potential to improve landscape quality for bats. In the present study, the greatest effect of increasing broadleaved woodland extent on a suite of edge specialist bat species was observed at low levels of broadleaved cover, up to proportions of approximately 20% of the available landscape. Roost selection by the majority of species tested was also positively associated with woodland proximity, but was not associated with patch size (assessed using the size of the nearest woodland patch). Together, the observed relationships with woodland extent and configuration suggest that, given a fixed amount of funding, edge specialist bats species will benefit equally from the creation of an extensive network of woodland patches in landscapes with little existing woodland cover, as from the enlargement of existing woodland patches. This is consistent with the preferential exploitation of woodland edge habitat and the highly mobile nature of the bat species tested here, but departs from recommendations that arise from the study of dispersal limited woodland specialist taxa, or from surveys of woodland biodiversity. A simulation of woodland colonisation suggested that small farm woodlands with closer links to existing woodland habitat will be more readily colonised by a wider range of species than isolated patches, and similar result have been shown in field studies of plant (Jacquemyn et al. 2003) and avian diversity (Opdam et al. 1995). Bird species richness is also affected by patch size, largely due to the absence of woodland specialists from smaller patches (Dolman et al. 2007). Such studies recommend that woodland creation schemes focus on enlarging woodland patches within existing woodland networks, but do not recommend the establishment of new woodland networks in landscapes with little existing woodland cover.

In England, the primary sources of funding for woodland creation are the English Woodland Grant Scheme (EWGS) and the Higher Level Stewardship scheme (HLS). HLS funds woodland creation on farmland in blocks up to 1ha each, and not exceeding 3ha in total, whereas the EWGS funds woodland creation of any size on private land. Both schemes are targeted and competitive.

EWGS grants are awarded on a points basis, based on regional priorities than can include native planting, the expansion of existing semi-natural woodland, or for specific woodland designs that benefit a UK Biodiversity Action Plan priority species (UK BAP, JNCC, 2007). Examples of appropriate species and suitable woodland designs are provided in the regional scoring guidance literature.

HLS targeting takes two forms; target areas and themes. Target areas are identified as containing nationally important landscape features, UK BAP priority habitats and priority species. Applications within these areas must meet the objectives outlined by the UK BAP. Outside target areas, application for the HLS must address one or more themes, which include increasing the resilience of UK BAP priority habitats to climate change, reversing farmland bird decline, and restoring populations of UK BAP priority species in non-priority habitats.

Pipistrellus pygmaeus, *R. hipposideros*, *P. auritus* and *N. noctula* are all BAP priority species in England, so both the EWGS and the HLS provide a mechanism by which woodland creation can be targeted to improve landscape quality for these species. However, the implementation of woodland creation for bat conservation is hindered by a lack of information describing appropriate woodland design for bats. Based on the findings of this study, I recommended that to conserve populations of the bat species assessed here, the extent of broadleaved woodland in the landscape should be increased, with benefits particularly marked in areas where broadleaved extent within a 1km radius is currently less than 20%. Land managers should aim to create an extensive network of woodland patches across the land holding, including small patches designed to take advantage of available land and increase the provision of woodland edge habitat. Patches should be spread throughout the holding so that no one patch is isolated, and distances between patches should not exceed 440m.

Incorporating these recommendations into the EWGS and HLS will meet action plan objectives of several UK BAP priority species, and also fulfil international obligations to protect and conserve bats.

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2.6 Appendix I

Table 2.5 Complete list of predictors assessed for inclusion in models relating roost location to the surrounding habitat. Cor. prop.= predictor excluded due to an unacceptable level of correlation with the proportion of habitat in the landscape (Pearson r^2 >0.5). Insuf. var. = predictor excluded due to insufficient variation (appearing in <10% of observations).

Predictor	Units	Description	Notes
Broadleaved:			
Proportion	%	Broad-leaved and mixed woodland with canopy cover greater than 20%, or scrub with cover greater than 30%	
Patch density	km^2		Cor. prop.
Mean patch area	km/km^2		Cor. prop.
Edge density	km		Cor. prop.
Mean perimeter-edge ratio			Cor. prop.
Mean distance to patch of same habitat type	km		Cor. prop.
Coniferous:			
Proportion	%	Coniferous woodland or plantation with canopy cover greater than 20%	
Patch density			Cor. prop.
Mean patch area	km^2		Cor. prop.
Edge density	km/km^2		Cor. prop.
Mean perimeter-edge ratio			Cor. prop.
Mean distance to patch of same habitat type	km		Cor. prop.
Arable:			
Proportion	%	Cereals, horticulture, perennial crops or unknown arable crops. Also includes freshly ploughed land and rotational setaside	
Improved:			
Proportion	%	Improved grassland and setaside grass	
Patch density			Cor. prop.
Mean patch area	km^2		Cor. prop.
Edge density	km/km^2		Cor. prop.
Mean perimeter-edge ratio			Cor. prop.
Mean distance to patch of same habitat type	km		Cor. prop.
Semi-natural:			
Proportion	%	Rough, calcareous and acid semi-natural grasslands and bracken	
Patch density			Cor. prop.
Mean patch area	km^2		Cor. prop.
Edge density	km/km^2		Cor. prop.
Mean perimeter-edge ratio			Cor. prop.
Mean distance to patch of same habitat type	km		Cor. prop.
Heath:			
Proportion	%	Dwarf and open shrub heath	Insuf. var.
Wetland:			
Proportion	%	Fen, marsh and swamp	Insuf. var.
Bog:			
Proportion	%		Insuf. var.
Montane:			
Proportion	%	Montane habitats	Insuf. var.

Table 2.5 continued.

Predictor	Units	Description	Notes
Bare ground:			
Proportion	%	Inland rock, bare ground and despoiled semi-natural areas	
Supra-littoral:			
Proportion	%	Supra-littoral rock and sediment	Insuf. var.
Littoral:			
Proportion	%	Littoral rock, sediment and saltmarsh	Insuf. var.
Distbroad	km	Euclidian distance from sample point to edge of nearest broadleaved cover	
Areabroad	km^2	Area of nearest broadleaved patch	
Distwater	km	Euclidian distance from sample point to nearest water body	
Elevation	m	Elevation of sample point	

2.7. Appendix II

Table 2.6 Results of AIC-based model selection across all possible combinations of explanatory predictors (candidate set of 511 models), using a 1km sample radius and home-range (HR) sample radius. Models shown are < Δ_i 2. For each model the number of estimable parameters (K), AIC score corrected for small sample size (cAIC$_c$), Akaike difference from the best model (Δ_i) and Akaike weight (w_i) are presented.

Model	K	cAIC$_c$	Δ_i	w_i
P. pipistrellus (1km sample radius)				
Distbroad + Distwater + Broadleaved + Arable + Improved	5	476.03	0.000	0.074
Distbroad + Distwater + Broadleaved + Coniferous + Arable + Improved	6	477.21	1.182	0.041
Distbroad + Broadleaved + Arable + Improved	4	477.27	1.242	0.040
Distbroad + Areabroad + Distwater + Broadleaved + Arable + Improved	6	477.51	1.482	0.035
Distbroad + Distwater + Elevation + Broadleaved + Arable + Improved	6	477.66	1.628	0.033
Distbroad + Distwater + Broadleaved + Arable + Improved + Semi-natural	6	477.80	1.773	0.030
P. pipistrellus (HR sample radius)				
Distbroad+ Distwater + Broadleaved + Arable + Improved	5	476.03	0	0.074
Distbroad + Distwater + Broadleaved + Coniferous + Arable + Improved	6	477.21	1.182	0.041
Distbroad + Broadleaved + Arable + Improved	4	477.27	1.242	0.040
Distbroad + Areabroad + Distwater + Broadleaved + Arable + Improved	6	477.51	1.482	0.035
Distbroad + Distwater + Elevation + Broadleaved + Arable + Improved	6	477.66	1.628	0.033
Distbroad + Distwater + Broadleaved + Arable + Improved + Semi-natural	6	477.80	1.773	0.030
P. pygmaeus (1km sample radius)				
Distbroad + Distwater + Elevation + Broadleaved + Improved	5	252.36	0.000	0.119
Distbroad + Distwater + Elevation + Broadleaved + Arable + Improved + Semi-natural	7	252.44	0.082	0.114
Distbroad + Distwater + Elevation + Broadleaved + Improved + Semi-natural	6	252.90	0.545	0.091
Distbroad + Distwater + Elevation + Broadleaved + Coniferous + Arable + Improved + Semi-natural	8	253.72	1.361	0.060
Distbroad + Distwater + Elevation + Broadleaved + Arable + Improved	6	253.83	1.474	0.057
Distbroad + Areabroad + Distwater + Elevation + Broadleaved + Improved	6	254.33	1.968	0.044

Table 2.6 continued.

Model	K	cAIC$_c$	Δ_i	w_i
P. pygmaeus (HR sample radius)				
Distbroad + Distwater + Elevation + Broadleaved + Improved + Semi-natural	6	254.64	0.000	0.134
Distbroad + Distwater + Elevation + Broadleaved + Coniferous + Improved + Semi-natural	7	255.65	1.014	0.081
Distbroad + Areabroad + Distwater + Elevation + Broadleaved + Improved + Semi-natural	7	255.83	1.194	0.074
Distbroad + Distwater + Elevation + Broadleaved + Improved	5	256.09	1.446	0.065
Distbroad + Distwater + Elevation + Broadleaved + Arable + Improved + Semi-natural	7	256.53	1.887	0.052
R. hipposideros (1km sample radius)				
Distbroad + Broadleaved + Semi-natural	3	246.77	0.000	0.065
Distbroad + Broadleaved + Arable + Improved	4	247.02	0.251	0.058
Distbroad + Broadleaved + Coniferous + Semi-natural	4	248.23	1.456	0.031
Distbroad + Distwater + Broadleaved + Semi-natural	4	248.39	1.619	0.029
Distbroad + Broadleaved + Arable + Semi-natural	4	248.40	1.628	0.029
Distbroad + Broadleaved + Improved + Semi-natural	4	248.46	1.691	0.028
Distbroad + Areabroad + Broadleaved + Semi-natural	4	248.52	1.746	0.027
Distbroad + Distwater + Broadleaved + Arable + Improved	5	248.52	1.751	0.027
Distbroad + Elevation + Broadleaved + Semi-natural	4	248.63	1.858	0.026
Distbroad + Broadleaved + Arable + Improved + Semi-natural	5	248.65	1.881	0.025
Distbroad + Areabroad + Broadleaved + Arable + Improved	5	248.67	1.901	0.025
R. hipposideros (HR sample radius)				
Distbroad + Broadleaved + Arable + Improved	4	258.48	0.000	0.044
Distbroad + Areabroad + Broadleaved + Arable + Improved	5	259.22	0.738	0.031
Distbroad + Broadleaved + Improved	3	259.48	0.994	0.027
Distbroad + Distwater + Broadleaved + Arable + Improved	5	259.53	1.050	0.026
Distbroad + Broadleaved + Semi-natural	3	259.77	1.284	0.023
Distbroad + Areabroad + Distwater + Broadleaved + Arable + Improved	6	260.26	1.772	0.018
Distbroad + Areabroad + Broadleaved + Improved	4	260.34	1.853	0.018
Distbroad + Broadleaved + Coniferous + Arable + Improved	5	260.46	1.976	0.016
Distbroad + Distwater + Broadleaved + Improved	4	260.48	1.999	0.016
P. auritus (1km sample radius)				
Distwater + Elevation + Broadleaved + Coniferous + Improved + Semi-natural	6	140.07	0.000	0.087
Areabroad + Distwater + Elevation + Broadleaved + Coniferous + Improved + Semi-natural	7	141.18	1.104	0.050
Distwater + Elevation + Broadleaved + Coniferous + Improved	5	141.26	1.191	0.048
Elevation + Broadleaved + Coniferous + Improved + Semi-natural	5	141.41	1.333	0.045
Distwater + Elevation + Broadleaved + Coniferous + Arable + Improved + Semi-natural	7	141.97	1.901	0.034
Areabroad + Distwater + Elevation + Broadleaved + Coniferous + Improved	6	142.03	1.961	0.033

Table 2.6 continued.

Model	*K*	cAIC$_c$	Δ_i	w_i
P. auritus (HR sample radius)				
Distwater + Elevation + Broadleaved + Coniferous + Improved + Semi-natural	6	150.34	0.000	0.055
Distwater + Elevation + Broadleaved + Arable + Improved	5	150.94	0.601	0.041
Distwater + Elevation + Broadleaved + Improved + Semi-natural	5	151.10	0.761	0.038
Distwater + Elevation + Broadleaved + Improved	4	151.24	0.905	0.035
Distbroad + Distwater + Elevation + Broadleaved + Coniferous + Improved + Semi-natural	7	151.56	1.220	0.030
Distwater + Elevation + Broadleaved + Coniferous + Improved	5	151.62	1.284	0.029
Distbroad + Distwater + Elevation + Broadleaved + Improved + Semi-natural	6	151.70	1.358	0.028
Distbroad + Distwater + Elevation + Broadleaved + Arable + Improved	6	151.91	1.566	0.025
Distwater + Elevation + Broadleaved + Arable + Improved + Semi-natural	6	151.95	1.611	0.025
Elevation + Broadleaved + Coniferous + Improved + Semi-natural	5	152.17	1.828	0.022
Distbroad + Distwater + Elevation + Broadleaved + Improved	5	152.17	1.832	0.022
Areabroad + Distwater + Elevation + Broadleaved + Coniferous + Improved + Semi-natural	7	152.26	1.916	0.021
E. serotinus (1km sample radius)				
Distbroad + Coniferous + Improved	3	105.16	0.000	0.061
Distbroad + Elevation + Coniferous + Improved	4	106.17	1.015	0.036
Distbroad + Arable + Improved	3	106.45	1.291	0.032
Distbroad + Coniferous + Arable + Improved	4	106.69	1.532	0.028
Distbroad + Improved	2	106.69	1.539	0.028
Distbroad + Elevation + Improved	3	106.91	1.756	0.025
Distbroad + Broadleaved + Coniferous + Improved	4	106.91	1.759	0.025
Distbroad + Elevation + Arable + Improved	4	106.95	1.790	0.025
Distbroad + Areabroad + Coniferous + Improved	4	107.15	1.995	0.022
E. serotinus (HR sample radius)				
Distbroad + Improved	2	111.34	0.000	0.053
Distbroad + Elevation + Improved	3	111.56	0.220	0.048
Distbroad + Elevation + Broadleaved + Improved	4	111.74	0.402	0.044
Distbroad + Broadleaved + Improved	3	112.63	1.286	0.028
Distbroad + Improved + Semi-natural	3	112.77	1.426	0.026
Distbroad + Elevation + Improved + Semi-natural	4	113.16	1.824	0.021
Distbroad + Elevation + Broadleaved + Improved + Semi-natural	5	113.20	1.859	0.021

Table 2.6 continued.

Model	K	cAIC$_c$	Δ_i	w_i
M. nattereri (1km sample radius)				
Distbroad + Areabroad + Broadleaved + Arable + Improved + Semi-natural	6	81.37	0.000	0.032
Distbroad + Broadleaved + Arable + Improved + Semi-natural	5	81.56	0.193	0.029
Distbroad + Arable + Improved + Semi-natural	4	81.94	0.572	0.024
Distbroad + Arable + Improved	3	82.22	0.852	0.021
Distbroad + Elevation + Arable + Improved + Semi-natural	5	82.25	0.876	0.021
Distbroad + Elevation + Broadleaved + Arable + Improved + Semi-natural	6	82.32	0.952	0.020
Distbroad + Areabroad + Elevation + Broadleaved + Arable + Improved + Semi-natural	7	82.67	1.301	0.017
Distbroad + Areabroad	2	82.89	1.514	0.015
Distbroad + Improved	2	83.15	1.783	0.013
Distbroad + Distwater + Arable + Improved	4	83.24	1.872	0.013
Distbroad + Areabroad + Elevation	3	83.25	1.877	0.013
Distbroad + Areabroad + Improved	3	83.25	1.877	0.013
Distbroad + Elevation	2	83.32	1.947	0.012
Distbroad + Areabroad + Distwater + Broadleaved + Arable + Improved + Semi-natural	7	83.33	1.954	0.012
M. nattereri (HR sample radius)				
Distbroad + Arable + Improved + Semi-natural	4	67.68	0.000	0.126
Distbroad + Elevation + Arable + Improved + Semi-natural	5	68.82	1.134	0.072
Distbroad + Coniferous + Arable + Improved + Semi-natural	5	69.20	1.518	0.059
Distbroad + Areabroad + Arable + Improved + Semi-natural	5	69.49	1.808	0.051
Distbroad + Broadleaved + Arable + Improved + Semi-natural	5	69.50	1.818	0.051
Distbroad + Distwater + Arable + Improved + Semi-natural	5	69.64	1.957	0.047

Chapter 3

Separating the effects of habitat extent and habitat aggregation on the incidence of bats in a fragmented landscape

Abstract

Habitat fragmentation is characterised by two processes, a reduction in habitat extent and the breaking apart of remaining habitat. To correctly assess the effect of habitat fragmentation on biodiversity, it is important to understand how species respond to these separate processes, yet few studies of habitat fragmentation distinguish between the two. Here I use data from a national survey of bat distribution in the UK to assess the independent effects of habitat extent and the aggregation of habitat patches on the incidence of four bat species; *Pipistrellus pipistrellus, Pipistrellus pygmaeus, Nyctalus noctula* and *Eptesicus serotinus*. The effect of scale on the relationships between bat incidence and landscape structure was assessed by fitting models at multiple spatial scales. The effect of habitat aggregation on bat incidence was weak when compared to habitat extent measured at an appropriate scale. Incidence of all four species was greater in landscapes with a higher proportion of broadleaved woodland cover. Only *P. pipistrellus* was affected by the aggregation of woodland patches. When broadleaved woodland exceeded 9% of the landscape, activity of *P. pipistrellus* was greatest in landscapes with more dispersed woodland patches. However in landscapes with a low extent of broadleaved woodland, *P. pipistrellus* activity was greatest when woodland patches were more aggregated. *Pipistrellus pygmaeus* and *N. noctula* incidence was positively associated with the proportion of improved grassland in the landscape. Both species preferred landscapes with dispersed grassland patches. *Pipistrellus pygmaeus, N. noctula* and *E. serotinus* were also positively associated with the proportion of coniferous woodland in the landscape. No one spatial scale captured all landscape scale habitat associations shown by each species. The findings of this study suggest that increasing the extent of broadleaved woodland should form the focus of bat conservation strategies at a landscape scale.

3.1. Introduction

Habitat fragmentation almost inevitably accompanies anthropogenic habitat alteration, and as a result has become a central topic ecological research (reviewed by Andrén 1994; Fahrig 2003; Saunders et al. 1991). The process of fragmentation can be characterised as a reduction in the extent of the original habitat and the breaking apart of remaining habitat, resulting in decreased patch size and increased patch isolation (Andrén 1994). In addition to the impact of habitat loss, fragmentation can have negative consequences for biodiversity as a result of, among other factors, the loss of species with large home-range requirements from remnant patches (Fahrig 2003), the disruption of gene flow between populations (Keller and Largiadèr 2003), increased habitat disturbance along patch edges (Beier et al. 2002), and the modification of ecosystem processes (Saunders et al. 1991). However, conservation actions designed to reduced the negative effects of habitat fragmentation are often hindered by a lack of knowledge regarding how species respond to the different components of the process.

Many commonly used measures of habitat fragmentation, such as patch density, patch size, patch isolation and edge density, are correlated with habitat extent in natural landscapes. As a result the relative effects of habitat loss and habitat disaggregation are hard to distinguish. Research to date suggests that the relationship between biodiversity and habitat loss is overwhelmingly negative, whereas the effects of habitat disaggregation are much weaker, and are at least as likely to be positive as negative (Fahrig 2003). Another little studied aspect of fragmentation is the interaction between habitat loss and habitat disaggregation. The results of simulations of landscape fragmentation suggest that population declines in landscapes with a high proportion of focal habitat are primarily a response to habitat loss, while the effects of habitat disaggregation are important only in landscapes with little remaining original habitat (Andrén 1994).

The response of bats to fragmentation has been studied extensively in tropical regions (eg. Bernard and Fenton 2007; Cosson et al. 1999; Estrada-Villegas et al.; Klingbeil and Willig 2009), and to a lesser extent in temperate landscapes (Ekman and de Jong 1996; Lesinski et al. 2007). However, very few studies have attempted to assess the independent effects of habitat loss and habitat disaggregation. Gorresen et al (Gorresen and Willig 2004; Gorresen et al. 2005) used residual regression to correct measures of landscape configuration for habitat extent in a study of Phyllostomid bats in the Atlantic forests of Paraguay. However, residual regression has been shown to produce biased estimates of effect size in the presence of colinearity (Freckleton 2002). No study of the response of bats to habitat fragmentation has employed metrics of fragmentation that are truly independent of habitat extent.

In this paper I utilise an index of habitat aggregation proposed by McGarigal et al (2002) that is independent of habitat extent, to assess the effects of landscape composition and configuration on incidence of four bat species. I use data from a national survey of bat activity in the UK to address the following hypotheses. 1) The activity of bats recorded along field transects will be more strongly associated with measures of habitat extent than with measures of habitat disaggregation. 2) The effect of habitat disaggregation on bat activity will vary according to the extent of focal habitat in the landscape. 3) The scale at which the landscape is characterised with impact the strength of the observed associations between habitat metrics and bat activity. As the scale at which UK bats respond to landscape structure is not known, models are fitted at series of nested scales in order to assess patterns of scale dependency.

3.2. Methods

3.2.1. Species ecology and range

This study models the landscape scale habitat associations of four vespertilionid bat species: *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, *Nyctalus noctula* and *Eptesicus serotinus*. *Pipistrellus pipistrellus* and *P. pygmaeus* are the smallest bats found in the UK, weighing between 3.5-8g (Schober and Grimmberger 1997). They forage close to vegetation, often around head height (Russ 1999). Both species are common and widespread in the UK, with a nationwide range (Richardson 2000), although the relative frequency of these two species varies across their range (see section 3.3). *N. noctula* and *E. serotinus* are among the largest British bats, weighing 19-40g and 14-33g respectively (Schober and Grimmberger 1997). *N. noctula* typically forages between 10-

40m, sometimes up to 70m, in open areas and above trees (Schober and Grimmberger 1997). It is fairly common throughout England and Wales, up to southern Scotland. *Eptesicus serotinus* forages from ground level up to heights of 5-10m, much closer to vegetation than *N. noctula* (Russ 1999). It is restricted to southern England and South Wales (Richardson 2000). Further details of the ecology and distribution of these species are provided in chapter 1.

3.2.2. Survey methodology

Species distribution data were derived from 544 field transects, surveyed between 1998-2007 as part of the National Bat Monitoring Programme (fig. 3.1). Trained volunteer surveyors were each assigned a 1km grid square, selected in 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. See Walsh et al. 2001 for further details of the stratification procedure). Despite the stratified-random design some landscape types, such as upland and wetland habitats, were underrepresented in the sample and associations with these habitat types could not be tested. Habitats for which associations could not be established should not be considered unimportant to bats. Within each square a transect of approximately 3km in length was mapped, following as closely as possible to a triangular route. Although transect routes deviated in most cases from the idealised route, biases in transect placement are expected to be constant across landscape types, so the analysis of landscape scale habitat associations should be minimally affected. Transect were split into twelve approximately equal sections. Beginning 20 minutes after sunset, surveyors walked the transect with a heterodyne detector tuned to 25 kHz, and noted 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 flies 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* < 21kHz, *E. serotinus* 25-32kHz, *P. pipistrellus* 44-48kHz, *P. pygmaeus* > 52kHz) 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 (± 3.9 SD) occasions. Transect routes were recorded on enlarged 1:25,000 Ordnance Survey maps, and digitised with reference to 1:25,000 OS raster tiles.

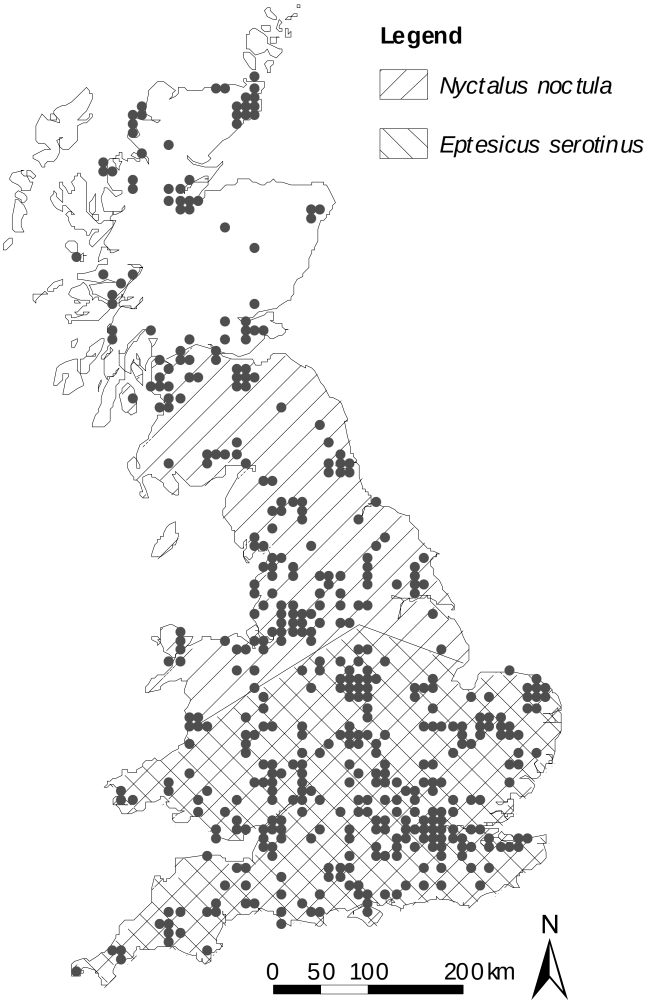


Figure 3.1. Distribution of field transects surveyed 1998-2007 as part of the National Bat Monitoring Programme, which were used in this study. Circles represent 10km grid squares containing at least one transect. Also shown are the minimum convex polygons used to delimit the range of *N. noctula* and *E. serotinus.* A nation-wide range was assumed for *P. pipistrellus* and *P. pygmaeus.*

Data from all point counts and transect sections were combined to provide a measure of species incidence per transect, to correspond to the resolution of available habitat data. The mean number of *P. pipistrellus* and *P. pygmaeus* passes per survey was calculated for each transect. Due to the relative rarity of *N. noctula* and *E. serotinus* along transects, incidence of these species could not be modelled as a continuous variable. The number of passes recorded along each transect was instead transformed into presence/absence, combining records from all surveys completed during the study period. To reduce false absences, transects along which a species was recorded, but where unidentified bats showing the characteristics of the species of interest were noted, were not used in the analysis of that species.

In this study I focus on landscape level predictors of species distribution, rather than bioclimatic factors that may set the limits of a species range. As such only sites within the range of each species were used for modelling. 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. Three non-roost records of *N. noctula* from the North Scottish coast were removed as probable vagrants. All sites were assumed to fall within the range of *P. pipistrellus* and *P. pygmaeus* (fig 3.1). The number of transects used to construct species distribution models for each species ranged from 266-526 (table 3.1.).

Table 3.1. Number of transects used to construct species distribution models for each species, and the percentage of transects along which each species occurred.

Species	N	Occupancy (%)
P. pipistrellus	526	83
P. pygmaeus	526	56
N. noctula	440	67
E. serotinus	266	49

3.2.3. Habitat Data

The habitat composition and configuration of the landscape was characterised at three spatial scales. Home-range size is likely to have a strong influence on the scale at which bats perceive landscape change, therefore data describing typical home-range size were gathered from published radio-telemetry studies. Despite large differences in maximal home-range size, the distance from the roost within which bats spent the majority of foraging time (the ‘core’ foraging radius) was relatively consistent between species (table 3.2). A sample radius of 1500m was chosen to represent the core foraging range of the species in this study, however, due to the lack of knowledge regarding the scale at which bats respond to landscape structure, data was also sampled at half and twice this distance from the transect.

Table 3.2. Literature describing bat foraging behaviour, used to inform choice of data extraction radius.

Species	Distance (km)	Note	Citation
P. pipistrellus	1.44	Mean distance from roost to core area of activity	Nicholls and Racey 2006a
	1.90	Mean distance from roost to furthest point travelled	Davidson-Watts and Jones 2006a
P. pygmaeus	0.69	Mean distance from roost to core area of activity	Nicholls and Racey 2006a
	1.94	Mean distance from roost to furthest point travelled	Davidson-Watts and Jones 2006a
	1.75	Maximum distance from roost to foraging site	Bartonicka et al. 2008a
N. noctula	3.82	Median of maximum distance individual lactating bats recorded from roost	Mackie and Racey 2007
	2.00	Radius of main activity of maternity colony	Schmidt 1988
	1.30	Mean distance from roost to frequently used foraging area	Kronwitter 1988
E. serotinus	1.70	Distance within which bats spent 91% of foraging time	Harbusch 2003
	1.25	Average distance from roost to foraging patch	Simon et al. 2004

Habitat data were derived from the Land Cover Map 2000 (LCM2000, Fuller et al. 2002); a 25m raster grid of 16 broad land cover types, classified using spectral reflectance parameters from satellite images. A concurrent field survey of 569 1km squares suggests LCM2000 identifies broad land cover types with an accuracy of *c.* 85% (Fuller et al. 2002, further details of classification accuracy are provided in chapter 1). Satellite data were collected between 1998 and 2001. Between 1998 and 2007 the change in UK land mass under the most extensive land cover types was considered small enough for LCM2000 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). The proportion of each LCM2000 habitat class was calculated at each sample scale. Measures of habitat fragmentation are often highly correlated with habitat extent, making an independent assessment of the effects of habitat loss and habitat disaggregation difficult. To overcome this difficulty, McGarigal et al. have developed an index of fragmentation termed *clumpiness*, that is independent of habitat extent (McGarigal et al. 2002). For a given landscape and focal habitat type, this index equals the deviation of the observed habitat distribution from that expected under a spatially random distribution of the same habitat extent, based on the number of like adjacencies between pixels. The index ranges from –1 when habitat is maximally disaggregated to 1 when habitat is maximally clumped, with zero representing a spatial random distribution. Here I use the terms *aggregation* and *disaggregation* to refer to the specific aspect of habitat fragmentation measured by the clumpiness index, and reserve the term *fragmentation* for the combined effect of habitat loss and habitat disaggregation. Aggregation of broadleaved woodland, improved grassland and semi-natural grassland was measured at each spatial scale, as previous studies have shown these habitat types to be positively associated with the bat species investigated here (Glendell and Vaughan 2002; Vaughan et al. 1997; Walsh and Harris 1996). The effect of habitat extent on the relationship between habitat aggregation and bat incidence was investigated by including the interaction of habitat proportion and the aggregation index. Mean elevation was calculated using the Ordnance Survey Panorama digital terrain model (50m raster, elevation recorded to the nearest metre). Spatial data processing was carried out using FRAGSTATS (McGarigal et al. 2002) and ArcGIS 9.2 (ESRI, Redlands CA).

3.2.4. Statistical analysis

Variation in bat activity was modelled using a GLM with a log link and a negative binomial error term for *Pipistrellus* species, and a logit link and binomial error term for *N. noctula* and *E. serotinus*. From the initial set of predictors (table 3.8, appendix 1), those which displayed insufficient variation to be modelled accurately (appearing in <10% of observations) were removed. Multicollinearity was assessed among the remaining predictors. Where necessary predictors were centred by subtracting the mean value from each observation to reduce colinearity between main effects and interaction terms. In England and Wales, semi-natural grassland is concentrated on marginal land, generally occurring at higher elevations. As a result semi-natural grassland and elevation were highly correlated when only data from these two countries were used, as for *N. noctula* and *E. serotinus.* For these species, the proportion of semi-natural grassland was removed from models in favour of retaining average elevation. All remaining predictors demonstrated acceptable levels of colinearity (squared Spearman correlation coefficients <0.5, Freckleton 2002).

Not all transects were surveyed every year. Population change over the study period could therefore cause variation in bat activity between transects surveyed over a differing subsets of years. To control for this source of variation, a mean population index was included in all models. This was calculated using the smoothed population trends estimated from NBMP field survey data (Bat Conservation Trust 2008). For each transect, a mean population index value was calculated by averaging the national index value over the years the transect was surveyed. The effect of survey effort on the likelihood of correctly establishing the presence of *N. noctula* and *E. serotinus* was controlled for by including transect length and the number of times each transect was surveyed in every *N. noctula* and *E. serotinus* model. Within their range (fig. 3.1), both *N. noctula* and *E. serotinus* demonstrated a decline in incidence with increasing latitude that was not sufficiently explained by the selected habitat predictors. Therefore northing, measured with reference to OSGB 36, was included in *N. noctula* and *E. serotinus* models. The final set of predictors used to model species incidence are shown in table 3.3.

Table 3.3. Environmental predictors used to model site occupancy

Predictor	Units	Description
Arable	%	Proportion of cereals, horticulture, perennial crops or unknown arable crops. Also includes freshly ploughed land and rotational setaside
Broadleaved	%	Proportion of broad-leaved and mixed woodland (canopy cover greater than 20%), or scrub (with cover greater than 30%)
CLUbroadleaved		Aggregation of broadleaved woodland habitat patches, represented by an index of 'clumpiness'.
Coniferous:	%	Proportion of coniferous woodland or plantation (canopy cover greater than 20%)
Improved	%	Proportion of improved grassland and setaside grass
CLUimproved		Aggregation of improved grassland habitat patches, represented by an index of 'clumpiness'.
Semi-natural	%	Proportion of rough, calcareous and acid semi-natural grasslands and bracken. (*P. pipistrellus* and *P. pygmaeus* only)
CLUsemi-natural		Aggregation of semi-natural grassland habitat patches, represented by an index of 'clumpiness' (*P. pipistrellus* and *P. pygmaeus* only)
Bare ground		Inland rock, bare ground and despoiled semi-natural areas
Built	%	Proportion of continuous urban, suburban and rural developed areas
Heath	%	Proportion of dwarf and open shrub heath
Water	%	Proportion of inland water
Elevation	m	Mean elevation of landscape, in metres above sea-level
Included in every model:		
Mean population index		National population index averaged over the years each site has been surveyed
Number of surveys		Number of surveys used to determine species presence (*N. noctula* and *E. serotinus* only)
Length	m	Transect length (*N. noctula* and *E. serotinus* only)
Northing	m	With reference to OSGB 36

At each spatial scale, all possible combinations of predictors and interaction terms were modelled, and averaged parameter estimates were calculated using the methods described by Burnham and Anderson (2002). 95% confidence intervals were constructed for each predictor using unconditional standard errors. The utility of each predictor within the averaged model was assessed based on whether the confidence interval of the coefficient estimate overlapped zero. The performance of models fitted using data at different spatial scales was compared using AICc score. Spatial autocorrelation of residuals was assessed using Moran's I. All analyses were performed using STATA 10 (StataCorp, TX).

3.3 Results

3.3.1. National patterns of activity

The mean number of bat passes recorded per survey varied greatly among transects for all study species. Activity of *P. pipistrelles* ranged from 0 to 67 passes per survey, with hotspots of high activity distributed patchily throughout England and Wales (fig. 3.2a). Activity was generally lower in Scotland. Activity of *P. pygmaeus* ranged from 0 to 62 passes per survey, showing discrete hotspots of high activity in areas such as central Scotland and the Norfolk Broads (fig. 3.2b). There was localised variation in the relative activity levels of *P. pipistrellus* and *P. pygmaeus* across much of their range. However, *P. pygmaeus* was the dominant species across central and west coast Scotland (fig 3.3).

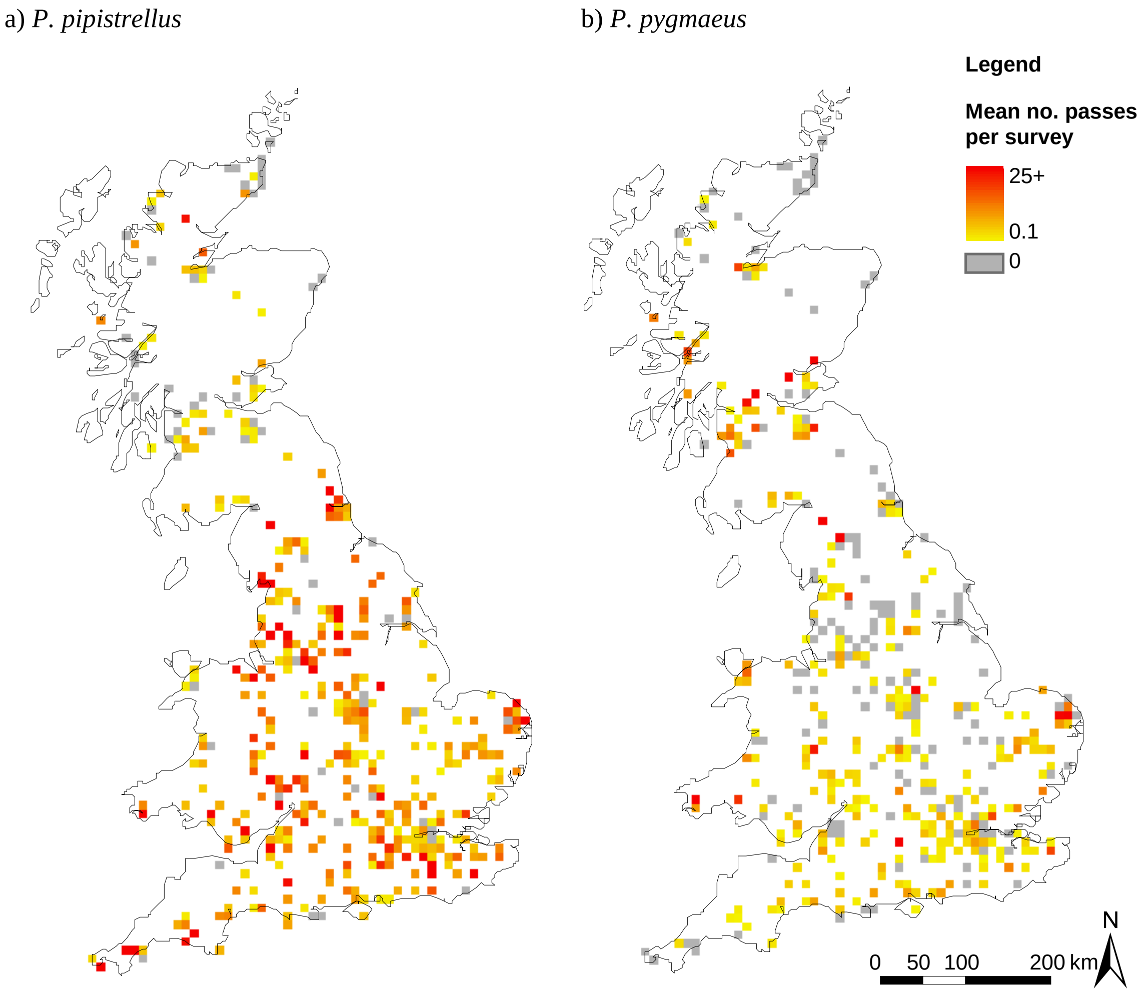


Figure 3.2 Variation in activity level of a) *P. pipistrellus* and b) *P. pygmaeus*. Each 10km grid square shows the mean number of passes recorded per survey per transect, averaged over all transects falling within that square. Grey squares represent grid squares that were surveyed, but where the species was not recorded.

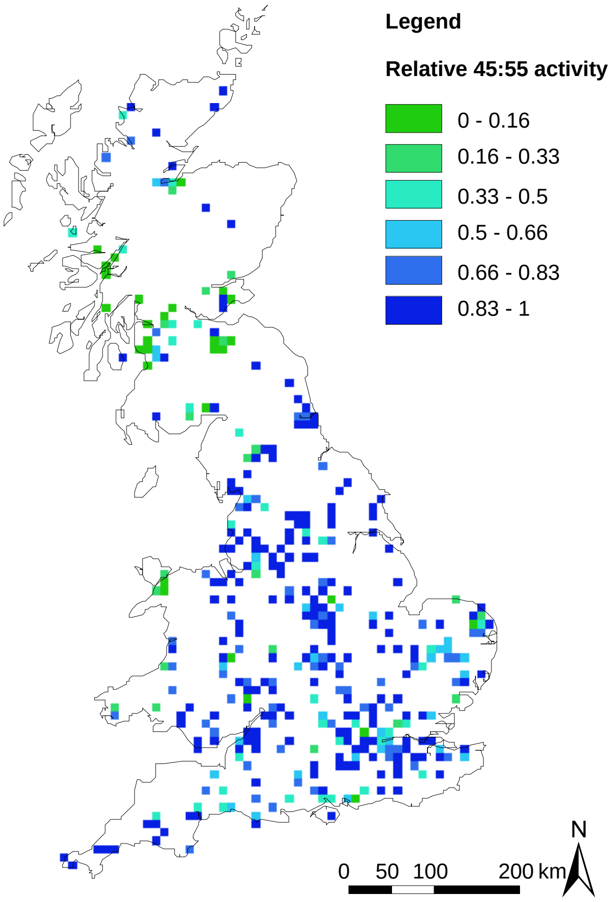
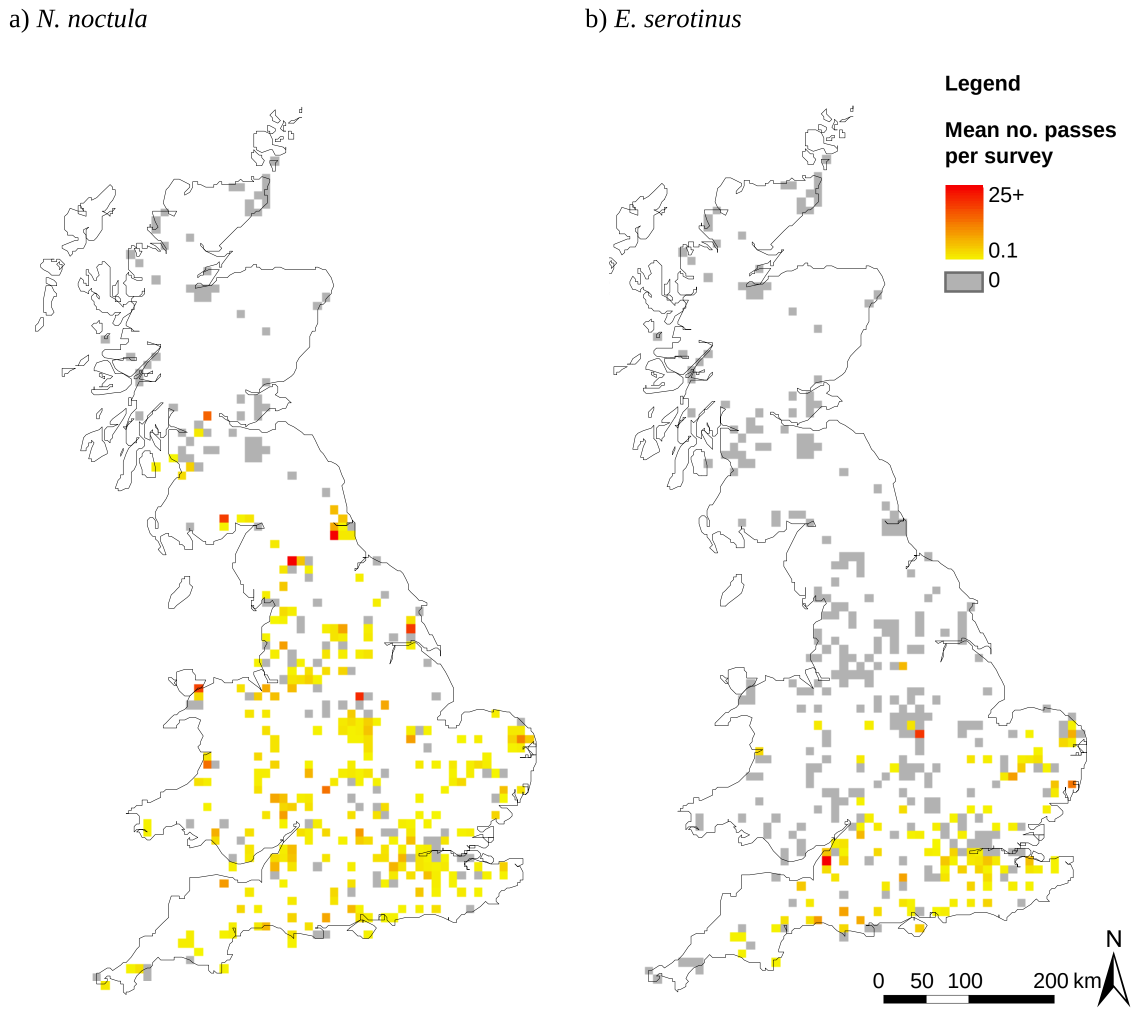


Figure 3.3 Relative activity levels of *P. pipistrellus* and *P. pygmaeus.* Each 10km grid square represents the ratio of the mean number of passes per species per transect, averaged over all transects that fall within the square. Blue squares represent areas dominated by *P. pipistrellus*, green squares represent areas dominated by *P. pygmaeus*.

Nyctalus noctula activity was low across England and Wales (fig. 3.4a). It was recorded rarely in southern and central Scotland, and was not recorded in northern Scotland. Within it's national range (fig. 3.1), it was present along 67% of transects, and mean activity per survey varied from 0 to 44 passes among transects. *Eptesicus serotinus* was encountered most frequently in southern and eastern England (fig. 3.4b). It was recorded less frequently in central England and Wales, and was not recorded in northern England or Scotland. Within it's range (fig. 3.1) it was recorded along 49% of transects, and mean activity per survey varied from 0 to 27 passes.


a) *N. noctula*

b) *E. serotinus*

Figure 3.4 Variation in activity level of a) *N. noctula* and b) *E. serotinus*. Each 10km grid square shows the mean number of passes recorded per survey per transect, averaged over all transects falling within that square. Grey squares represent grid squares that were surveyed, but where the species was not recorded.

3.3.2. Landscape metrics

Model residuals showed low levels of spatial dependency (Moran's *I* –0.003-0.042, where a value of 0 equals a spatially random pattern of residual variation, and 1 equals perfect spatial correlation). There was a weak but significant spatial dependency in *E. serotinus* model residuals (Moran's *I* 0.038-0.042, $p < 0.001$), however, this level of dependency was not large enough to require corrective measures (Legendre 1993).

3.3.2.1. P. pipistrellus and P. pygmaeus

Variation in *P. pipistrellus* and *P. pygmaeus* activity along field transects was best explained using metrics of landscape structure measured within 750m of the transect. There was a trend of increasing AICc score, and decreasing model performance, as the scale used to measure landscape structure increased (table 3.4 and table 3.5). *Pipistrellus pipistrellus* activity was negatively associated with the proportion of heath at all three spatial scales. Activity was positively associated with the proportion of broadleaved woodland measured at 1500m and 3000m from the transect. At 750m from the transect, the averaged coefficient of the proportion of broadleaved woodland was distinct from zero at the 90% confidence level ($\beta = 0.015$, 90% CI 0.002-0.028), but not at the 95% level. An effect of habitat aggregation was seen only at the largest spatial scale (fig. 3.5). At low proportions of broadleaved woodland, activity decreased as woodland became increasingly disaggregated. At proportions of woodland greater than 9%, the opposite relationship was seen, activity here was higher in landscapes with more disaggregated woodland. Habitat aggregation of both broadleaved woodland and improved grassland was greater than 0.5 in all landscapes, indicating these habitats were more clumped than would be expected under a spatially random distribution. Such a result is expected when grain (pixel) size is small relative to patch size, as in this study.

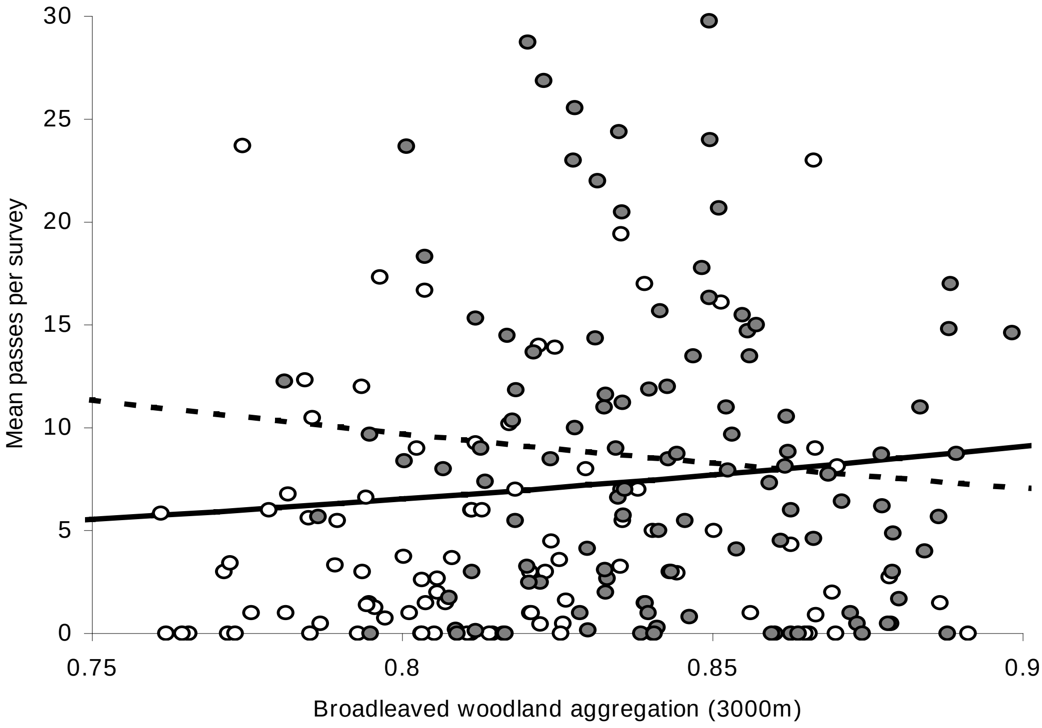


Figure 3.5 *Pipistrellus pipistrellus* activity in relation to the aggregation of broadleaved woodland, measured within a 3000m radius of the transect. The fitted relationship is shown for 5% broadleaved woodland (lower quartile, *solid line*) and 13% broadleaved woodland (upper quartile, *dashed line*). *Open circles* represent observations within the lower quartile of broadleaved woodland extent (1-5%). *Filled circles* indicate observations within the upper quartile (13-37%). Noise was added to the x-axis so that all data points were visible.

Across all three spatial scales, *P. pygmaeus* activity was positively associated with the proportion of improved grassland and coniferous woodland in the landscape, and at the two smaller scales, was also positively associated with the proportion of broadleaved woodland and negatively associated with the average elevation of the landscape. At the largest spatial scale, *P. pygmaeus* activity was negatively associated with the aggregation of improved grassland (fig. 3.6). Activity increased as improved grassland habitat became more disaggregated. This association was not affected by the proportion of improved grassland in the landscape. No effect of woodland aggregation was seen.

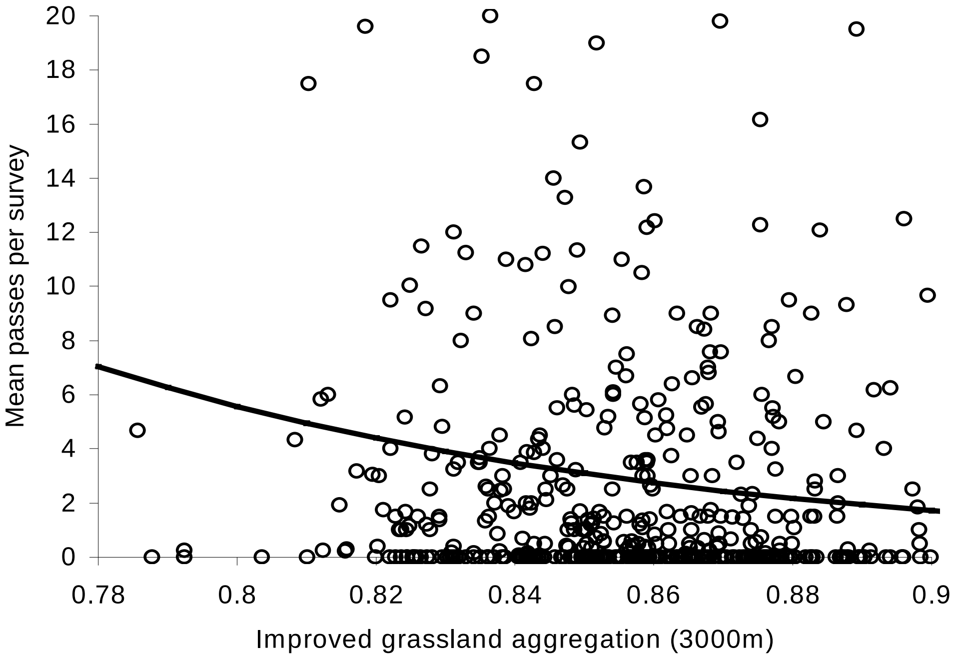


Figure 3.6 *Pipistrellus pygmaeus* activity in relation to the aggregation of improved grassland, measured within a 3000m radius of the transect. Noise was added to the x-axis so that all data points were visible.

3.3.2.2. N. noctula and E. serotinus

For *N. noctula,* variation in incidence among transects was best explained by landscape metrics calculated within 750m of the transect (table 3.6). For *E. serotinus* models constructed using data from within 750m and 3000m were both well supported (table 3.7). However there was no clear trend in model performance across spatial scales for either species. Incidence of both species was positively associated with the proportion of broadleaved woodland at every spatial scale, and coniferous woodland at the 3000m scale. A negative association between the proportion of the landscape containing urban or suburban development within 750m was shown by *N. noctula.* This species was positively related to the proportion of improved grassland at 1500m and 3000m from the transect, but not 750m. However, at the smaller scale *N. noctula* incidence was related to the aggregation of improved grassland; this species was more likely to occur in landscapes with more dispersed grassland habitat (fig. 3.7). The only other landscape metric associated with the incidence of *E. serotinus* was the average elevation of the landscape. *Eptesicus serotinus* was more likely to occur along transects at lower elevations, measured at all three spatial scales.

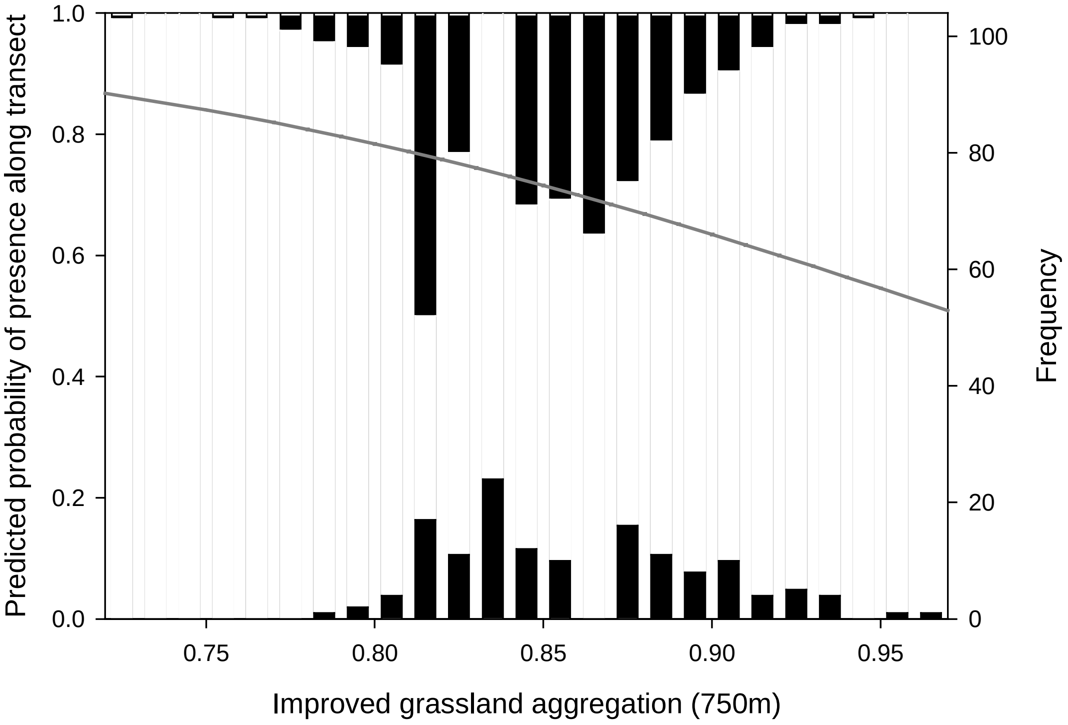


Figure 3.7 Predicted probability of encountering *N. noctula*, in relation to the aggregation of improved grassland measured within 750m of the transect. At each level of aggregation, the frequency of transects where *N. noctula* was present are plotted on the upper axis, and where absent on the lower axis.

Table 3.4 Results of GLM analysis relating mean activity level of *P. pipistrellus* along transects to the composition and configuration of the surrounding landscape, measured at three spatial scales. Parameters shown are averaged coefficient estimates, unconditional standard errors and 95% confidence intervals of the averaged coefficients calculated over all possible combinations of explanatory predictors and interaction terms. For each model, Moran's *I* measure of the spatial autocorrelation of residuals, AIC score corrected for small sample size (AICc) and Akaike difference from the best model (Δ_i) are presented. Coefficient estimates with 95% confidence intervals that do not include zero are shown in bold.

	750m				1500m				3000m			
			95% CI				95% CI				95% CI	
Predictor	β	SE	Lower	Upper	β	SE	Lower	Upper	β	SE	Lower	Upper
Arable	0.002	0.003	-0.004	0.008	0.001	0.002	-0.004	0.006	0.001	0.002	-0.004	0.005
Broadleaved	0.015	0.008	-7.50E-5	0.030	**0.017**	**0.009**	**0.000**	**0.034**	**0.033**	**0.011**	**0.011**	**0.055**
CLUbroadleaved	-1.793	1.393	-4.522	0.937	-0.985	1.803	-4.518	2.548	-0.384	2.264	-4.821	4.053
CLUbroadleaved*Broadleaved	-0.103	0.087	-0.273	0.068	-0.235	0.153	-0.534	0.064	**-0.808**	**0.287**	**-1.371**	**-0.245**
Coniferous	-2.25E-4	0.003	-0.006	0.005	-2.15E-4	0.002	-0.005	0.004	-0.002	0.003	-0.008	0.004
Improved	0.002	0.003	-0.004	0.009	0.003	0.003	-0.004	0.009	0.006	0.004	-0.002	0.014
CLUimproved	-2.316	1.571	-5.395	0.763	-4.362	2.264	-8.800	0.075	-2.457	2.090	-6.553	1.640
CLUimproved*Improved	0.006	0.012	-0.017	0.029	0.070	0.061	-0.049	0.189	0.141	0.103	-0.062	0.343
Semi-natural	0.006	0.004	-0.003	0.014	0.006	0.006	-0.006	0.018	1.45E-5	0.002	-0.005	0.005
CLUsemi-natural	-0.746	1.361	-3.413	1.922	-2.403	1.707	-5.748	0.942	0.060	0.531	-0.982	1.101
CLUsemi-natural*Semi-natural	0.012	0.019	-0.026	0.050	0.123	0.083	-0.040	0.286	0.003	0.006	-0.008	0.014
Bare ground	0.010	0.013	-0.015	0.036	0.009	0.015	-0.020	0.039	-0.001	0.014	-0.028	0.026
Built	-0.007	0.004	-0.014	0.000	-0.006	0.003	-0.012	0.001	-0.006	0.003	-0.013	0.001
Heath	**-0.041**	**0.009**	**-0.059**	**-0.022**	**-0.032**	**0.009**	**-0.049**	**-0.016**	**-0.033**	**0.008**	**-0.049**	**-0.016**
Water	-0.008	0.009	-0.026	0.010	-0.045	0.025	-0.094	0.003	-0.060	0.035	-0.129	0.009
Elevation	6.95E-5	2.90E-4	-4.99E-4	6.38E-4	-3.33E-5	3.25E-4	-6.69E-4	6.03E-4	1.92E-4	3.13E-4	-4.23E-4	8.06E-4
Mean population index	**0.017**	**0.003**	**0.012**	**0.023**	**0.018**	**0.003**	**0.012**	**0.023**	**0.016**	**0.003**	**0.011**	**0.021**
Moran's I	0.040	p = 0.083			0.036	p = 0.092			0.034	p = 0.100		
AICc	3149				3224				3266			
Δ_i	0.000				75.724				116.962			

Table 3.5 Results of GLM analysis relating mean activity level of *P. pygmaeus* along transects to the composition and configuration of the surrounding landscape, measured at three spatial scales. Parameters shown are averaged coefficient estimates, unconditional standard errors and 95% confidence intervals of the averaged coefficients calculated over all possible combinations of explanatory predictors and interaction terms. For each model, Moran's *I* measure of the spatial autocorrelation of residuals, AIC score corrected for small sample size (AICc) and Akaike difference from the best model (Δ_i) are presented. Coefficient estimates with 95% confidence intervals that do not include zero are shown in bold.

	750m				1500m				3000m			
			95% CI				95% CI				95% CI	
Predictor	β	SE	Lower	Upper	β	SE	Lower	Upper	β	SE	Lower	Upper
Arable	0.001	0.003	-0.005	0.006	0.002	0.004	-0.005	0.009	-1.77E-4	0.004	-0.009	0.009
Broadleaved	**0.036**	**0.012**	**0.014**	**0.059**	**0.035**	**0.015**	**0.005**	**0.065**	0.019	0.014	-0.008	0.045
CLUbroadleaved	-0.767	2.138	-4.957	3.424	0.227	2.642	-4.950	5.405	1.915	3.619	-5.178	9.008
CLUbroadleaved*Broadleaved	0.007	0.062	-0.115	0.129	0.002	0.079	-0.152	0.157	0.028	0.097	-0.162	0.218
Coniferous	**0.021**	**0.010**	**0.001**	**0.040**	**0.032**	**0.013**	**0.006**	**0.058**	**0.045**	**0.016**	**0.015**	**0.076**
Improved	**0.021**	**0.006**	**0.009**	**0.034**	**0.023**	**0.008**	**0.008**	**0.039**	**0.023**	**0.008**	**0.006**	**0.039**
CLUimproved	-2.470	2.716	-7.794	2.853	-5.607	4.254	-13.944	2.730	**-11.758**	**4.957**	**-21.475**	**-2.042**
CLUimproved*Improved	0.067	0.065	-0.060	0.193	0.118	0.112	-0.102	0.338	0.206	0.169	-0.126	0.538
Semi-natural	4.92E-4	0.004	-0.008	0.009	0.004	0.007	-0.010	0.018	0.013	0.010	-0.006	0.033
CLUsemi-natural	0.634	2.146	-3.571	4.840	1.217	2.736	-4.146	6.580	-1.041	1.509	-3.998	1.917
CLUsemi-natural*Semi-natural	-0.014	0.022	-0.058	0.030	-0.072	0.073	-0.215	0.071	-0.059	0.062	-0.180	0.063
Bare ground	0.004	0.014	-0.023	0.031	0.014	0.024	-0.033	0.060	0.002	0.022	-0.041	0.045
Built	-0.001	0.003	-0.006	0.005	0.001	0.004	-0.006	0.008	0.003	0.005	-0.006	0.012
Heath	-3.96E-4	0.004	-0.008	0.007	0.001	0.005	-0.009	0.011	-0.006	0.007	-0.020	0.008
Water	0.007	0.013	-0.018	0.032	0.012	0.019	-0.025	0.048	-0.012	0.022	-0.054	0.031
Elevation	**-0.004**	**0.001**	**-0.007**	**-0.002**	**-0.003**	**0.001**	**-0.006**	**-0.001**	-0.002	0.001	-0.005	0.000
Mean population index	**0.078**	**0.031**	**0.017**	**0.138**	**0.081**	**0.031**	**0.020**	**0.142**	**0.065**	**0.031**	**0.004**	**0.126**
Moran's I	-0.003	p = 0.483			0.001	p = 0.463			0.006	p = 0.382		
AICc	2108				2147				2174			
Δ_i	0.000				38.594				65.705			

Table 3.6 Results of GLM analysis relating the presence of *N. noctula* along transects to the composition and configuration of the surrounding landscape, measured at three spatial scales. Parameters shown are averaged coefficient estimates, unconditional standard errors and 95% confidence intervals of the averaged coefficients calculated over all possible combinations of explanatory predictors and interaction terms. For each model, Moran's *I* measure of the spatial autocorrelation of residuals, AIC score corrected for small sample size (AICc) and Akaike difference from the best model (Δ_i) are presented. Coefficient estimates with 95% confidence intervals that do not include zero are shown in bold.

	750m				1500m				3000m			
			95% CI				95% CI				95% CI	
Predictor	β	SE	Lower	Upper	β	SE	Lower	Upper	β	SE	Lower	Upper
Arable	0.002	0.004	-0.006	0.009	0.007	0.005	-0.003	0.017	0.011	0.007	-0.002	0.024
Broadleaved	**0.033**	**0.016**	**0.003**	**0.064**	**0.037**	**0.017**	**0.003**	**0.071**	**0.061**	**0.025**	**0.012**	**0.110**
CLUbroadleaved	-4.868	2.878	-10.509	0.773	-1.229	1.703	-4.568	2.109	-6.600	4.008	-14.456	1.256
CLUbroadleaved*Broadleaved	0.011	0.081	-0.148	0.169	-0.036	0.065	-0.164	0.092	-0.058	0.144	-0.340	0.223
Coniferous	0.002	0.005	-0.008	0.012	0.028	0.018	-0.007	0.063	**0.062**	**0.026**	**0.010**	**0.113**
Improved	0.011	0.007	-0.002	0.025	**0.022**	**0.008**	**0.005**	**0.039**	**0.028**	**0.010**	**0.009**	**0.047**
CLUimproved	**-7.371**	**3.435**	**-14.103**	**-0.640**	-3.668	4.059	-11.623	4.288	-9.366	5.338	-19.827	1.096
CLUimproved*Improved	-0.016	0.035	-0.085	0.053	-0.047	0.063	-0.170	0.076	0.031	0.074	-0.114	0.176
Bare ground	0.005	0.017	-0.029	0.038	-0.020	0.029	-0.077	0.037	-0.012	0.030	-0.072	0.047
Built	**-0.013**	**0.006**	**-0.025**	**-0.001**	-0.003	0.005	-0.012	0.006	0.001	0.005	-0.009	0.010
Heath	-0.009	0.011	-0.030	0.012	-0.006	0.010	-0.025	0.013	-0.012	0.014	-0.039	0.016
Water	0.006	0.016	-0.025	0.036	0.003	0.016	-0.028	0.034	0.013	0.026	-0.037	0.064
Elevation	-9.09E-4	8.79E-4	-0.003	8.14E-4	-5.52E-4	6.91E-4	-0.002	8.01E-4	-5.49E-4	7.23E-4	-0.002	8.68E-4
Mean population index	-0.004	0.011	-0.026	0.017	-0.006	0.010	-0.027	0.014	-0.008	0.010	-0.028	0.013
No. surveys	**0.165**	**0.037**	**0.093**	**0.237**	**0.174**	**0.036**	**0.102**	**0.245**	**0.172**	**0.036**	**0.101**	**0.242**
Length	-3.45E-5	2.02E-4	-4.31E-4	3.62E-4	-2.22E-5	1.99E-4	-4.13E-4	3.68E-4	-3.14E-5	2.02E-4	-4.27E-4	3.64E-4
Northing	**-3.34E-6**	**7.90E-7**	**-4.89E-6**	**-1.79E-6**	**-2.89E-6**	**7.73E-7**	**-4.40E-6**	**-1.37E-6**	**-2.56E-6**	**8.06E-7**	**-4.14E-6**	**-9.77E-7**
Moran's I	0.034	p = 0.075			0.036	p = 0.056			0.03	p = 0.086		
AICc	486				504				500			
Δ_i	0.000				18.293				13.941			

Table 3.7 Results of GLM analysis relating the presence of *E. serotinus* along transects to the composition and configuration of the surrounding landscape, measured at three spatial scales. Parameters shown are averaged coefficient estimates, unconditional standard errors and 95% confidence intervals of the averaged coefficients calculated over all possible combinations of explanatory predictors and interaction terms. For each model, Moran's *I* measure of the spatial autocorrelation of residuals, AIC score corrected for small sample size (AICc) and Akaike difference from the best model (Δ_i) are presented. Coefficient estimates with 95% confidence intervals that do not include zero are shown in bold.

	750m				1500m				3000m			
			95% CI				95% CI				95% CI	
Predictor	β	SE	Lower	Upper	β	SE	Lower	Upper	β	SE	Lower	Upper
Arable	0.004	0.006	-0.007	0.015	0.006	0.006	-0.006	0.019	0.012	0.009	-0.006	0.030
Broadleaved	**0.061**	**0.021**	**0.020**	**0.102**	**0.080**	**0.025**	**0.032**	**0.129**	**0.112**	**0.035**	**0.043**	**0.181**
CLUbroadleaved	-5.188	3.653	-12.349	1.973	-3.032	2.854	-8.626	2.561	-1.681	3.477	-8.495	5.134
CLUbroadleaved*Broadleaved	-0.254	0.231	-0.708	0.199	-0.119	0.148	-0.409	0.171	-0.733	0.547	-1.806	0.340
Coniferous	0.020	0.014	-0.007	0.048	0.031	0.018	-0.005	0.067	**0.090**	**0.045**	**0.002**	**0.178**
Improved	0.002	0.006	-0.010	0.014	0.005	0.007	-0.009	0.019	0.009	0.010	-0.011	0.029
CLUimproved	-4.271	3.610	-11.346	2.805	-0.794	2.158	-5.024	3.436	-0.206	2.487	-5.080	4.668
CLUimproved*Improved	0.006	0.021	-0.035	0.046	-0.016	0.026	-0.067	0.034	-0.002	0.017	-0.036	0.031
Bare ground	-0.016	0.031	-0.076	0.045	-0.010	0.032	-0.073	0.053	0.016	0.046	-0.075	0.106
Built	-0.011	0.007	-0.025	0.003	-0.005	0.007	-0.019	0.009	0.001	0.010	-0.018	0.020
Heath	-0.057	0.040	-0.136	0.022	-0.055	0.042	-0.137	0.028	-0.164	0.085	-0.330	0.001
Water	-0.010	0.015	-0.039	0.020	-0.017	0.023	-0.063	0.029	-0.018	0.032	-0.080	0.043
Elevation	**-0.006**	**0.003**	**-0.011**	**-0.001**	**-0.007**	**0.003**	**-0.012**	**-0.002**	**-0.007**	**0.003**	**-0.013**	**-0.001**
Mean population index	**0.058**	**0.022**	**0.016**	**0.101**	**0.052**	**0.021**	**0.011**	**0.093**	**0.050**	**0.022**	**0.008**	**0.092**
No. surveys	0.058	0.033	-0.007	0.123	0.055	0.033	-0.009	0.119	0.057	0.034	-0.009	0.123
Length	-7.18E-6	2.32E-4	-4.63E-4	4.48E-4	-5.43E-5	2.32E-4	-5.09E-4	4.01E-4	-9.96E-5	2.37E-4	-5.63E-4	3.64E-4
Northing	**-5.60E-6**	**2.05E-6**	**-9.61E-6**	**-1.58E-6**	**-4.97E-6**	**2.06E-6**	**-9.02E-6**	**-9.29E-7**	**-4.74E-6**	**2.32E-6**	**-9.29E-6**	**-1.90E-7**
Moran's I	0.042	$p < 0.001$			0.04	$p < 0.001$			0.038	$p < 0.001$		
AICc	331				341				329			
Δ_i	1.580				11.480				0.000			

3.4. Discussion

3.4.1. Landscape level associations with habitat extent

The incidence of all four bat species was positively associated with the proportion of broadleaved woodland in the landscape, at either the 90% or 95% confidence level, at every spatial scale tested with the exception of the model fitted for *P. pygmaeus* at 3000m. It was the only habitat to be consistently associated with incidence of all four species, and confirms that the positive association with broadleaved woodland demonstrated at patch level by previous studies of most UK bat species is also observed at a landscape scale (Russ and Montgomery 2002; Vaughan et al. 1997; Walsh and Harris 1996). The influence of broadleaved woodland on the distribution of a broad suite of bat species is discussed further in chapter 2.

The proportion of improved grassland was positively associated with incidence of *P. pygmaeus* at all three spatial scales and *N. noctula* at the two larger scales, again indicating a fairly consistent association with this habitat type. The habitat classification scheme used in this study defines improved grassland as grassland swards dominated by productive grass species, managed by reseeding, fertilizer treatment and/or weed control (Jackson 2000). 97% of improved grassland in the UK is agriculturally productive (Fuller et al. 2002), of that, 43% is used for cattle pasture, 32% for sheep pasture and 20% for hay or silage (Carey et al. 2008). *Nyctalus noctula* is often observed foraging over pasture (Mackie and Racey 2007; Vaughan et al. 1997), so an association with improved grassland is expected. Conversely *P. pygmaeus* is most often shown to avoid grassland habitats (Bartonicka et al. 2008b; Nicholls and Racey 2006b; Russ and Montgomery 2002). However, *P. pygmaeus* is strongly associated with linear habitat elements such as tree lines and hedgerows (Downs and Racey 2006; Glendell and Vaughan 2002; Oakeley and Jones 1998; Russ et al. 2003). The network of linear habitat features that subdivide grassland landscapes (at a greater density than in comparable arable habitat, Carey et al. 2008), may explain the landscape-level association between *P. pygmaeus* and improved grassland. *Pipistrellus pipistrellus* is also strongly associated with linear features (Verboom and Huitema 1997; Walsh and Harris 1996) but did not show an association with improved grassland. However, it is much more of a generalist forager than *P. pygmaeus* (Sattler et al. 2007), and its presence in almost all landscape types may mask habitat associations at a landscape scale. Of note is the lack of an association between *E. serotinus* and the proportion of improved grassland in the landscape. At patch level, this species shows a strong association with pasture (Catto et al. 1996; Robinson and Stebbings 1997), however this association was not observed in this study at a landscape scale. The use of pasture by *E. serotinus* is opportunistic, being particularly related to the presence of fresh cattle dung (Catto et al. 1996). It may be that such transient habitat associations are not readily revealed at a landscape scale.

A further association demonstrated at patch level by previous studies, but not apparent at a landscape scale in the present study, was the association between *P. pygmaeus* and water bodies (Davidson-Watts et al. 2006b; Nicholls and Racey 2006b). Features less than 50m in length or 0.5ha in area were not captured by the habitat map used to quantify landscape structure. As such, small water features were not represented by the inland water habitat category, with the result that the inland water habitat category may have been too low resolution to appropriately model the associations between bats and water features.

The present study found a positive association between *P. pygmaeus* and coniferous woodland extent measured at all spatial scales, and a positive association between *N. noctula, E. serotinus* and coniferous woodland extent that largest spatial scale. This is in contrast to studies which assess species occurrence within habitat patches, where coniferous woodland is either used in proportion to availability (Russ and Montgomery 2002), or avoided (Racey and Swift 1985; Walsh and Harris 1996). The avoidance of coniferous woodland by bats has been attributed a paucity of roosting opportunities and the low abundance of invertebrate prey supported by contiguous plantations (Fahy and Gormally 1998; Winter 1983). However, a population of *M. nattereri* was found to make extensive use of coniferous woodland as foraging habitat when the availability of roosting opportunities was increased by the provision of artificial bat boxes (Mortimer 2006). This indicates that coniferous woodland can provide suitable foraging habitat for bats. The species examined in the current study all show a preferences for areas of open woodland (Kanuch et al. 2008; Kusch et al. 2004; Sattler et al. 2007), and in particular forage along woodland edge in preference to woodland interior (Kanuch et al. 2008;

Nicholls and Racey 2006b; Rachwald 1992). Where open canopy, clearings and edges exist within coniferous woodland, invertebrate diversity and abundance are increased (Butterfield et al. 1995) and can be comparable to broadleaved woodland (Day et al. 1993; Woodcock et al. 2003). UK forestry policy requires all new woodland to include at least 10% open space, and that the open space content of existing woodland be brought in line with this standard where possible (Forestry Commission 2004). It also requires that woodland edges, rides and open spaces are managed with the needs of biodiversity conservation in mind. As a result landscapes that contain a greater cover of coniferous woodland may also provide a greater density of the woodland; this may explain the positive association between coniferous woodland and foraging incidence observed in this study.

A negative association between the proportion of heath in the landscape and the incidence of *P. pipistrellus* was seen at all spatial scales tested. Heath in this study was characterised by the presence of ericaceous and gorse shrub cover, and an absence of tree cover. When heath occurs in upland areas it is generally used less than would be expected by bats, as a result of its exposed nature and typically lower insect densities than lowland habitat (Russ and Montgomery 2002; Walsh and Harris 1996). This may explain the negative association between *P. pipistrellus* incidence and heath shown here. Negative habitat associations involving the other bat species assessed in this study would be harder to demonstrate, due to their relative scarcity across all habitat types.

3.4.2. Habitat aggregation

The relationship between bat incidence and habitat aggregation, independent of habitat extent, was assessed for two focal habitat types: broadleaved woodland and improved grassland. Effects of habitat aggregation were found for three of the four species tested. However, in contrast to measures of habitat extent, associations with habitat aggregation at the 95% confidence level were seen at only one of the three spatial scales tested (750m for *N. noctula* and 3000m for *P. pipistrellus* and *P. pygmaeus*), and appeared only once in a best performing model. It is unlikely that habitat aggregation would effect bat incidence at a single, discrete spatial scale, rather this finding suggests that the independent effect of habitat aggregation is weak overall, relative to the effect of habitat extent when measured at an appropriate scale. Similarly weak effects of habitat configuration, relative to habitat loss, have been reported across a broad range of taxa (Fahrig 2003).

Two species, *P. pygmaeus* and *N. noctula,* were positively associated with the proportion of improved grassland in the landscape. Both of these species were also associated with grassland aggregation; in both cases bat incidence increased as improved grassland habitat became more dispersed. An interaction between aggregation and extent was not supported. A negative association with improved grassland aggregation may be explained by a preference for grassland edge habitat. In the UK, improved grassland is often bordered by linear features such as hedgerows and tree-lines. As noted above, *P. pygmaeus* is strongly associated with such features, and may therefore benefit from grassland disaggregation. Insect abundance is increased adjacent to linear features, particularly in the presence of trees (Lewis 1969, 1970; Merckx et al. 2010; Merckx et al. 2009), and this effect extends into the adjacent field by up to 10 times the height of the feature (Lewis 1969), so linear features may also benefit bats that do not directly forage along the feature itself.

An association with broadleaved woodland aggregation was shown by *P. pipistrellus* when measured within 3000m of the transect, however the direction of the relationship was dependent on the extent of broadleaved woodland in the landscape. At proportions of broadleaved woodland above 9%, *P. pipistrellus* incidence was greater in landscapes with more dispersed woodland. *Pipistrellus pipistrellus* can be characterised as a woodland edge specialist, found more often foraging along woodland edge than in the woodland interior (Kanuch et al. 2008; Nicholls and Racey 2006b). A preference for woodland edge over woodland interior may explain why, at higher proportions of broadleaved woodland, *P. pipistrellus* actually benefits from woodland disaggregation. Positive associations between bat incidence and forest fragmentation have also been observed in tropical forest systems, generally involving species able to exploit successional or matrix habitats (Gorresen and Willig 2004; Ochoa 2000). A study of bat assemblages on islands in Lake Gatún, Panama, found edge-sensitivity, represented by the difference in captures at edge relative to interior sites, was the strongest ecological correlation of sensitivity to fragmentation (Meyer et al. 2008). A preference for edge habitat may therefore ameliorate the negative effects of fragmentation.

The opposite relationship with broadleaved woodland aggregation was seen at low woodland extents. Here *P. pipistrellus* incidence was greater in landscapes in which broadleaved woodland was more clumped. Several studies that model population persistence in simulated landscapes have found the negative effects of habitat disaggregation become more marked at lower extents of focal habitat (Fahrig 1998; Flather and Bevers 2002), and a review of the literature suggests this may also be the case for birds and mammals inhabiting island systems (Andrén 1994). However other studies, both theoretical and empirical, have failed to detect an interaction between habitat extent and disaggregation (Fahrig 1997; Trzcinski et al. 1999; Villard et al. 1999). Although there is clear ecological explanation as to why *P. pipistrellus* may benefit from habitat disaggregation at high woodland extents, the processes which may lead to detrimental effects at low extents are not clear. The index of aggregation used in this study is based on the number of like adjacencies between habitat pixels, and as a result it represents the break up of large patches into smaller habitats more closely than it does the increasing distances between patches. However, it is unlikely that P. pipistrellus is negatively affected by patch size. This species forages in edge habitat, and shows an equal association with woodland edge as it does with other structurally similar habitats such as tree-lines (Verboom and Huitema 1997). In addition it does not rely on woodland for roosting opportunities (Dietz et al. 2009). A similar response to broadleaved aggregation was not shown by other species tested, despite positive associations between the incidence of every species and woodland extent. I therefore suggest that this result is interpreted with caution.

3.4.3. Scale dependency

Variation in the relationship between incidence and landscape structure, and with individual measures of landscape composition and configuration, has been shown by many taxa, including bats (Gorresen et al. 2005), bees (Steffan-Dewenter et al. 2002) and birds (Mitchell et al. 2001; Söderström and Pärt 2000), and most often corresponds to variation in home range size.

For the two species with the smallest home ranges, *P. pipistrellus* and *P. pygmaeus*, models fitted at the smallest spatial scale performed better than models at the larger two spatial scales. The home range of *Pipistrellus pipistrellus* and *P. pygmaeus* tends to extend approximately 3-4km from the roost, although the majority of foraging effort is concentrated into a ‘core’ area usually within 2km of the roost (Bartonicka et al. 2008a; Davidson-Watts and Jones 2006a; Feyerabend and Simon 2000; Nicholls and Racey 2006a). This finding shows that *P. pipistrellus* and *P. pygmaeus* respond to landscape structure at a scale smaller even than their core foraging range. The trend for better model performance at smaller scales was less distinct for *N. noctula*, and completely absent for *E. serotinus*, the two species with the largest home ranges (approximately 10km and 7km from the roost, respectively, Catto et al. 1996; Harbusch 2003; Mackie and Racey 2007; Meschede and Heller 2000; Robinson and Stebbings 1997; Simon et al. 2004). It therefore appears that the scale at which bats respond to the landscape is linked to home range size, although the optimal scale at which to measure the effect of landscape structure may lie below the core foraging range of the species.

The strength of the relationship between bat incidence and measures of landscape composition and configuration varied across scales, with no one scale capturing all associations demonstrated by each species. For example, associations between the two *Pipistrellus* species and measures of habitat aggregation, and between *N. noctula* and *E. serotinus* and the proportion of coniferous woodland, were seen only at the largest spatial scale. This suggests that bats respond to different habitat types and different measures of landscape structure at different scales. However, with data for only four bat species, general patterns of spatial dependency are hard to determine.

3.4.4. Conservation implications

Of the nine habitat types assessed in this study, broadleaved woodland was the only habitat positively associated with incidence of all four bat species, suggesting that the provision of broadleaved woodland should form the focus of bat conservation strategies at a landscape scale. The lack of clear evidence for a negative effect of broadleaved woodland disaggregation suggests that increasing the extent of woodland should be prioritised, rather than altering its configuration. This study also highlights the potential of improved grassland and coniferous woodland to provide foraging habitat for bats. In particular, consideration should be given to the role of boundary features in influencing habitat quality for bats in pastoral landscapes. Incorporating bat conservation measures within agricultural and forestry policy will help meet international obligations to conserve these species (e.g. EC Habitats Directive, Council Directive 92/43/EEC). However, response to landscape structure varied by species and by scale. Conservation actions assessed at one scale may not achieve equivalent results when applied at a different scale, and the benefits will not apply equally to all species.

This study demonstrates that the effect of habitat loss can differ in both strength and direction from the effect of habitat disaggregation. Future studies of bat-habitat relationships at a landscape scale should seek to distinguish between the effects of landscape composition and configuration. Such an approach will prevent the negative consequences of habitat loss being erroneously attributed to habitat disaggregation, which may in fact have negligible, or even positive effects on bat populations.

3.5. References

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3.6 Appendix I

Table 3.8. Complete list of predictors assessed for inclusion in models bat incidence along transect to the composition and configuration of the surrounding landscape. Cor. = predictor excluded due to an unacceptable level of correlation with a retained predictor (Pearson r^2 >0.5), insuf. var. = predictor excluded due to insufficient variation (appearing in <10% of observations).

Predictor	Units	Description	Notes
Broadleaved	%	Proportion of broad-leaved and mixed woodland (canopy cover greater than 20%), or scrub (with cover greater than 30%)	
CLUbroad		Aggregation of broadleaved woodland, represented by an index of 'clumpiness'.	
Coniferous:	%	Proportion of coniferous woodland or plantation (canopy cover greater than 20%)	
Arable	%	Proportion of cereals, horticulture, perennial crops or unknown arable crops. Also includes freshly ploughed land and rotational setaside	
Improved	%	Proportion of improved grassland and setaside grass	
CLUimproved		Aggregation of improved grassland, represented by an index of 'clumpiness'.	
Semi-natural	%	Proportion of rough, calcareous and acid semi-natural grasslands and bracken.	Corr. (*N. noctula* and *E. serotinus* only)
CLUsemi-natural		Aggregation of semi-natural grassland, represented by an index of 'clumpiness'	Not included in *N. noctula* or *E. serotinus* models due to the removal of proportion of semi-natural grassland
Heath	%	Proportion of dwarf and open shrub heath	
Wetland	%	Proportion of fen, marsh and swamp	Insuf. var
Bog	%	Proportion of bog habitat	Insuf. var
Montane	%	Proportion of montane habitats	Insuf. var
Bare ground		Inland rock, bare ground and despoiled semi-natural areas	
Built	%	Proportion of continuous urban, suburban and rural developed areas	
Supra-littoral	%	Proportion of supra-littoral rock and sediment	Insuf. var
Littoral	%	Proportion of Littoral rock, sediment and saltmarsh	Insuf. var
Water	%	Proportion of inland water	
Elevation	m	Mean elevation of landscape, in metres above sea-level	
Included in every model:			
Mean population index		National population index averaged over the years each site has been surveyed	
Number of surveys		Number of surveys used to determine species presence (*N. noctula* and *E. serotinus* only)	
Length	m	Transect length (*N. noctula* and *E. serotinus* only)	

Chapter 4

Optimising the conservation benefits of hedgerows: how the physical characteristics of linear features and the proximity of foraging habitat affect their use by bats

Abstract

Within agricultural landscapes, linear features such as hedgerows and tree-lines provide valuable habitat for many species. Agri-environment schemes offer financial incentives for the creation and management of hedgerows in order to provide an environmental improvement in rural landscapes. Optimising the biodiversity benefits provided by these features maximises the effectiveness of these schemes. Here, I use data from a national acoustic bat survey to examine the incidence of four bat species adjacent to linear features in rural areas. The use of linear features is 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 categorised into three types: hedgerows without trees, hedgerows with sparse trees (comprising < 50% tree canopy) and tree-lines (>50% tree canopy). Occurrence of *Pipistrellus pipistrellus* was higher adjacent to linear features than in open areas, and all types of linear feature had a similar effect. The use of linear features by *Pipistrellus pygmaeus* depended on tree density and the proximity of woodland; only linear features containing trees were consistently beneficial to *P. pygmaeus* across all distances from woodland. The use of linear features by *P. pipistrellus* and *P. pygmaeus* was not affected by hedgerow width or by the presence of water. The incidence of *Nyctalus noctula* and *Eptesicus serotinus* was unaffected by the density of linear features of any type. Agri-environment schemes do not currently provide compensation for the establishment of hedgerow trees. The effectiveness of hedgerow management for biodiversity could be improved by measures that encourage the establishment and retention of hedgerow trees.

4.1. Introduction

Hedgerows and tree-lines are a common feature of agricultural landscapes worldwide, and play a key role in sustaining rural biodiversity. They increase structural heterogeneity, landscape connectivity and botanical diversity, and provide breeding sites, food resources and cover for foraging and local movement of 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 species associated with farmland that have undergone widespread population declines across Britain and Europe (Robinson and Sutherland 2002).

Intensification of agriculture over the last 60 years has led to the widespread removal of hedgerows and tree-lines. Since 1940, hedgerows have been removed from the American Midwest at a rate of between 0.6% and 3% per annum (Baltensperger 1987), while a study of medieval field patterns in the Czech Republic recorded a 71% reduction in hedgerow length between 1950 and 2005 (Sklenicka et al. 2009). In the UK, large scale removal of hedgerows began in the 1960s (Robinson and Sutherland 2002) with the loss of approximately 600,000km, or 60% of total length, between 1960 and 1993 (Robinson 1997), and a further loss of 12 000km, or 1.7% of total length, between 1998-2007 (Carey et al. 2008). Neglect is also having a detrimental effect on UK hedgerows. Between 1998-2007 the length of hedgerows classified as ‘managed’ by the UK Countryside Survey declined by 6.2% (Carey et al. 2008). Only 41% of UK hedgerows surveyed between 2006-2008 were classified as being in favourable condition (Wolton 2010). The primary causes of poor condition were nutrient enrichment, excessive gaps, and insufficient height or width as a result of excessive trimming.

In the EU, both the EC Habitats Directive (Council Directive 92/43/EEC) and Common Agricultural Policy (Cross compliance regulations EC No. 73/2009) require the protection of linear features. In the UK, basic standards of protection and management are required by national legislation (the Forestry Act 1967, the Hedgerow Regulations 1997) and the Single Farm Payment Scheme. Additional financial incentives to manage hedgerows for the benefit of biodiversity are provided by agri-environment schemes.

The effectiveness of such incentives, both in terms of cost and biodiversity gain, can be improved by an understanding of how the benefits provided by linear features are affected by factors such as physical structure and landscape context.

Many European bat species make preferential use of hedgerows and tree-lines (Downs and Racey 2006; Entwistle et al. 1996; Glendell and Vaughan 2002; Limpens et al. 1989; Limpens and Kapteyn 1991; Pocock and Jennings 2008; Racey and Swift 1985; Robinson and Stebbings 1997; Russ et al. 2003; Russ and Montgomery 2002; Walsh and Harris 1996). These features provide foraging habitat for insectivorous bats (Racey and Swift 1985; Walsh and Harris 1996), they harbour greater insect densities than open habitats (Lewis 1969, 1970), and are structurally similar to the woodland edges preferred by many bat species (Kanuch et al. 2008; Kusch et al. 2004; Nicholls and Racey 2006). They may also function to increase landscape connectivity, providing a commuting route between foraging patches that is sheltered from predators and the elements (Limpens et al. 1989; Verboom and Spoelstra 1999). There is also evidence that the density of linear habitat in the landscape may influence bat distribution. Oakeley and Jones (1998) found *Pipistrellus pygmaeus* maternity roosts were located in areas with a greater density of hedgerows with emergent trees than was found around randomly selected points, and Verboom and Huitema (1997) found the number of *Eptesicus serotinus* passes recorded along linear elements was positively associated with the density of linear landscape elements (woodland edge, hedgerows and tree-lines) within a 1x1km square. 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* species) 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 by bats. 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 affect on *Pipistrellus pipistrellus* activity (Verboom and Huitema 1997). Studies that make a distinction between hedgerows and tree-lines point to a general preference for tree-lines over hedgerows, although the effect of emergent trees within hedgerows is not known. For example, Russ and Montgomery (Russ and Montgomery 2002) found *P. pipistrellus*, *P. pygmaeus* and *Nyctalus leisleri* activity was greater alongside tree-lines than would be predicted by their availability, while hedgerows were used according to availability by *P. pipistrellus* and less than would be predicted by their availability by *P. pygmaeus* and *N. leisleri.* Downs and Racey (Downs and Racey 2006) found activity (*P. pipistrellus, P. pygmaeus* and *Myotis daubentonii* combined) alongside linear features was highest along woodland edges and streams, and lowest along hedgerows, the latter type used less than would be expected. In a study of linear feature use in the Netherlands, it was noted that *P. pipistrellus* was not observed foraging along features less than 6m high, also suggesting a greater association with tree-lines as apposed to hedgerows (Verboom and Huitema 1997).

In this study I investigate how the use of linear features by bats in rural landscapes is affected by the physical characteristics of the feature and the proximity of foraging habitat. I use data from a national survey of bat distribution in the UK to relate the incidence of four bats species, *P. pipistrellus, P. pygmaeus, Nyctalus noctula* and *E. serotinus,* to hedgerow width, the density of hedgerow trees, the presence of water and the proximity of preferred foraging habitat, represented here as the distance to the nearest woodland fragment. If linear features function primarily as commuting routes, I would expect the association between bats and linear features to increase with increasing proximity to woodland. However, if linear features also provide foraging habitat, the use of linear features would either be unaffected by woodland proximity, or would be greater in locations further from woodland.

4.2. Methods

The distribution and ecology of the study species are described in chapters 1 and 3.

4.2.1. Survey methodology and sample construction

Species incidence was recorded along 315 field transects distributed across the UK, surveyed between 1998-2007 as part of the National Bat Monitoring Programme, a nationwide survey using standardised methodology (NBMP, Walsh et al. 2001). Each transect was approximately 3km long, and was divided into twelve approximately equal sections. Surveyors walked the transect with a heterodyne bat detector, beginning 20 minutes after sunset, and recorded the number of *N. noctula* and *E. serotinus* ‘passes’ heard along each section. At the end of each section, surveyors completed a two minute point count, noting the number of *P. pipistrellus* and *P. pygmaeus* passes heard. Each transect was walked twice during July, and surveys were repeated each year. Further details of the survey methodology are provided in chapter 3. Transect routes were recorded on enlarged 1:25 000 Ordnance Survey maps, and digitised with reference to 1:25 000 raster OS data tiles.

Species presence along each transect section and at each point count was determined by combining data from all surveys undertaken between 1998-2007. Occasionally transects routes were altered between years. If the new point count or transect section was within 10m of the original location (measured from the centroid of the transect section), data from the new and original sections were combined when determining species presence. If the new point count or transect section differed by more than 10m from the original location, it was treated as a separate section. To reduce falsely assigned absences, those point counts or transect sections where the study 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. Species range was delimited as described in chapter 3. This study focuses on the use of linear features by bats in rural areas as distinct from linear features in urban areas, such as street trees and gardens, which are subject to different legislation and management pressures. Rural habitats included all habitat classes except urban and suburban areas, as defined by the Landcover Map 2000 (Fuller et al. 2002). All point counts that fell within a rural habitat class, or transect sections with greater than 75% of their length within rural habitat classes, were included in the analysis. The final sample size and incidence of each species (ranging from 44-10%, table 4.1) was sufficiently large to permit multivariate logistic regression analysis.

Table 4.1. Number of points count/transect sections used in the analysis, the number of transects they are drawn from, and the percentage of sections occupied.

Species	Points/Sections	Transects	Percentage of points/sections occupied
P. pipistrellus	2357	291	44%
P. pygmaeus	2354	291	19%
N. noctula	2170	219	21%
E. serotinus	1607	161	10%

4.2.2 Detection radii

A bat heard on a detector may be located some distance from the observer. As such, habitat data was sampled from within the ‘detection radius’ of each point count and 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. A roost of each species was identified, and monitored at dusk to identify commonly used flight paths. Echolocation calls made by bats as they emerge from the roost can differ from ‘typical’ search phase echolocation calls, so a point was chosen at a distance from the roost where calls were overwhelmingly of the typical kind. One surveyor remained on the flight path, while a second surveyor moved perpendicular to the flight path until passing bats (as indicated by the first surveyor) could no longer be heard on the detector, and the distance between the two surveyors was measured. To ensure the most inclusive buffer was used, the maximum distance measured (rounded up to the nearest 5m), was chosen to represent the detection radii of the species. Fresh batteries were used each night, and estimates were not made during rain or mist, due to the increased attenuation caused by high humidity. For *P. pipistrellus, P. pygmaeus* and *E. serotinus*, passes by at least twenty bats were assessed on two separate nights, for *N. noctula,* six passes were used. Roosts were located within Norfolk and Suffolk, in eastern England. The detection radii (and range of distances measured) for each species were: *P. pipistrellus* 20m (14-19m) and *P. pygmaeus* 20m (14-18.5m), *E. serotinus* 35m (27-32m) and *N. noctula* 75m (66-73m). This resulted in sample areas of 0.13 ha for the *Pipistrellus* species, surveyed using point counts, and of approximately 56.7 ha for *N. noctula* and 22.2 ha for *E. serotinus,* based on the average transect section length of 262m.

4.2.3. Habitat data

Linear features were digitised from GoogleEarth orthorectified and georeferenced aerial photographs with a resolution of 50cm per pixel or better, taken over the period 1999-2008. 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 0.4-3.5m. Locations differed by on average 2.0m, and by no more 3.8m.

All linear features comprising shrubs or trees, less than 30m wide and located within 75m of a transect were digitised. Digitised linear features were assumed to represent a random sample of linear features available across 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. Features were classified as either hedgerows without trees, hedgerows with sparse trees, or tree-lines (see table 4.2 for category definitions). Trees were distinguished from shrubs by their open grown canopy, extending beyond that of the shrub component of the feature. The continuity/gappiness of the feature was also estimated, however there was insufficient variation in this characteristic to include it as an explanatory predictor in the analysis. As such, only continuous or near continuous features (features with gaps less than 20m wide and comprising no more than 50% gaps in total), were used in the analysis. Where present, the width of the shrub component of the linear feature was also classified, as either narrow (<2m), medium (2-5m) or wide (>5m). In the absence of information describing the response of bats to variation in linear feature characteristics, category definitions were based on the observed variation in width, continuity and tree density, as determined by a visual inspection of aerial photographs from across the UK. 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 20m.

Each point count was classified according to the type of linear features present within the detection radius, or as an ‘open area’ if no linear features were present within 40m (table 4.2). Point counts that did not fall into any category were removed from the dataset (table 4.1). Transect sections covered a far greater area than point counts, so rather than categorising each section according to linear feature type, the density of linear features of each type within the detection radius was calculated.

The proximity of woodland habitat was derived from OS MasterMap. Woodland is defined within OS MasterMap as an area in which individual trees are no more than 30m apart. Patch sizes ranged from 26km^2 to less than 10m^2 (mean 0.02km^2), representing all woodland types from relatively continuous woodland blocks to highly fragmented small farm woodlands. Distance to the nearest patch of broadleaved or mixed woodland, and distance to the nearest woodland patch of any type (broadleaved, mixed or coniferous) were measured from the point count location or mid point of the transect section. Distances were square root transformed for analysis. Both woodland measures were highly correlated (Spearman *r* >0.8). Coniferous woodland can provide foraging habitat for bats (Mortimer 2006 and chapter 3), so distance to the nearest woodland patch of any type was chosen as the more inclusive measure of foraging habitat proximity. Easting and northing (OSGB 36) were measured from the point count location or mid point of the transect section. Additional explanatory predictors measured only at point counts included width of hedgerows and the presence of water within the detection radius, the latter determined from OS MasterMap data. As a result of the large area sampled by each transect section, it was not considered appropriate to use data collected 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 for by including the number of separate surveys at each point or transect section, and for *N. noctula* and *E. serotinus*, section length. 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 a 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 2008). For each transect the mean population index of each species was calculated by averaging the national index value over the years the transect was surveyed. Previous analysis of NBMP data suggests that site occupancy is strongly influenced by landscape context (chapters 2 and 3), therefore the proportion of broadleaved woodland and improved grassland within 1.5km of each transect was calculated from the Landcover Map 2000, (Fuller et al. 2002), a description of this dataset is provided in chapter two). All predictors demonstrated acceptable levels of colinearity (squared Spearman correlation coefficient <0.5 (Freckleton 2002). Spatial data processing was carried out using ArcGIS 9.2 (ESRI, Redlands CA).

Table 4.2. Summary of predictors used to model the effect of linear feature characteristics on the incidence of bats

	Units	Description
Predictors included in *Pipistrellus* models		
Hedgerow width	Categorical	
Narrow		Less than 2m wide
Medium		2-5m wide
Wide		Greater than 5m wide
Feature type	Categorical	
Hedgerow without trees		Shrubby linear feature without trees
Hedgerow with sparse trees		Shrubby linear feature with a tree canopy comprising less than 50% of its length
Tree-line		Linear feature with a tree canopy comprising more than 50% of its length, with or without a shrub understorey
Open area		Reference category. No linear features within 40m
Distwood	sqrt(m)	Distance from point count location to nearest woodland patch
Water	0/1	Presence of water features within detection radius
Predictors included in *N. noctula* and *E. serotinus* models		
Feature density (entered into models as a group of three predictors)		
Hedgerows without trees	km/km^2	Density of hedgerows without trees within detection radius of transect section. Category definition as *Pipistrellus* sp.
Hedgerows with sparse trees	km/km^2	As above
Tree-lines	km/km^2	As above
Distwood	sqrt(m)	Distance from mid-point of transect section to nearest woodland patch
Control covariates included in every model		
Easting	m	With reference to OSGB 36
Northing	m	As above
Number of surveys		Number of surveys used to determine species presence
Length	m	Transect section length (*N. noctula* and *E. serotinus* only)
Mean population index		National population index averaged over the years each site has been surveyed
Broadleaved woodland	%	Proportion of broadleaved woodland within 1.5km of the transect
Improved grassland	%	Proportion of improved grassland within 1.5km of the transect

4.2.4. Model structure and statistical analysis

Hierarchical logistic regression was used to relate incidence of bats to the characteristics of linear features, with transect ID fitted as the random intercept to allow for dependence between points located along the same transect (Rabe-Hesketh and Skrondal 2008). The effect of hedgerow width on the incidence of *Pipistrellus* bats was assessed first, using the subset point counts with hedgerows within the detection radius. The importance of hedgerow width to *Pipistrellus* bats was assessed by comparing the

AIC*c* score of a null model containing only control covariates to one that in addition contained a categorical predictor describing hedgerow width (for classification see table 4.2). The effect of medium and wide hedgerows was estimated relative to narrow hedgerows. The importance of each level of hedgerow width was assessed based on whether the 95% confidence interval of the coefficient estimate overlapped zero.

The remaining predictors were assessed using a model averaging procedure incorporating the full dataset. The effect of woodland proximity and the presence of water (*Pipistrellus* species only) on the use of linear features by bats was modelled by including the interactions *feature type*distwood* and *feature type*water*. In addition, variation in the use of linear features across the UK was assessed by modelling *feature type*easting* and *feature type*northing*. A candidate set of models comprising all possible combinations of predictors and interaction terms was fitted, and average parameter estimates were calculated using the methods described by Burnham and Anderson (2002). For analysis, the effect of feature type was estimated relative to *open*. Where necessary, predictors were centred by subtracting the mean value from each observation to reduce colinearity between main effects and interaction terms. The relative importance of each predictor within the averaged model was assessed by summing the Akaike weight of each candidate model in which that predictor appeared. 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 selection probabilities requires that each predictor appears with a similar frequency within the candidate set. This creates a problem when the candidate set contains interactions, as the main effects will appear in twice as many models as the interaction terms. To create a balanced candidate set, the importance of the interactions terms was first assessed over all possible combinations of explanatory predictors (39 models for *Pipistrellus* species and 13 models for *N. noctula* and *E. serotinus*, control covariates listed in table 4.2 were included in every model). An interaction term was deemed to be supported if it appeared within the subset of substantially supported models (Δ_i <2, (Burnham and Anderson 2002), and the 95% confidence interval of the averaged coefficient estimate did not overlap zero. Supported interaction terms were retained, and all models in which the main effect appeared without the associated interaction term were removed from the candidate set. Where these conditions were not met, there was considered to be little support for inclusion of the interaction term within the averaged model, and all models containing the interaction term were removed from the candidate set. Averaged parameter estimates and selection probabilities were then recalculated over this new candidate set of models. All analyses were performed using STATA 10 (StataCorp, TX).

4.3. Results

4.3.1. Bat species abundance

Pipistrellus pipistrellus was the most commonly encountered of the two *Pipistrellus* species, present at twice as many point counts locations (44%) as *P. pygmaeus* (present at 19% of point count locations, table 4.1). 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, while *E. serotinus* occurred along 10% of transect sections.

4.3.2. UK linear feature stock

In total 891km of linear features were mapped. Of the total length of mapped features, 95% were continuous or near continuous, classified as comprising less than 50% gaps and with no gaps greater than 20m. 43% of the continuous or near continuous features were classified as hedgerows without trees, 11% as hedgerows with sparse trees and 46% as tree-lines. 38% of hedgerows were less than 2m wide, 42% were between 2m and 5m wide, and 20% were greater than 5m wide.

4.3.3. The use of linear features by P. pipistrellus and P. pygmaeus

Hedgerow width

The incidence of *P. pipistrellus* and *P. pygmaeus* along hedgerows was not affected by hedgerow width, represented here using three categorical levels; narrow, medium and wide. The addition of a predictor describing hedgerow width to the null model resulted in an increase in AIC*c* score ($\Delta_i > 3$ for both species, table 4.3), indicating that the inclusion of hedgerow width does not improve the explanatory power of the null model, and an association between bat incidence and hedgerow width is therefore unlikely.

Table 4.3 Comparison of the performance of the null model (containing only the control covariates listed in table 4.2) with a model that in addition contains a categorical predictor describing hedgerow width, estimated over the subset of point counts containing hedgerows.

Model	*K*	AIC$_c$	Δ_i
P. pipistrellus (*n*=758)			
Null model	8	815.40	0
Null model + hedge width	10	818.83	3.430
P. pygmaeus (*n*=757)			
Null model	8	658.92	0
Null model + hedge width	10	662.57	3.655

The 95% confidence intervals of the effect of medium and wide hedgerows, estimated relative to narrow hedgerows, overlapped zero (table 4.4). This suggests that the effect of medium and wide hedgerows on bat incidence does not differ from that of narrow hedgerows, providing further evidence that *P. pipistrellus* and *P. pygmaeus* do not discriminate between hedgerows of different widths.

Table 4.4 Parameter estimates for the logistic regression model relating bat incidence at point counts to hedgerow width.

			95% CI	
Predictor	ß	SE	Lower	Upper
P. pipistrellus				
Hedgerow width (with reference to narrow hedgerows)				
Medium	-0.170	0.263	-0.685	0.345
Wide	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
P. pygmaeus				
Hedgerow width (with reference to narrow hedgerows)				
Medium	0.077	0.321	-0.552	0.707
Wide	-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

Physical characteristics and woodland proximity

For *P. pipistrellus,* models containing interaction terms did not receive substantial support within the candidate set representing all possible combinations of explanatory predictors and interactions (table 4.9, appendix I). Additionally the 95% confidence intervals of the averaged regression coefficients for every interaction term overlapped zero (table 4.10, appendix I). Models containing interaction terms were removed from the candidate set and Akaike weights were recalculated over the remaining seven models (table 4.5).

Table 4.5 Results of AIC-based model selection across a candidate set of models predicting the occurrence of *P. pipistrellus* and *P. pygmaeus* at point count locations. Candidate set was defined after assessing the importance of interaction terms (Appendix I). For each model the number of estimable parameters (K), AIC score corrected for small sample size (cAIC$_c$), Akaike difference from the best model (Δ_i) and Akaike weight (w_i) are presented.

Model [1]	K	cAIC$_c$	Δ_i	w_i
P. pipistrellus				
Feature type + distwood + water	13	2368.51	0.000	0.556
Feature type + distwood	12	2368.98	0.464	0.441
Feature type + water	12	2380.57	12.059	0.001
Feature type	11	2381.56	13.042	0.001
Distwood + water	10	2402.64	34.125	2.16E-08
Distwood	9	2408.04	39.526	1.45E-09
Water	9	2426.24	57.724	1.63E-13
P. pygmaeus				
Feature type + distwood + feature type*distwood	15	1808.13	0.000	0.710
Feature type + distwood + water + feature type*distwood	16	1809.93	1.793	0.290
Water	9	1834.91	26.774	1.09E-06

1. All models included site fitted as a random intercept, and the control covariates easting, northing, number of surveys, mean population index, proportion of broadleaved woodland and proportion of improved grassland within 1.5km. See table 4.2 for predictor definitions.

Incidence of *P. pipistrellus* at point counts adjacent to hedgerows without trees, hedgerows with sparse trees and tree-lines was higher than at point counts in open areas (fig. 4.1). The 95% confidence intervals of the averaged coefficient estimates of feature type overlapped substantially (table 4.6), suggesting that the strength of association between *P. pipistrellus* and all three types of linear feature is similar. Feature type had a selection probability of almost one, indicating very strong support for the importance of this predictor. The importance of distance to the nearest woodland patch also received very strong support ($\Sigma w_i = 0.998$). Incidence of *P. pipistrellus* increased as distance to the nearest woodland patch decreased. The lack of support for an interaction between feature type and distance to the nearest woodland indicates that the use of linear features by *P. pipistrellus* is not affected by woodland proximity. Interactions between feature type and easting, northing and the presence of water also received little support, indicating that the association of *P. pipistrellus* with linear features is independent of the presence of water, and remains constant across the UK. The main effect of water on *P. pipistrellus* incidence also received little support ($\Sigma w_i = 0.558$, 95% CI of averaged coefficient -0.075-0.367).

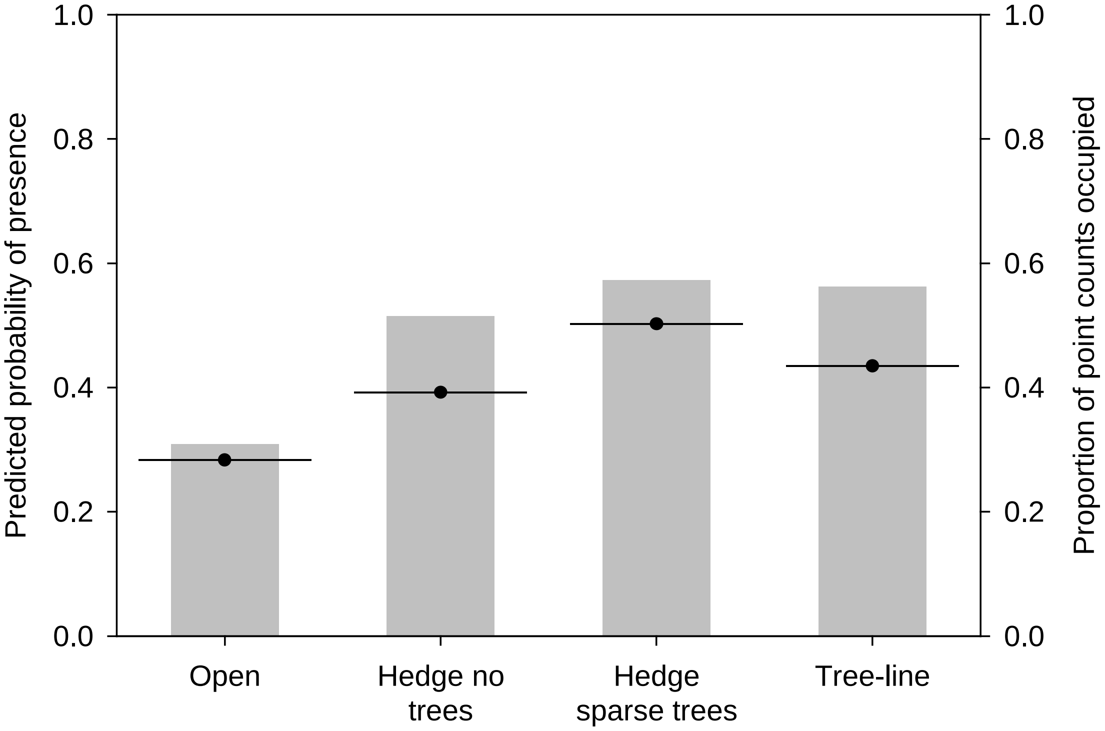

Figure 4.1 The predicted probability of encountering *P. pipistrellus* in open areas and adjacent to different types of linear features (*points*), and the proportion of point counts in each category at which *P. pipistrellus* occurred (*bars*).

For *P. pygmaeus*, the only interaction supported was between feature type and distance to the nearest woodland patch (table 4.9 and 4.10, Appendix I). A new candidate set was constructed in which feature type and distance to nearest woodland were constrained to appear alongside their interaction, and the remaining interaction terms were omitted (table 4.5). Averaged coefficients and selection probabilities were recalculated over this new candidate set (table 4.6).

The use of linear features by *P. pygmaeus* was dependent on both the type of feature and the proximity of woodland. The selection probability for the group of three predictors (*feature type*, *distwood* and *feature type*distwood*) was >0.999, indicating very strong support. In open areas, the probability of encountering *P. pygmaeus* declined as the distance to the nearest woodland patch increased (figure 4.2). Incidence of *P. pygmaeus* along tree-lines was consistently higher than in open areas both close to and further from woodland. The effect of hedgerows without trees on incidence of *P. pygmaeus* depended entirely on the proximity of woodland. In close proximity to woodland, incidence adjacent to hedgerows without trees was no higher than in open areas. At approximately 100m from woodland, the presence of hedgerows without trees resulted in a marginal increase in incidence relative to open areas, and this effect strengthened as the distance to the nearest woodland patch increased. The presence of hedgerows with sparse trees resulted in a greater increase in *P. pygmaeus* incidence relative to open areas, and this effect was seen across a greater range of woodland proximity. However, fewer point counts were available to test this relationship in comparison to the other feature types. As a result the averaged coefficient of the interaction term had a relatively wide confidence interval that included zero (table 4.6), so we can have less confidence that the relationship between bat incidence and hedgerows with sparse trees takes the exact form shown in figure 4.2. As with *P. pipistrellus,* the incidence of *P. pygmaeus* at point count locations was not affected by the presence of water ($\Sigma w_i = 0.288$), and the lack of support for the other interaction terms indicates that the association between *P. pygmaeus* and linear features was not altered by the presence of water or by geographical location.

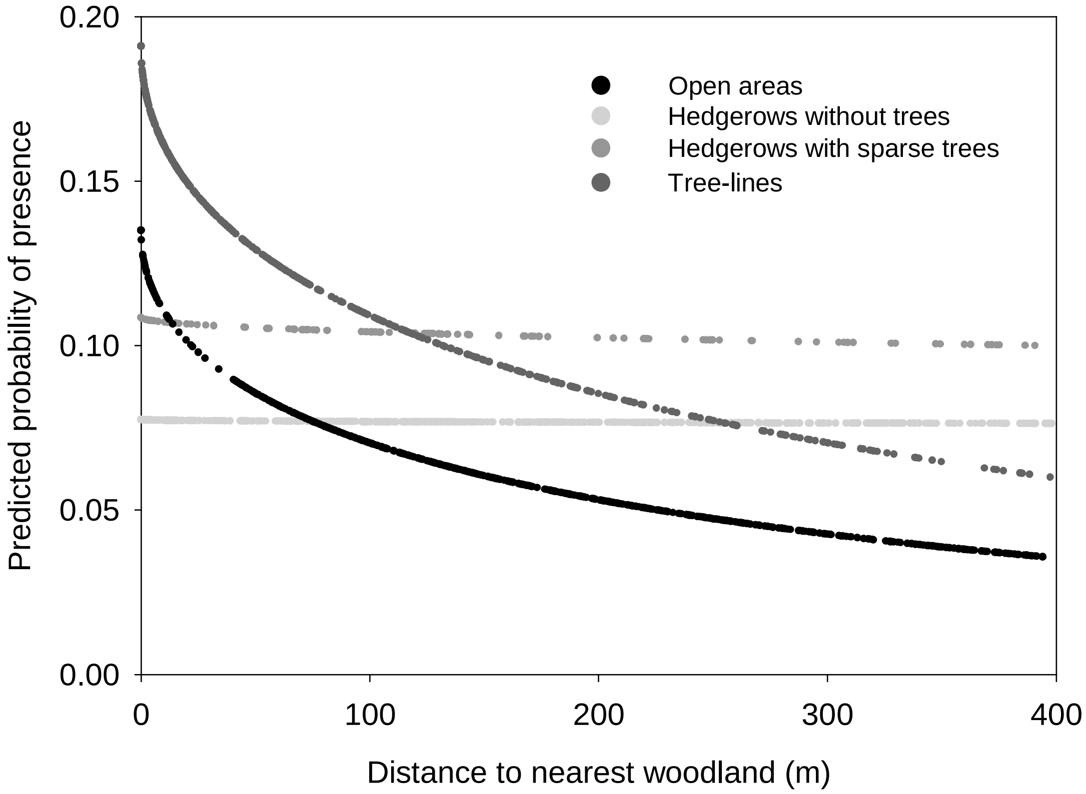

Figure 4.2 The relationship between distance to the nearest woodland patch and the predicted probability of encountering *P. pygmaeus*, shown for point counts in open areas and adjacent to different types of linear feature.

Table 4.6 Averaged coefficient estimates, unconditional standard errors, selection probabilities (Σw_i) and 95% confidence intervals of the averaged coefficients calculated for *P. pipistrellus* and *P. pygmaeus* over all models retained after the importance of interaction terms has been assessed.

				95% CI	
Predictor	ß	SE	Σw_i	Lower	Upper
P. pipistrellus					
Feature type			>0.999		
Hedgerow without trees	0.489	0.138		0.219	0.760
Hedgerow with sparse trees	0.937	0.212		0.521	1.353
Tree-line	0.664	0.147		0.376	0.952
Distwood	-0.040	0.011	0.998	-0.062	-0.018
Water	0.146	0.113	0.558	-0.075	0.367
Easting	1.83E-06	1.17E-06		-4.60E-07	4.13E-06
Northing	-1.17E-06	6.20E-06		-1.30E-05	1.10E-05
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-04	0.028
P. pygmaeus					
Feature type			>0.999		
Hedgerow without trees	0.288	0.167		-0.039	0.615
Hedgerow with sparse trees	0.611	0.232		0.156	1.066
Tree-line	0.450	0.179		0.099	0.801
Distwood	-0.072	0.020	>0.999	-0.111	-0.033
Feature type*distwood			>0.999		
Hedgerow without trees*distwood	0.072	0.024		0.025	0.119
Hedgerow with sparse trees*distwood	0.068	0.035		-0.001	0.137
Tree-line*distwood	0.007	0.025		-0.042	0.056
Water	0.028	0.060	0.288	-0.090	0.146
Number of surveys	0.162	0.031		0.101	0.223
Mean population index	0.067	0.050		-0.031	0.165
Easting	2.04E-06	1.56E-06		-1.00E-06	5.09E-06
Northing	8.33E-07	8.09E-07		-7.50E-07	2.42E-06
Broadleaved woodland	0.054	0.021		0.013	0.095
Improved grassland	0.014	0.010		-0.006	0.034

4.3.4. The use of linear features by N. noctula and E. serotinus

No interaction terms were supported for inclusion in the candidate set of models used test the relationship between linear features and incidence of *N. noctula* and *E. serotinus* (table 4.9 and 4.11, appendix I). Three models remained in the candidate set following the removal of interaction terms (table 4.7).

Table 4.7 Results of AIC-based model selection across a candidate set of models predicting the occurrence of *N. noctula* and *E. serotinus* along transect sections. Candidate set was defined after assessing the importance of interaction terms (Appendix I). For each model the number of estimable parameters (K), AIC score corrected for small sample size (cAIC$_c$), Akaike difference from the best model (Δ_i) and Akaike weight (w_i) are presented.

Model	K	cAIC$_c$	Δ_i	w_i
N. noctula				
Distwood	10	1818.00	0.000	0.826
Feature density + distwood	13	1821.70	3.702	0.130
Feature density	12	1823.83	5.832	0.045
E. serotinus				
Distwood	10	846.42	0.000	0.908
Feature density + distwood	13	851.04	4.625	0.090
Feature density	12	858.39	11.964	0.002

Incidence of both species along transect sections increased as the distance from the transect to the nearest woodland patch decreased (table 4.8). The large Akaike weight of the model containing only this predictor lends strong support to it being the best model within the candidate set for both species (w_i=0.826 for *N. noctula* and w_i=0.908 for *E. serotinus*, table 4.7). The predictor was also strongly supported within the averaged model ($\Sigma\ w_i > 0.900$). The group of predictors describing the density of linear features within the detection radius of the transect section had a low selection probability for both species ($\Sigma\ w_i < 0.2$) and the 95% confidence interval of each predictor included zero (table 4.8). Thus, this analysis provides no evidence that *N. noctula* or *E. serotinus* make preferential use of the linear feature types assessed here.

Table 4.8 Averaged coefficient estimates, unconditional standard errors, selection probabilities (Σw_i) and 95% confidence intervals of the averaged coefficients calculated for *N. noctula* and *E. serotinus* over all models retained after the importance of interaction terms has been assessed.

				95% CI	
Predictor	ß	SE	Σw_i	Lower	Upper
N. noctula					
Feature density			0.174		
Hedgerow without trees	-0.002	0.003		-0.009	0.005
Hedgerow with sparse trees	0.008	0.009		-0.009	0.025
Tree-line	-0.001	0.003		-0.007	0.005
Distwood	-0.024	0.011	0.955	-0.046	-0.001
Number of surveys	-3.42E-07	1.60E-06		-3.47E-06	2.79E-06
Section length	-1.77E-06	9.94E-07		-3.72E-06	1.82E-07
Mean population index	0.167	0.030		0.108	0.226
Easting	2.66E-04	6.16E-04		-9.41E-04	1.47E-03
Northing	-1.47E-03	1.63E-02		-0.033	0.030
Broadleaved woodland	0.016	0.019		-0.022	0.054
Improved grassland	0.011	0.010		-0.009	0.032
E. serotinus					
Feature density			0.092		
Hedgerow without trees	6.26E-05	1.98E-03		-3.81E-03	3.93E-03
Hedgerow with sparse trees	0.001	0.004		-0.006	0.008
Tree-line	0.002	0.002		-0.003	0.007
Distwood	-0.066	0.020	0.998	-0.106	-0.026
Number of surveys	1.09E-05	2.52E-06		5.94E-06	1.58E-05
Section length	-9.99E-06	3.12E-06		-1.61E-05	-3.88E-06
Mean population index	0.043	0.038		-0.031	0.117
Easting	1.75E-03	8.25E-04		1.29E-04	3.36E-03
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

4.4. Discussion

4.4.1. Associations with linear features

Hedgerows and tree-lines are widely assumed to be beneficial to bats. However, this study demonstrates that the association between bats and linear features varies among species. *Pipistrellus pipistrellus* and *P. pygmaeus* were positively associated with the presence of hedgerows and tree-lines, while no evidence was found of an association between *N. noctula* and *E. serotinus* and linear feature density. *Nyctalus noctula* and *E. serotinus* are thought to be less dependent on linear features than other bat species, as they often forage in open habitats (Glendell and Vaughan 2002; Kanuch and Kristin 2005; Limpens et al. 1989; Vaughan et al. 1997; Zukal and Rehak 2006). Pocock and Jennings (2008) found *N. noctula* activity was greater within fields than along field boundaries, and although *E. serotinus* has been observed commuting along linear features (Robinson and Stebbings 1997), its incidence in detector surveys is not as strongly associated with the presence of linear features as *Pipistrellus* species (Pocock and Jennings 2008; Verboom and Huitema 1997). However, the lack of association between the larger bat species and linear features seen in this study may also be an artefact of the use of acoustic detectors as survey tools. Calls of *N. noctula* and *E. serotinus* carry further that 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). In the current study, this problem was compounded by the pooling of records along transect sections, further increasing the area from which a bat pass may have originated. Nevertheless, if a strong association between the incidence of either of the larger bat species and the extent of linear features in the landscape existed, it is likely that it would have been seen in this study.

4.4.2. The use of linear features by Pipistrellus species

The use of linear features by *P. pipistrellus* was not affected by tree density. The presence of hedgerows without trees, hedgerows with sparse trees and tree-lines all provided a similar increase in incidence relative to open areas. In contrast, the use of linear features by *P. pygmaeus* was affected by both the type of linear feature and the distance of the feature from the nearest woodland patch. Tree-lines and hedgerows with sparse trees were consistently associated with an increase in *P. pygmaeus* incidence, whereas the effect of hedgerows lacking trees was only comparable to linear features containing trees in areas located at distance from woodland. This suggests that *P. pygmaeus* prefers linear features that contain trees, and that hedgerows without trees are utilised only when other, higher quality habitats are unavailable. By increasing both the height and volume of a linear feature, hedgerow trees provide greater shelter from predators and the elements (Limpens et al. 1989; Verboom and Spoelstra 1999), and also provide better foraging opportunities, as insect accumulation in the lee of hedgerows increases with increasing feature height (Lewis 1967). Both the abundance and diversity of macro-moths is increased in the vicinity of hedgerow trees (Merckx et al. 2009), primarily to the additional shelter they provide in agricultural landscapes (Merckx et al. 2010). Hedgerow trees also provide additional microhabitats, such as senescing and dead wood, that can increase invertebrate abundance and diversity

(DEFRA 2010). The greater association between incidence and the presence of trees shown by *P. pygmaeus* suggests a possible mechanism which may at least partly explain the differing habitat selection of *P. pygmaeus* and *P. pipistrellus* (Davidson-Watts et al. 2006; Nicholls and Racey 2006; Sattler et al. 2007).

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 both these species and woodland habitats (Davidson-Watts et al. 2006; Glendell and Vaughan 2002; Nicholls and Racey 2006; Russ et al. 2003; Russ and Montgomery 2002; Vaughan et al. 1997; Walsh and Harris 1996). However, the association with linear features was not increased in close proximity to woodland, as would be expected if linear features were used solely as commuting routes connecting foraging patches. It is therefore likely that linear features also provide foraging habitat for bats, functioning as a substitute for woodland edge habitat in areas lacking woodland.

The remaining linear attributes tested in this study, hedgerow width and the presence of water, did not affect the use of linear features by either *Pipistrellus* species. The lack of an association with water, either adjacent to linear features or in open areas, is perhaps surprising given the association with riparian habitat shown by both species in previous studies, particularly by *P. pygmaeus*, (Davidson-Watts et al. 2006; Nicholls and Racey 2006). In this study water was represented by water features mapped by OS MasterMap, including very small features such as field drains and ditches that are unlikely to be associated with significant riparian habitat, and may be too small to influence choice of foraging patch. Hedgerow width may fail to influence the use of linear features if, it is feature height, and not width, that is the physical characteristic of primary importance to bats. Nationwide data describing linear feature height were not available to this study. Further research investigating the relationship between feature height and the use of linear features by bats is needed, in particular to assess the relative benefits of increasing hedgerow height in comparison to increasing the density of hedgerow trees.

4.4.3. Conservation implications

In this study, *P. pipistrellus* and *P. pygmaeus* both showed positive associations with linear features, while *N. noctula* and *E. serotinus* did not. These associations were consistent across the UK. So while policies that promote the management of linear features have the potential to benefit bat populations nationally, not all species will benefit equally.

This study suggests that the presence of trees within hedgerows increases the quality of the hedgerow for *P. pygmaeus*, a priority species in the UK Biodiversity Action Plan (JNCC 2007). Hedgerow trees have also been shown to increase the abundance and diversity of birds (Hinsley and Bellamy 2000; Walker et al. 2005), although, as in the current study, species-specific responses to tree density have been reported. Green et al. (1994) found the incidence of Linnet *Carduelis cannabina,* Common whitethroat *Sylvia communis* and Lesser whitethroat *S. curruca*, was negatively affected by increasing tree density, and a study by DEFRA (2010) found ground nesting species, including Red-legged partridge *Alectoris rufa*, Meadow pipit *Anthus pratensis* and House sparrow *Passer domesticus,* were more abundant in short, treeless hedges.

Article 10 of the EC Habitats Directive (Council Directive 92/43/EEC) requires that the management of linear landscape features be considered within the land-use policies of the member states, however the conservation of hedgerow trees and tree-lines is neglected by current conservation legislation. In the UK, hedgerows are protected under the Hedgerow Regulations 1997, the Good Environmental and Agricultural Condition requirements of UK agricultural policy, and hedgerow management is addressed by current UK agri-environments schemes. Tree-lines do not receive the same protection. The Hedgerows Regulations do not apply to lines of trees without a shrub understorey, and as the Regulations are concerned only with hedgerow destruction and not degradation, they do not explicitly prohibit the removal of trees associated with hedgerows so long as the shrub portion of the hedgerow remains intact. The removal of trees in the UK is controlled by a system of felling licenses (Forestry Act 1967, as amended), and Tree Preservation Orders (Town and Country Planning Act 1990). However, these schemes only apply to the removal of more than 5 cubic metres of wood in the former case, and only to trees clearly visible from public rights of way in the latter, so neither offer a practical means of protecting hedgerow trees or tree-lines. These features are therefore vulnerable to loss. Over 40% of the length of linear features mapped as part of this study were lacking trees. In the UK, successive surveys have noted a 6.6% decline in hedgerow trees over the last two decades (Carey et al. 2008; Haines-Young et al. 2000). Thirty percent of the remaining hedgerow tree population is now over 100 years old, while the number of newly established trees declined by 40% between 1990-1998 (Haines-Young et al. 2000). This suggests a lack of recruitment is a major cause of the decline. In order to stabilise the current UK population of 1.6 million isolated hedgerows trees, it is estimated that 30,000 trees must be established annually. Currently this figure stands at between 10-15,000, so further declines in the hedgerow tree population are possible (DEFRA 2010). Establishment of new emergent trees in hedgerows is hindered by the additional costs to farmers created by such features. Hedgerow trees are an impediment to mechanical trimming, while tree-lines cover a greater basal area and cast a larger shadow over adjacent crops than an intensively managed hedgerow. However, financial compensation for the provision of hedgerows trees is rarely provided by EU agri-environment schemes. As a result, the decline in the population of hedgerow trees is expected to continue, with negative consequences for *P. pygmaeus* populations in rural landscapes.

This study demonstrates that hedgerow management has the potential to affect the distribution of *P. pipistrellus* and *P. pygmaeus* in rural landscapes, and *P. pygmaeus* will benefit from an increased provision of hedgerow trees. Legislation which specifically restricts the removal of tree-lines and hedgerow trees, combined with agri-environment options that encourage the establishment and management of these features, will benefit *Pipistrellus* bat populations and secure these valuable landscape resources for the future.

4.5 References

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4.6 Appendix I

Table 4.9 Results of AIC-based model selection across all possible combinations of explanatory predictors and interaction terms. Models shown are the 95% confidence set of models with which $\Sigma w_i \geq 0.95$. For each model the number of estimable parameters (K), AIC score corrected for small sample size (cAIC$_c$), Akaike difference from the best model (Δ_i) and Akaike weight (w_i) are presented.

Model	K	cAIC$_c$	Δ_i	w_i
P. pipistrellus (*N*= 2357)				
Feature type + distwood + water	13	2368.51	0.000	0.377
Feature type + distwood	12	2368.98	0.464	0.299
Feature type + distwood + water + feature type*northing	16	2371.63	3.114	0.079
Feature type + distwood + feature type*northing	15	2372.09	3.577	0.063
Feature type + distwood + water + feature type*water	16	2372.92	4.411	0.042
Feature type + distwood + water + feature type*distwood	16	2373.61	5.099	0.029
Feature type + distwood + feature type*distwood	15	2373.97	5.454	0.025
Feature type + distwood + water + feature type*easting	16	2374.07	5.562	0.023
Feature type + distwood + feature type*easting	15	2374.56	6.046	0.018
P. pygmaeus (*N*= 2354)				
Feature type + distwood + feature type*distwood	15	1808.13	0.000	0.457
Feature type + distwood + water + feature type*distwood	16	1809.93	1.793	0.186
Feature type + distwood + feature type*distwood + feature type*northing	18	1811.12	2.983	0.103
Feature type + distwood + feature type*distwood + feature type*easting	18	1812.77	4.635	0.045
Feature type + distwood + water + feature type*distwood + feature type*northing	19	1812.90	4.770	0.042
Feature type + distwood + water + feature type*distwood + feature type*water	19	1812.94	4.809	0.041
Feature type + distwood + feature type*distwood + feature type*easting + feature type*northing	21	1813.37	5.234	0.033
Feature type + distwood	12	1814.32	6.192	0.021
Feature type + distwood + water + feature type*distwood + feature type*easting	19	1814.60	6.466	0.018
Feature type + distwood + water + feature type*distwood + feature type*easting + feature type*northing	22	1815.21	7.074	0.013
N. noctula (*N*= 2170)				
Distwood	10	1818.00	0.000	0.497
Feature density + distwood + feature density*distwood + feature density*northing	19	1821.23	3.231	0.099
Feature density + distwood + feature density*northing	16	1821.49	3.493	0.087
Feature density + distwood + feature density*distwood	16	1821.66	3.656	0.080
Feature density + distwood	13	1821.70	3.702	0.078
Feature density + feature density*northing	15	1823.31	5.314	0.035
Feature density	12	1823.83	5.832	0.027
Feature density + distwood + feature density*easting	16	1823.91	5.907	0.026
Feature density + distwood + feature density*easting + feature density*northing	19	1824.20	6.203	0.022
Feature density + distwood + feature density*distwood + feature density*easting	19	1824.53	6.536	0.019
E. serotinus (N= 1607)				
Distwood	10	846.42	0.000	0.783
Feature density + distwood	13	851.04	4.625	0.078
Feature density + distwood + feature density*distwood	16	851.66	5.239	0.057
Feature density + distwood + feature density*distwood + feature density*easting	19	852.54	6.121	0.037

Table 4.10 Averaged coefficient estimates, unconditional standard errors, selection probabilities (Σw_i) and 95% confidence intervals of the averaged coefficients calculated for *P. pipistrellus* and *P. pygmaeus* over all possible combinations of explanatory predictors and interaction terms

	P. pipistrellus				*P. pygmaeus*			
			95% Confidence Interval				95% Confidence Interval	
Predictor	ß	SE	Lower	Upper	ß	SE	Lower	Upper
Feature type								
Hedgerow without trees	0.496	0.14	0.222	0.77	0.284	0.169	-0.047	0.614
Hedgerow with sparse trees	0.934	0.216	0.511	1.358	0.616	0.24	0.146	1.086
Tree-line	0.662	0.149	0.37	0.953	0.501	0.183	0.142	0.86
Distwood	-0.04	0.011	-0.062	-0.019	-0.07	0.022	-0.113	-0.028
Water	0.159	0.123	-0.082	0.4	0.029	0.078	-0.123	0.181
Feature type*distwood								
Hedgerow without trees*distwood	-8.39E-04	1.68E-03	-4.13E-03	2.45E-03	0.069	0.023	0.023	0.114
Hedgerow with sparse trees* distwood	1.31E-03	2.73E-03	-4.05E-03	6.67E-03	0.064	0.034	-0.002	0.131
Tree-line*distwood	7.98E-04	1.67E-03	-2.48E-03	4.08E-03	0.006	0.024	-0.04	0.052
Feature type*water								
Hedgerow without trees*water	-0.022	0.028	-0.077	0.033	-0.009	0.024	-0.056	0.038
Hedgerow with sparse trees*water	0.014	0.032	-0.048	0.076	-0.034	0.044	-0.12	0.053
Tree-line*water	0	0.019	-0.037	0.037	0.021	0.03	-0.038	0.081
Feature type*easting								
Hedgerow without trees*easting	8.50E-09	7.91E-08	-1.46E-07	1.63E-07	8.90E-08	1.99E-07	-3.00E-07	4.78E-07
Hedgerows with sparse tree*easting	8.37E-08	1.43E-07	-1.96E-07	3.63E-07	3.20E-07	3.83E-07	-4.30E-07	1.07E-06
Tree-line*easting	2.45E-08	8.42E-08	-1.41E-07	1.90E-07	1.78E-07	2.51E-07	-3.15E-07	6.70E-07
Feature type*northing								
Hedgerow without trees*northing	2.19E-07	2.28E-07	-2.27E-07	6.65E-07	-4.57E-08	2.07E-07	-4.50E-07	3.59E-07
Hedgerow with sparse trees*northing	1.32E-07	2.80E-07	-4.17E-07	6.81E-07	5.36E-07	5.36E-07	-5.14E-07	1.59E-06
Tree-line*northing	-2.20E-08	1.44E-07	-3.04E-07	2.60E-07	1.85E-07	2.51E-07	-3.07E-07	6.78E-07
Easting	1.79E-06	1.19E-06	-5.36E-07	4.12E-06	1.91E-06	1.63E-06	-1.28E-06	5.09E-06
Northing	-1.24E-06	6.58E-07	-2.53E-06	4.85E-08	7.46E-07	8.56E-07	-9.31E-07	2.42E-06
Number of surveys	0.228	0.027	0.176	0.281	0.163	0.031	0.103	0.223
Mean population index	0.037	0.005	0.026	0.047	0.068	0.05	-0.031	0.167
Broadleaved woodland	0.014	0.016	-0.018	0.046	0.055	0.021	0.014	0.095
Improved grassland	0.014	0.007	-1.73E-04	0.029	0.014	0.01	-0.005	0.034

Table 4.11 Averaged coefficient estimates, unconditional standard errors, selection probabilities (Σw_i) and 95% confidence intervals of the averaged coefficients calculated for *N. noctula* and *E. serotinus* over all possible combinations of explanatory predictors and interaction terms.

	N. noctula				*E. serotinus*			
			95% Confidence Interval				95% Confidence Interval	
Predictor	ß	SE	Lower	Upper	ß	SE	Lower	Upper
Feature density								
Hedgerow without trees	-0.004	0.009	-0.022	0.015	0	0.005	-0.01	0.009
Hedgerow with sparse trees	0.024	0.02	-0.017	0.064	0.002	0.009	-0.016	0.02
Tree-line	-0.002	0.009	-0.019	0.015	0.001	0.006	-0.01	0.013
Distwood	-0.023	0.011	-0.046	-0.001	-0.066	0.021	-0.107	-0.026
Feature denisty*distwood								
Hedgerow without trees*distwood	7.35E-04	7.64E-04	-7.63E-04	2.23E-03	3.38E-04	4.12E-04	-4.70E-04	1.15E-03
Hedgerow with sparse trees* distwood	8.17E-04	8.00E-04	-7.51E-04	2.39E-03	-5.63E-04	8.23E-04	-2.18E-03	1.05E-03
Tree-line*distwood	1.05E-03	1.33E-03	-1.57E-03	3.67E-03	-5.68E-04	6.26E-04	-1.79E-03	6.58E-04
Feature denisty*easting								
Hedgerow without trees*easting	1.32E-08	2.15E-08	-2.90E-08	5.53E-08	5.52E-09	1.48E-08	-2.34E-08	3.45E-08
Hedgerows with sparse tree*easting	-3.72E-08	4.94E-08	-1.34E-07	5.96E-08	-4.69E-09	2.91E-08	-6.17E-08	5.23E-08
Tree-line*easting	-1.57E-08	2.14E-08	-5.76E-08	2.62E-08	3.05E-08	3.18E-08	-3.18E-08	9.29E-08
Feature denisty*northing								
Hedgerow without trees*northing	3.40E-08	4.10E-08	-4.63E-08	1.14E-07	4.56E-10	3.76E-09	-6.92E-09	7.83E-09
Hedgerow with sparse trees*northing	1.63E-07	1.44E-07	-1.19E-07	4.46E-07	-2.57E-09	7.23E-09	-1.67E-08	1.16E-08
Tree-line*northing	-3.32E-08	3.85E-08	-1.09E-07	4.22E-08	-1.50E-10	4.06E-09	-8.11E-09	7.81E-09
Easting	-4.89E-07	1.62E-06	-3.67E-06	2.69E-06	1.09E-05	2.52E-06	5.94E-06	1.58E-05
Northing	-1.71E-06	1.01E-06	-3.68E-06	2.65E-07	-1.00E-05	3.12E-06	-1.61E-05	-3.90E-06
Number of surveys	0.166	0.03	0.107	0.224	0.043	0.038	-0.031	0.118
Length	2.46E-04	6.21E-04	-9.72E-04	1.46E-03	1.76E-03	8.28E-04	1.40E-04	3.39E-03
Mean population index	-0.001	0.016	-0.033	0.031	0.046	0.027	-0.007	0.099
Broadleaved woodland	0.015	0.02	-0.023	0.054	-0.002	0.025	-0.05	0.047
Improved grassland	0.011	0.011	-0.01	0.032	0.031	0.018	-0.004	0.066

Chapter 5

Concluding remarks

5.1. Habitat associations of UK bats

5.1.1. Habitat associations at landscape and local scales

This thesis examined the habitat associations of seven bat species, representing two families and six genera. Landscape scale habitat associations were investigated using two approaches. The first compared the habitat surrounding bat roosts to that generally available (roost selection, chapter 2), and the second related the incidence of bats along transects to the habitat composition and configuration of the surrounding landscape (chapters 3 and 4). Species specific responses to landscape structure were demonstrated using both approaches, and these are discussed in the relevant data chapters. However, associations common among species and between approaches were also evident.

The availability of broadleaved woodland affected both roost selection and foraging incidence of every species assessed in this thesis. Of the six species for which roost location data were available, *Pipistrellus pipistrellus, Pipistrellus pygmaeus, Rhinolophus hipposideros* and *Plecotus auritus* were more likely to roost in landscapes with a greater proportion of broadleaved woodland. Foraging incidence data were available for four species; *P. pipistrellus, P. pygmaeus, Nyctalus noctula* and *Eptesicus serotinus*. All four species were encountered more frequently in landscapes with a greater proportion of broadleaved woodland. Woodland proximity had strong effects on both roost location and foraging incidence; *P. pipistrellus*, *P. pygmaeus, R. hipposideros, E. serotinus* and *Myotis nattereri* all roosted closer to broadleaved woodland than would be expected by chance, and all species for which data were available were encountered along transects more frequently as the distance to the nearest woodland patch (broadleaved and coniferous woodland combined) decreased. There was little evidence of an effect of woodland patch size on the bat species assessed here. The size of the nearest broadleaved patch did not affect the roost location of any species, and evidence of a negative effect of broadleaved woodland disaggregation (the breaking up of larger patches into smaller patches) on foraging incidence was equivocal.

Roost selection and foraging incidence of a number of species were also affected by the availability of improved grassland. *Pipistrellus pipistrellus, P. pygmaeus, P. auritus, E. serotinus* and *M. nattereri* were all more likely to select roosts in landscapes with a greater proportion of improved grassland, and *P. pygmaeus* and *N. noctula* were both more frequently encountered in landscapes with a greater proportion of improved grassland. Only two of these species, *N. noctula* and *E. serotinus,* are known to regularly forage over grassland habitats (Catto et al. 1996; Mackie and Racey 2007; Vaughan et al. 1997). For the remaining species, *P. pipistrellus, P. pygmaeus, P. auritus* and *M. nattereri,* the association with improved grassland may reflect the higher density hedgerows and tree-lines found in grassland landscapes, when compared to other rural landscape types (Haines-Young et al. 2000). The potential importance of linear boundary features to bats is also suggested by the fact that incidence of *P. pygmaeus* and *N. noctula* was higher in landscapes with more dispersed improved grassland patches.

When the effect of linear features on bat incidence was assessed, two species, *P. pipistrellus, P. pygmaeus* were found to occur more frequently adjacent to linear features than in open areas, while *N. noctula* and *E. serotinus* were unaffected by the density of linear features in the landscape. The use of linear features by *Pipistrellus* species was not affected by hedgerow width or the presence of water, and *P. pipistrellus* was unaffected by the density of trees within the linear feature. However, incidence of *P. pygmaeus* was highest adjacent to linear features that contained trees. Tree density is strongly associated with the abundance and species richness of small mammals and birds within linear features (Gelling et al. 2007; Macdonald and Johnson 1995; Parish et al. 1994; Walker et al. 2005) although, unlike *Pipistrellus* species, hedgerow size (height, width or volume) is also of major importance (Arnold 1983; Macdonald and Johnson 1995; Michel et al. 2007; Parish et al. 1994). In general, abundance and species richness of birds are positively associated with tree density, however at species level some birds display the opposite relationship; the abundance of Linnet *Carduelis cannabina,* Whitethroat *Sylvia communis* and Lesser whitethroat *Sylvia curruca,* is negatively affected by increasing tree density (Green et al. 1994). Other taxa, including

Lepidoptera and ground beetles Carabidae are primarily affected by landscape context and the composition of the herbaceous layer, rather than hedgerow structure (Dover and Sparks 2000; Dover 1999; Petit and Usher 1998), although a study by Merckx et al. (2009) showed the abundance and diversity of larger moth species was positively related to the presence of hedgerow trees.

5.1.2. Scale of landscape perception

Very little is known about the scale at which bats respond to changes in landscape composition and configuration. In this thesis landscape metrics were measured at multiple spatial scales to assess variation in habitat associations with scale. No one scale was best at explaining all associations between bats and the surrounding landscape, rather the most appropriate scale depended on the biotic response variable in question (roost location or foraging incidence), the mobility of the species and the specific habitat metric considered.

The landscape scale which best explained the foraging incidence of bats appeared to be linked to species mobility. Landscape measures were calculated within 750m, 1500m and 3000m of field transects. The two species with the smallest home ranges (*P. pipistrellus* and *P. pygmaeus*, home range of approximately 3-4km, table 2.1**)** were most strongly associated with the surrounding landscape measured at the smallest spatial scale. However, no clear trend in model performance across the range of scales tested was apparent for the two species with the largest home ranges (*N. noctula* and *E. serotinus*, home range of approximately 10km and 7km respectively, table 2.1 and Mackie and Racey 2007).

For the majority of species, roost selection was better explained by the landscape within 1km of the roost than by the landscape within the maximum foraging radius of the colony. However, this was not the case for *M. nattereri*, the species with the greatest propensity to switch roosts. Roost selection by *M. nattereri* was better explained using data measured across the home range of the colony, possibly as a result of the regular use of a number of roosts located throughout the home range. It is therefore recommended that studies of roost selection involving species that regularly move between roosts should quantify the landscape at a scale equivalent to the maximum home range of the species, in addition to any other spatial scales considered.

5.2. Conservation implications and recommendations

The conservation implications of this thesis primarily concern the provision of broadleaved woodland and linear features within the UK landscape. As recommendations are drawn from a national dataset, they can be expected to be applicable across the UK (although see section 5.4.1. for a discussion of regional patterns of habitat use).

5.2.1. Broadleaved woodland in the UK

The findings of this thesis indicate that the availability of broadleaved woodland plays a central role in determining landscape suitability for the bats. This study supports the continued reforestation of the UK, with an emphasis on broadleaved planting, that is currently encouraged by grants available through the Woodland Grant Scheme and Higher Level Stewardship scheme (Forestry Commission 2009; Natural England 2010). However, there is also the opportunity to introduce specific woodland creation guidelines into these schemes to benefit bat conservation. Measures should primarily focus on increasing broadleaved woodland extent, particularly in landscapes with little existing broadleaved cover. Schemes should aim to create an extensive network of woodland patches, including small patches designed to make efficient use of available land and maximise the provision of edge habitat. The creation of woodland patches isolated by more than 440m from existing cover should be avoided.

These actions will benefit populations of edge specialist bat species, including the species assessed in this thesis, and help meet the objectives of the UK Biodiversity Action Plan (UK BAP, JNCC 2007). However true woodland specialist bats, such as *Myotis bechsteini* and *Barbastella barbastellus,* also occur in the UK, and their requirements must also be considered. Both *M. bechsteini* and *B. barbastellus* roost and forage primarily within broadleaved woodland (Kanuch et al. 2008; Meschede and Heller 2000; Sierro 1999). *Myotis bechsteini* roosts in old woodpecker holes and tree cavities (Meschede and Heller 2000) within woodlands with a high proportion of oak (Kanuch et al. 2008). *Barbastella barbastellus* roosts behind loose bark, and to a lesser extent in tree cavities (Meschede and Heller 2000; Russo et al. 2005) within unmanaged woodland, roosting less often than would be expected in open woodland and areas containing pasture, given the availability of these habitats (Russo et al. 2004). Both species regularly move between roosts (Meschede and Heller 2000; Russo et al. 2005), and so both require woodland patches containing sufficient numbers of mature or senescent trees with cavities and loose bark. Such requirements are likely to be met only in large, long established woodland patches. Abundance of *B. barbastellus* was shown to increase with increasing forest patch size within an agricultural landscape in Poland (Lesinski et al. 2007), and while little is known about the effect of patch isolation on these two species, the movement of *M. bechsteini* was shown to be impeded by a motorway cutting through a forest patch, suggesting this species is unwilling to cross open areas (Kerth and Melber 2009). In areas adjoining existing populations of these species, woodland creation schemes should prioritise the enlargement of existing woodland patches, and forestry practices should be adopted that increase availability of mature and senescent trees.

5.2.2. *Linear habitat features*

The management of linear features offers further opportunities to improve landscape quality for bats, and to meet the objectives of the UK BAP. Increasing the availability of linear features will benefit *P. pipistrellus* and *P. pygmaeus* in rural landscapes, and *P. pygmaeus*, a UK BAP priority species, will benefit from increasing provision of hedgerow trees. Hedgerow management is already a part of both the Entry Level and Higher Level Stewardship schemes (Natural England 2008, 2010). The addition of options to these schemes that compensate farmers for the provision of hedgerows trees is recommended.

5.3. Utility of National Bat Monitoring Program data

This thesis demonstrates that, although designed to monitor population trends, NBMP data can also be used to provide valuable insights into the habitat use of UK bats.

Perhaps the greatest benefit of the data is the national extent, which, together with a multi-species scope, allows bat-habitat relationships to be assessed in a manner that is of relevance to national policy development.

The NBMP is made possible by the efforts of a large group of skilled and committed volunteers. However, the use of volunteers rather than paid professionals necessarily imposes limits on the data that can be collected. In order to maintain volunteer involvement, survey time and the number of repeat visits are kept to the minimum required to detect significant population trends, as indicated by power analysis of data collected during the first three years of the program (Walsh et al. 2001). Reduced survey effort can reduce precision, in this case by inflating the number of false absences reported by field surveys. However, problems of reduced precision along any particular survey were overcome by the large overall sample size.

In order to maximise the sensitivity of the monitoring program to population trends, survey methods were designed to optimise species encounter rate. For the rarer species monitored by the field survey (*N. noctula* and *E. serotinus*) this necessitated the use of transect surveys rather than points counts. However, pooling species records along transect sections compounds problems caused by the large detection range of these species, as discussed in chapter 4. This may prevent the identification of small scale habitat relationships for *N. noctula* and *E. serotinus* using current NBMP data. However, this may be overcome by the use of broad band detector technology. Currently heterodyne detectors are used during the field survey. They must be tuned to a specific sound frequency, and so can only detect bat species that echolocate at or near that frequency. In contrast, broadband detectors can monitor all frequencies, and therefore all species, simultaneously. This would allow *N. noctula* and *E. serotinus* to be monitored alongside *Pipistrellus* spp. during the point counts, providing fine resolution distribution data for these species. Simultaneous monitoring also increases survey efficiency, which may allow overall survey effort to be increased. The most recent NBMP surveys (Bats and Roadside Mammals, Woodland and Nathusius’ pipistrelle survey, Bat Conservation Trust 2009) all employ broadband detectors, and are therefore likely to provide high quality data for assessing bat-habitat associations as their coverage expands.

The need to prioritise population monitoring has also restricted the amount of additional data, including habitat data, that can be collected. Though the original survey protocols included estimates of percentage cover of basic habitat types, the collection of habitat data was discontinued due to a lack of funds and the poor quality of habitat data returned (Walsh et al. 2001). The scope of habitat analysis is therefore limited by the availability of national datasets. Although the Landcover Map 2000 is suitable for analysis at landscape scale, local habitat data is currently restricted to features mapped by Ordnance Survey (MasterMap). This may change when the latest version of the Landcover Map is released in 2010. This will integrate remote sensed land cover data with MasterMap landscape parcels (Centre for Ecology & Hydrology 2010), providing a comprehensive habitat map with a fine resolution suitable for patch level analysis. However, comprehensive national data that provide habitat quality and other within-patch measures are still lacking.

Both colony counts and field survey data are affected by the non-random selection of sample sites. This does not affect the use of survey data for its primary purpose, the estimation of population trends, but does have implications when used to assess habitat associations (discussed further in sections 2.2 and 3.2). A number of habitat types were underrepresented in the analysis of both roost selection and incidence along field transects. Targeted sampling by future surveys would allow the use of these habitats to be investigated.

Finally, NBMP methodology does not distinguish between bats of different sex or reproductive status. The extent to which sex and reproductive status affect habitat selection has not been established for the majority of species, however, there is evidence that during pregnancy and lactation, female bats may be restricted to habitats able to support their increased energetic demands, whereas non-reproductive females and males can make use of more marginal habitats (Cryan et al. 2000; Dietz et al. 2006; Mackie and Racey 2007; Senior et al. 2005). The BCT is currently trialling a survey method to help establish the presence of reproductive females within a roost, using a second set of counts in late summer designed to detect an increase in the number of emerging bats as young become volant. Combining reproductive females with non-reproductive females and males for analysis may make habitat associations harder to distinguish, but will not undermine the validity of results.

5.4. Future directions

The analysis of NBMP data at a national scale has yielded useful insights into bat habitat use, and indicates that this approach could be successfully applied to other datasets collected by the NBMP. This will increase the suite of species for which national recommendations are available, including rarer species such as *M. bechsteinii* and *B. barbasatellus*. However there are many aspects of bat habitat use that can only be effectively addressed by the collection of specific datasets at a smaller scale , including the effect of habitat quality, prey availability, associations with underrepresented habitat types (see section 5.3), biotic interactions and seasonal changes (e.g. Crampton and Barclay 1998; Erickson and West 2003; Fukui et al. 2006).

5.4.1. Regional analysis

Species-habitat relationships can vary geographically and with landscape context. Robinson et al. (2001) demonstrated that the relationship between the abundance of some farmland birds species and the extent of arable habitat within a 1km^2 area depends on the availability of arable land in the surrounding landscape. In general, positive associations were strongest, and negative associations weakest, in landscapes where arable land was rare. The effects of habitat configuration (patch size and isolation) are also expected to be stronger in landscapes with a low extent of suitable habitat, based on threshold effects for contiguity observed in simulated landscapes (Andrén 1994). An effect of landscape context on farmland bird-habitat relationships was not shown by Whittingham et al. (2007), however, models fitted in one geographic region of the UK performed poorly when tested with data from other regions, suggesting that farmland bird habitat associations varied regionally (Whittingham et al. 2007). Modelling national data necessarily sacrifices some regional accuracy for generality, a compromise required of most national conservation policy. However, the relevance of relationships modelled at a national scale will be enhanced by an assessment of the extent to which national bat-habitat asscoiations vary between regions and landscape types. In this thesis, geographical variation in the use of linear features by bats was assessed by modelling the interaction between easting, northing and selected habitat predictors. When an all subsets modelling approach in used, as in this thesis, the number of candidate models increases exponentially with each additional predictor. As such, the addition of easting, northing and associated interaction terms was only possible when the set of habitat predictors was limited, as in chapter 4. Where the set of habitat predictors exceeded nine, as was the case in chapters 2 and 3, the addition of geographical variables resulted in an impractically large candidate set of models. An alternative approach to assessing geographical variation in modelled relationships is to subdivide the data into regions, and fit a different model for each region. Such an approach could yield valuable information about the general applicability of the landscape scale habitat associations revealed by this thesis. It will be particularly valuable to examine how the positive association with broadleaved woodland demonstrated by all species in this study varies between regions with different woodland cover.

5.4.2. Landscape change

The NBMP currently has thirteen years of field survey data, covering 584 sites. Of these, 111 sites have been monitored for five years or more, raising the possibility that population response to landscape change could be examined. Reliable landscape scale estimates of habitat change will be available for the first time with the release of the latest version of the CEH Landcover Map (Centre for Ecology & Hydrology 2010), which can be compared to the previous version created between 1998-2001 (Fuller et al. 2002). At a pixel level the two datasets are not directly comparable, as habitat patches in LCM2000 were identified by grouping pixels with similar reflectance parameters, whereas the latest version uses landscape parcels defined by OS MasterMap. However, at a landscape scale these two datasets should provide a robust measure of habitat change.

This thesis aims to extend the knowledge of the factors that determine bat distribution by drawing together habitat relationships across a range of rarely-studied scales. In demonstrating key habitat associations, it is my hope that this thesis can further the conservation of these enigmatic animals.

5.5. References

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