Landscape conservation for Irish bats & species specific roosting characteristics

The Centre for Irish Bat Research

University College Dublin & Queen's University Belfast

School of Biological Sciences

Mathieu G. Lundy + W. Ian Montgomery

&

Bat Conservation Ireland

Ulex House, Drumheel, Lisduff, Virginia, Co. Cavan

www.batconservationireland.org

Niamh Roche + Tina Aughney

Citation: Lundy MG, Aughney T, Montgomery WI, Roche N (2011) Landscape conservation for Irish bats & species specific roosting characteristics. Bat Conservation Ireland.

ACKNOWLEDGEMENTS

This work was funded by Bat Conservation Ireland, The Northern Ireland Environment Agency and the following County Councils in the Republic of Ireland: Clare, Donegal, Dún Laoghaire-Rathdown, Galway, Kerry, Kildare, Kilkenny, Laois, Longford, Louth, Mayo, Meath, Monaghan, Offaly, Roscommon, Sligo, South Dublin, Waterford, Wexford and Wicklow.

Special thanks to Liam Lysaght and staff at the National Biodiversity Data Centre for their helpful contribution to the project.

Thanks also to Ruth Carden, Donna Cassidy, Jennifer Firth, Naomi Kingston, Declan Looney, Deirdre Lynn, Ferdia Marnell, Damian McFerran, Cliona O'Brien and staff at the Heritage Council, Lynn Rendle, Catherine Snijder, Mark Wright and staff of CIBR in Queen's University Belfast and University College Dublin for support, advice and data gathering.

Thanks to The Vincent Wildlife Trust for generously contributing many lesser horseshoe and other species records in the west of Ireland.

We would like to thank the volunteer surveyors who annually survey for the Car-based Bat Monitoring Scheme, the All-Ireland Daubenton's Waterways Survey and the Brown Long-eared Roost Monitoring Scheme and to those who participated in the BATLAS 2010 survey. We are especially grateful to those who continue to contribute time and effort to collecting bat records and who share their data with the scientific community. Without their efforts the present insights into the ecology and status of bats in Ireland would not be possible.

Finally, much appreciation to Bat Conservation Ireland's dedicated and enthusiastic committee.

CONTENTS

OVERVIEW

Through this project we aim to provide a landscape conservation guide for Irish bat species. Using an existing database of species records, collated and maintained by Bat Conservation Ireland, we apply analysis of the habitat and landscape associations of all species that commonly occur in Ireland namely; common pipistrelle, soprano pipistrelle, Nathusius' pipistrelle, Leisler's bat, Daubenton's bat, Natterer's bat, whiskered bat, brown long-eared bat and the lesser horseshoe bat. Through this project we aim to provide a guide to the key habitat associations of bats to help understand their habitat requirements in Ireland. Applying this specifically with the unique Irish fauna allows both similarities to and differences from other regions to be identified; in turn we can develop tailored management prescriptions for Irish species.

We identify the geographical areas that are suitable for individual species and summarize the associations that result in these patterns. For each species, the 'core favourable area' is identified. We also examine the roosting habitat associations of each species. Roosts are central to ensuring continued favourable conservation status of bats in Ireland. The roosting habitat is examined by delineating the area around roosts and comparing it with areas where roosts are not known to occur. Finally, we also describe patterns of selection for specific aspects of roost type, such as building types or wall construction material. This combination of analyses provides a picture of the broad scale geographic patterns of occurrence and local roosting habitat requirements for Irish bats.

The results show that, for the majority of species, suitable areas exist in all regions of Ireland. The lesser horseshoe bat and rarely recorded Nathusius' pipistrelle are exceptions with more restricted distributions. We also identify those species with widespread occurrence, but whose presence at a given location is determined by immediate small scale habitat character, such as the Daubenton's bat. Complex, species specific, patterns of roosting habitat association are shown. However, some generalisations can be made such as selection for broadleaf woodland habitat, mixed forestry and avoidance of anthropogenically modified areas, such as areas of agriculture and conifer forestry. Some species show selection of only a few of the recorded roost parameters. This may reflect the highly site specific nature of roost selection and may mean that making broad generalisations is difficult. Known individual roosts are, therefore, likely to represent extremely important conservation units for bat species.

The core areas we identify are those areas where a species is expected and effort should be made to maintain them. However, areas outside the core area should not be discounted as unimportant. Indeed the occurrence of the species in these areas may be reliant on small fragments of favourable area which are vulnerable to any environmental change, individual locations within regions should be assessed on their own merit. The synthesis of these combined analyses demonstrates the complex nature of bats' habitat requirements, with occurrence dependent on a combination of broad landscape patterns, local roosting conditions and roost character.

INTRODUCTION

Many populations of bat species have undergone long term declines across continental Europe (Stebbings 1988). Nine species of bat occur regularly in Ireland and all are protected by national and European Union (EU) legislation. The foraging habitats chosen by a species reflect both its ability to catch prey in different environments, depending on echolocation calls and wing morphology (Norberg & Rayner 1987), and also the quality of the foraging habitat in providing sufficient insect prey (Fenton 1990). All species of bat that occur in Ireland are listed on Annex IV of the EU Habitats Directive (92/43/EEC), defined as species in need of strict protection, with the Lesser horseshoe (*Rhinolophus hipposideros*) included on Annex II, as a species requiring special protection measures including designation of Special Areas of Conservation (SACs). A primary aim of the Habitats Directive is that the favourable conservation status of species should be maintained or restored. We present analyses of the landscape associations, roosting habitat and roost characteristics of all Irish bat species as a means of better understanding their geographic patterns of occurrence and habitat requirements.

Modelling species' distributions offers an alternative to direct mapping, allowing the prediction of species' current, future and past distributions (Guisan & Zimmerman 2000; Thomas *et al.* 2004). The models derived can be used in assessment of a species' conservation status (Thomas *et al.* 2004). Deviations from predictions can be used to both identify environmental impacts and also gaps in our knowledge. In addition, modelled predictions of response to conditions beyond those currently experienced, indicate likely modifications to species' distributions in response to environmental change (e.g. Lundy *et al.* 2010). The outputs can also be used to identify and define priority conservation areas or indeed sites suitable for reintroductions (e.g. Wilson *et al.* 2010). Species' Distribution Models (SDM) provide a generalisation of species – habitat associations. However, small scale variation and plasticity in response to environmental conditions means that these are used as a general guide to broad scale patterns. The suitability of any given location should also be assessed on its own merit and on a case by case basis. For example, a small area of marginally suitable habitat in a landscape of broadly unfavourable landscape may be more important to a species than a marginally suitable habitat in a broadly favourable landscape.

The predictions of SDMs are based on estimating the suitability of an area for a species using correlations with environmental variables. However, the suitability of an area is not related to the availability of habitat at any one given location but to the context of the surrounding landscape habitat structure, size and shape (Virkkala 1991; Jokimaki & Huhta 1996; Bennett *et al.* 2006). Species respond to heterogeneous landscapes at multiple scales which combine to determine presence and population processes (e.g. Fryxell *et al.* 2005). In the current project, we apply a multi-scale approach that allows the immediate habitat to be placed in the context of the surrounding landscape (Wiens 1989; Jokimaki & Huhta 1996). Multi-scale methods can identify species specific relationships with aspects of habitat spatial scale (McAlpine *et al.* 2006; Lundy and Montgomery 2010a). We have applied this approach for all bat species occurring in Ireland. The overarching aim of the present report is to provide a guide to the key habitat associations of bats to help understand their habitat requirements in Ireland. Additionally we characterise the landscape component of roosting by delineating habitat around roosts and establish patterns of roost selection. It is important to apply this study within Ireland, using the records of species accumulated, to ensure that accurate management prescriptions are defined specifically for the Irish bat community. Inaccurate prescriptions may be developed if these are based on data from other geographic regions due to ecological and genetic differences in species present, and because of Ireland's unique landscape structure. However, being able to draw on similarities with the associations observed in other regions and can help develop a consensus (Heer *et al.* 2005) and can also help identify the uniqueness in patterns of the Irish fauna.

Defining the geographical ranges of bat species can be difficult due to their nocturnal and elusive behaviour (Walsh & Harris 1996; Vaughan *et al.* 1997). Developing SDMs is particularly useful for examining the ecology of bat species (Jaberg & Guisan 2001; Rebelo *et al.* 2010). Utilising low resolution land cover data does not allow prediction of individual locations of species' occurrence but provides an overview of the distribution of favourable habitat at a landscape level. At a fine scale level, the availability of suitable roosts is likely to determine occurrence at individual locations (Kunz & Fenton 2003). Indeed, it is likely that ideal foraging habitat may exist in some areas where suitable roosts are not present. Whilst significantly improved understanding of habitat selection can be achieved using fine scale, high resolution habitat mapping at individual sites, the application of this to broad patterns of landscape favourability is limited, particularly when incorporating habitat information from mixed resolutions and with incomplete coverage. The foraging range of bats, for example, can be several kilometres from roosts and this should be considered when interpreting the predictions of landscape models as bats may commute from roosts in favourable roosting habitat to discrete areas of favourable foraging habitat.

Bat species have specific roost requirements (Marnell & Presetnik 2010) based on, for example, thermal conditions (Lourenço & Palmeirim 2004; Smith & Racey 2005) and avoidance of predators linked to the manoeuvrability of individual species (Jones & Rydell 1994). Throughout the year, bats may use a variety of roosts of different types depending on changing metabolic and social requirements. In late spring, breeding females seek warm areas to minimise the energy cost of maintaining a high body temperature whilst caring for dependent young. There are many exceptions, however, and species have been recorded from a wide variety of situations. Some species are particularly closely associated with natural structures but man-made structures are regularly used by bats across Europe. The roosting dependence of European bats was reviewed by Marnell and Presetnik (2010).

Within Ireland, the majority of bat roosts are in buildings. In other parts of their range, outside Ireland, their roosting associations can be markedly different; for instance, the Leisler's bat (*Nyctalus leisleri*) in Europe is considered to be highly dependent on tree roosts (Marnell & Presetnik 2010) whereas, in Ireland, tree roosts remain rarely recorded. We present analyses of the patterns of roost selection across all species of Irish bats. By combining analysis of landscape associations, roosting habitat and roost selection, we hope to further the understanding of the ecology of Irish bats and provide a guide to the key differences in landscape and roost associations of all species.

METHODS

Species' records and predictor variables

Bat Conservation Ireland (http://www.batconservationireland.org/) maintains a database of species' occurrence records. This database was devised in 2004 with funding from The Heritage Council and populated with records with funding from the Heritage Council and the National Parks and Wildlife Service. It is a MySql database that is designed to be compatible with Recorder 6. Records fit into one of three categories: Roosts, Transects or Ad-Hoc Observations. Since 2005 records have been entered from state-funded surveys, results of studies by independent ecologists, academic institutions and monitoring schemes administered by Bat Conservation Ireland, among others. Over 17,000 records had been entered by winter 2010. In order to ensure a high standard in the database, records from experienced bat researchers were accepted for entry to it, along with validated monitoring records collected by volunteers. Confirmed bat records collected by individuals with little or no experience in bat identification are entered into the database as 'species unidentified' so these records were not selected for inclusion in the present study. Since whiskered (*Myotis mystacinus*) and Brandt's (*M. brandtii*) bats are indistinguishable based on echolocation calls, records for these similar species were entered in the database under the whiskered/Brandt's category. However, due to the confirmed rarity of Brandt's bat in Ireland (CIBR 2011) the records are assumed to mostly or wholly refer to whiskered bats, hence all records in this category are ascribed to whiskered bats. For this study, all unique records attributed to a defined species, collected between 2000 and 2009, were collated for analysis of landscape association. Records including incidental records and roost records were included from across Ireland. For analysis of roosting habitat associations and roosting characteristics, only maternity roosting records were used. No extant roosts are known for Nathusius' pipistrelle (*P. nathusii*) in Ireland, however, so roost habitat association and roost characterisation analyses were carried out on the remaining eight species.

Variables used in the model to predict occurrence included land cover (http://www.eea.europa.eu), topography (http://www.diva-gis.org/Data), climate (http://www.worldclim.org/), riparian habitat (http://www.diva-gis.org/Data) and soil pH (http://eusoils.jrc.ec.europa.eu/). In addition, a variable encompassing human influence (http://sedac.ciesin.columbia.edu/wildareas) was used to compensate for bias in survey effort due to the distribution of human population / human activity. Corine land cover data was used to provide land cover data for the entire island. At present the ability to incorporate fine scale site specific habitat surveys into coarse regional and all-Ireland land cover assessment remains problematic. All variables used are summarised in Table 1. Predictor layers were constructed on grids of increasing spatial scale of size = 0.5km, 1.5km, 2.5km, 4.5km, 6.5km, 10.5km, 20.5km. These scales were selected to represent a gradient from likely foraging areas of individual bats / colonies to descriptive of the regional landscape.

Construction of landscape models

A Maximum Entropy Model (MEM) was fitted in MaxEnt 2.2 (Philips & Dudík 2008). Maximum Entropy modelling is a framework for integrating information from many heterogenous information sources for classification. MaxEnt works on the principle of generating probability distributions and does not require absence points in the framework. Using the MaxEnt method allows species' records that have not been collected in a systematic survey to be analysed. The results help explain patterns of species' occurrence and predict where species might occur. The method builds relationships of species' occurrence, similar to correlations, of different forms such as linear and quadratic, with environmental predictor layers. The outputs of this type of modelling can provide extremely accurate models of bat species' occurrence (Rebelo *et al.* 2007).

Individual MEM's were constructed for each bat species. A MEM was constructed to select the most relevant spatial scale for each spatial variable. To do this, all scales of single variables and a human bias layer were included. The human bias layer accounts for differences in rates of discovery of records due to different densities of human activity in remote regions. A single spatial scale was selected for each variable defined as that which made the largest percentage contribution to the model. A final model was constructed for each species including all variables at their selected spatial scale and non-spatial variables. Regularization values were selected as default (=1) and a convergence threshold set to $t = 10^{-5}$ and maximum number of iterations of $i = 500$. Regularization values define how closely the species' records are assumed to correlate to the environmental values. In the case where a very close relationship is expected, a value less than 1 is used. For weak relationships a value greater than 1 is used. In our case we can be confident that a record is of a bat occurring within a 500m grid (the smallest scale). The convergence threshold and number of iterations define the precision of the model's estimation of associations and the number of times the model will be applied to estimate associations.

Within the MEMs, two relationship forms are constructed; linear and quadratic. To aid interpretation, the responses of species' occurrence are classified as linear, where an increase / decrease in the probability of occurrence is matched to the increase or decrease in a land cover value (Figure 1a); or quadratic, where an optimum point is reached after which the probability of occurrence declines (Figure 1b). In the Results section we summarise these relationships as either coming from a positive or negative linear association or as having a quadratic form.

Table 1: Variables used for modelling the associations of Irish bat species. Those variables with a spatial component are shown.

Explanatory variables			Description	Spatial scale						
Type	**Name**	**Units**		**500m**	**1.5km**	**2.5km**	**4.5km**	**6.5km**	**10.5km**	**20.5km**
Land cover	Arable	m^2	Coverage of non-irrigated arable land.	✓	✓	✓	✓	✓	✓	✓
	Bare rock	m^2	Coverage of bare rock.	✓	✓	✓	✓	✓	✓	✓
	Bog, marsh, moor & heath	m^2	Coverage for a composite of bog, marsh, moor and heath.	✓	✓	✓	✓	✓	✓	✓
	Broad-leaved woodland	m^2	Coverage of broad-leaf woodland.	✓	✓	✓	✓	✓	✓	✓
	Coastal habitats	m^2	Coverage of coastal habitat.	✓	✓	✓	✓	✓	✓	✓
	Coniferous plantations	m^2	Coverage of conifer woodland.	✓	✓	✓	✓	✓	✓	✓
	Forest	m^2	Coverage for a composite of broad-leaved woodland, coniferous plantations and mixed forest.	✓	✓	✓	✓	✓	✓	✓
	Freshwater	m^2	Coverage of open water.	✓	✓	✓	✓	✓	✓	✓
	Mixed agriculture	m^2	Coverage for a composite of complex cultivation patterns and land principally occupied by agriculture with significant natural vegetation.	✓	✓	✓	✓	✓	✓	✓
	Mixed forest	m^2	Coverage of vegetation formation composed principally of trees, including shrub and bush under storeys, where neither broad-lived nor coniferous species predominate.	✓	✓	✓	✓	✓	✓	✓
	Natural grass	m^2	Coverage of low productivity grassland. Often situated in areas of rough, uneven ground. Frequently includes rocky areas, briars and heath.	✓	✓	✓	✓	✓	✓	✓
	Pasture	m^2	Coverage of dense grass cover, of floral composition, dominated by Graminaceae, not under a rotation system. Mainly for grazing, but the fodder may be harvested mechanically. Includes areas with hedges	✓	✓	✓	✓	✓	✓	✓
	Scrub	m^2	Bushy or herbaceous vegetation with scattered trees. Can represent either woodland degradation or forest regeneration / recolonization.	✓	✓	✓	✓	✓	✓	✓
	Sparse vegetation	m^2	Coverage of scattered vegetation is composed of gramineous and/or ligneous and semi-ligneous species.	✓	✓	✓	✓	✓	✓	✓
	Urban	m^2	Coverage of man made structures and transport network.	✓	✓	✓	✓	✓	✓	✓
Topography	Altitude	m	Elevation above sea level in metres.	✓						
Climate	$Temp_{min}$	^oC	Minimum temperature of the coldest month.	✓						
	$Temp_{max}$	^oC	Maximum temperature of the warmest month.	✓						
	$Precipitation_{annual}$	mm	Total annual precipitation.	✓						
	Seasonality	Index	Standard deviation of mean monthly temperatures *100.	✓						
Other	Riparian corridor	m	Total length of river and water body edge including lakes, reservoirs, ponds, rivers, streams and canals in metres.	✓	✓	✓	✓	✓	✓	✓
	Soil pH	pH	Mean soil pH.	✓	✓	✓	✓	✓	✓	✓
	Human influence layer	Index	Human Influence Index comprising population density, rail networks, major roads, navigable rivers, coastal shore lines, night-time stable light emissions, urban land cover and agriculture.	✓						

A random selection of 20% of records was used to test the predictive capability. These records were not used to build the model but were used after each model was constructed to determine accuracy. The number of species' records used to develop the MEM is given below in the summary of associations. The model fit was tested using Receiver Operating Characteristic (ROC) curve analysis and the Area Under the Curve (AUC) statistic (Fielding & Bell 1997). The AUC statistic provides a measure of how well the constructed model can predict if a species will occur in a given location, as a percentage correct classification rate.

The constructed model was projected across the entire area and the average probability calculated on a 5 km grid. The values of habitat suitability were scaled, ranging from 0 – unsuitable to 100 – highly suitable. The values of grid squares where species records exist were collated. These represent the range of habitat suitability values the species can tolerate. From this range a threshold value was calculated above which other areas are predicted as suitable for a species to occur. A threshold value equal to the lower 10^{th} percentile of the range is commonly used as a conservative threshold (Pearson *et al.* 2007). We calculated this threshold for each species and identified the entire land area with a habitat suitability score above this as the species' core area .

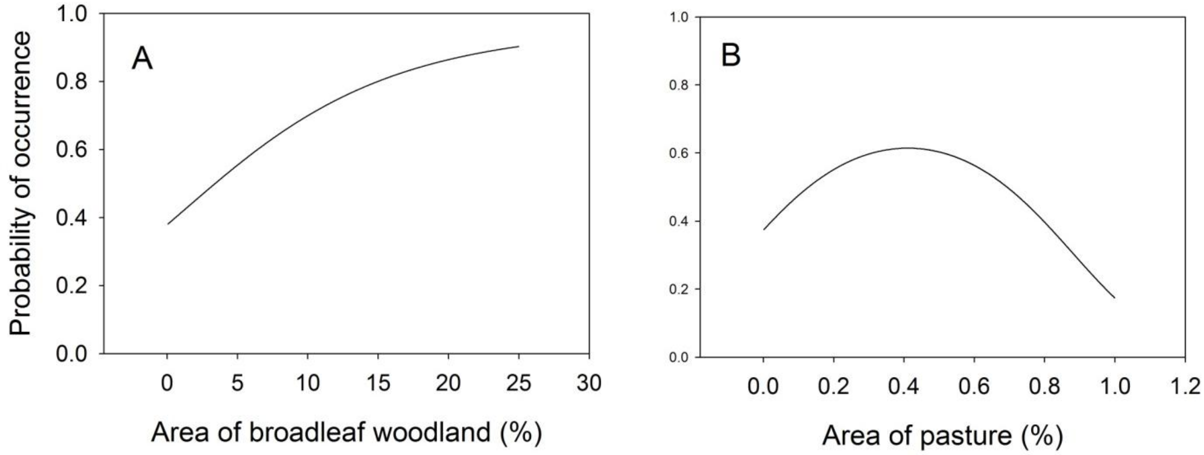


Figure 1.A. A modelled response form classified as 'linear', showing a positive relationship between the probability of occurrence of whiskered bat and the area of broadleaf woodland. B. A relationship classified as 'quadratic' between the probability of occurrence of whiskered bat and the area of pasture.

Analysis of roosting habitat pattern

For all known maternity roosts the area 5 km around roosts was delineated and the area of land cover variables calculated. Random locations were generated, which fell outside the 5 km area around roosts. Comparison of the land cover composition around roosts and in the randomly selected non-roost areas allows examination of roosting habitat selection. To achieve this, selection ratios (ωi) were used to provide a measure of the selection / avoidance of habitats (Manly *et al*. 2003).

Selection ratios provide a measure of occurrence of a land cover type in the immediate vicinity of roosts in comparison to how common that land cover type occurs in all areas. This helps account for different relative abundance of land cover types. For instance, if there was no selection / avoidance of a land cover it would be expected that the area of this land cover would be equal at both roosts and non-roost locations. Selection for a land cover type is reflected by a ωi of greater than 1, whereas avoidance is assumed with ratios below 1. We calculated ωi for each habitat type and each species assuming that all roosts are independent (Manly *et al.* 2003). The significance of selection ratios was calculated using Chi-square tests with Bonferroni correction.

Roosting characteristics

A number of standard parameters are entered to the Bat Conservation Ireland database when bat roosts in man-made structures are identified. These are categorised under Building type, Insulation, Roof lining, Roof material, Wall lining, and Wall material. The frequency of occurrence of these descriptive roost parameters was collated for all known maternity roosts. Using *wi*, the selection / avoidance of roost characteristics was calculated after Manly *et al*. (2003). Individual species' *wi* was compared to roost characteristics over all species. Tree roost characteristics were not analysed due to a paucity of records. Where a habitat is not present at any roosts, it is not possible to interpret values of *wi* because the method relies on comparing the levels of variation in used and available roosts.

RESULTS

Landscape Association Models

The variables that make the largest percentage contribution to the MEM of each species are summarised in Table 2. The selected spatial scales and relationships with predictor variables are shown in Table 2 along with the AUC and threshold value for the core area. The number of records used in the construction of each model can be found in Table 3.

The AUC values for models constructed for Irish bats ranged from 68.4 to 94.0%. An AUC value of 50% corresponds to a model which has equal rates of correct to incorrect predictions indicative of weak associations with variables used in the MEM. The AUC values derived for the Irish bat MEMs suggest that useful predictive models were constructed for all species.

No single spatial scale was selected as the most relevant for all species. However, there is a trend within land cover variables for selection of the smallest scale (0.5km grid) for variables such as riparian habitat and urban land cover. For Daubenton's bat (*M. daubentonii*), and soprano pipistrelle (*Pipistrellus pygmeaus*) land cover variables only from the smallest (0.5km grid) are selected, suggesting widespread distribution but with occurrence at a given location determined by local conditions. In contrast, the lesser horseshoe bat is associated with the largest spatial scale (20.5km grid) suggesting regional patterns of occurrence. All other species selected variables from a mix of scales indicative of a combination of regional variation in occurrence and important associations with local habitat.

The associations with habitat types revealed some consistent patterns across species. In general, bog, marsh and heath have negative associations, whilst broadleaf woodland, mixed forest and riparian habitats have positive associations with bat occurrence. Furthermore, small amounts of urban cover, when selected, are a positive determinant of some species, whilst large amounts of urban cover are negatively associated with occurrence, evident from a quadratic relationship.

The outputs of MEM models will be projected onto maps of habitat suitability for each bat species available through the National Biodiversity Data Centre (http://www.biodiversityireland.ie). A summary of the modelled core areas is shown in Table 3.

Table 2: The selected predictive variables used in Maximum Entropy Modelling (MEE) modelling of species' occurrence. The relationships; positive associations (**+ve**), negative associations (**-ve**) and quadratic (+ve/-ve) with variables are shown. The spatial scales (km) are shown in brackets. The Area Under the Curve (AUC) statistic provides the percentage correct classification of the model.

	Brown long-eared	Common pipistrelle	Soprano pipistrelle	Nathusius' pipistrelle	Lesser horseshoe bat	Leisler's bat	Daubenton's bat	Whiskered bat	Natterer's bat
Arable	-	-	-	-	**-ve** (20.5)	-	-	-	-
Bog, marsh and heath	**-ve** (0.5)	**-ve** (0.5)	-	**-ve** (2.5)	-	**-ve** (0.5)	**-ve** (0.5)	**-ve** (1.5)	**-ve** (0.5)
Broadleaf	**+ve** (0.5)	**+ve** (0.5)	**+ve** (0.5)	**+ve** (0.5)	**+ve** (20.5)	**+ve** (1.5)	**+ve** (0.5)	**+ve** (1.5)	**+ve** (0.5)
Mixed forestry	**+ve** (20.5)	**+ve** (20.5)	-	-	**+ve** (20.5)	**+ve** (20.5)	-	**+ve** (0.5)	**+ve** (20.5)
Pasture	-	-	-	+ve/-ve (0.5)	-	-	-	+ve/-ve (1.5)	+ve/-ve (1.5)
Riparian	**+ve** (0.5)	**+ve** (0.5)	**+ve** (0.5)	-	-	**+ve** (0.5)	**+ve** (0.5)	-	**+ve** (0.5)
Scrub	-	-	-	-	-	-	-	+ve/-ve (2.5)	-
Urban	+ve/-ve (0.5)	+ve/-ve (0.5)	+ve/-ve (0.5)	-	-	+ve/-ve (0.5)	+ve/-ve (0.5)	+ve/-ve (0.5)	-
Freshwater	-	-	-	+ve/-ve (10.5)	-	-	-	-	-
Altitude	-	-	**-ve**	-	-	-	**-ve**	-	-
AUC	78.2	78.1	74.9	68.4	94.0	73.9	80.8	83.3	79.2

Table 3: Core areas of Irish bat species, number of records for each species used in Landscape Association Model and roost habitat association/roost characterisation model constructions.

Species	Total No. records (Landscape Association Models)	Core Area (km^2)	Total No. Maternity Roost Records (Roost Habitat & Roost Characteristic Models)
Brown long-eared	611	49929	78
Common pipistrelle	1419	56485	27
Soprano pipistrelle	1896	62020	59
Nathusius' pipistrelle	37	13543	N/A
Lesser horseshoe bat	494	5993	121
Leisler's bat	1122	52820	22
Daubenton's bat	1159	41285	13
Whiskered bat	134	29222	9
Natterer's bat	256	52864	10

**Note – Area of Ireland taken as = 84062km²*

Roosting habitat selection and Roost character

In general, broadleaf woodland, mixed forest, scrub and freshwater are habitats selected by roosting bats (Table 4). Conifer forestry, arable land cover, natural grassland and mixed agriculture, in contrast, are avoided. In addition, bog, marsh and heath habitats are avoided by all bats species, except Daubenton's bat, which appears to be associated with this habitat. The number of maternity roost records used in constructing these models for the eight species are shown in Table 3.

Analysis of roost feature selection by Irish bats demonstrates low levels of selection / avoidance for specific features across species (Table 5). Brown long-eared (*Plecotus auritus*), lesser horseshoe and Daubenton's bats tend to avoid roosting in houses whilst brown long-eared bats select church buildings. In terms of selecting roosts with and without insulation, only Daubenton's show significant avoidance of insulated buildings and select non-insulated buildings. Roof material was not found to be a determinant of a roost selection but there is a complex pattern with roof lining and no consistent patterns across species. Only the brown long-eared bat shows any preference for roosts with particular wall lining with selection of stonework. All species, except Natterer's bat (*M. nattereri*), are associated with a specific wall material. There is a contrast in this regard between the common (*Pipistrellus pipistrellus*) and soprano pipistrelle, where the former selects for stone material and the latter for brick material. For most other species, there is significant avoidance of brick material and selection for stone.

Table 4: Significant roosting habitat selection ratios (*wi*) of Irish bat maternity roosts with standard errors. Values > 1 indicate significant selection of habitats whilst *wi* < 1 indicate avoidance.

	Brown long-eared	Common pipistrelle	Soprano pipistrelle	Lesser horseshoe bat	Leisler's bat	Daubenton's bat	Whiskered bat	Natterer's bat
Arable	-	**0.47**±0.1	-	-	**0.26**±0.1	-	-	
Bog, marsh and heath	**0.43**±0.1	-	-	**0.22**±0.1	**0.19**±0.1	**2.80**±0.4	**0.36**±0.1	**0.34**±0.1
Broadleaf	**3.38**±0.5	-	**4.06**±0.7	**6.36**±2.0	**1.23**±0.1	-	**4.12**±0.8	**4.12**±0.8
Mixed agriculture	**0.58**±0.1	-	-	**0.61**±0.1	**0.32**±0.1	**0.60**±0.1	-	
Conifer	-	**0.38**±0.1	-	-	**0.39**±0.1	-	-	
Freshwater	-	-	**4.05**±0.7	-	**2.41**±0.4	-	-	
Natural grassland	**0.12**±0.1	**0.21**±0.2	-	-	-	-	**0.22**±0.1	**0.22**±0.1
Mixed forestry	-	-	**5.30**±1.4	-	**3.12**±0.5	-	**1.89**±0.3	**1.89**±0.3
Pasture	-	**1.25**±0.1	-	-	-	-	-	
Scrub	**1.20**±0.1	-	-	-	-	-	**2.10**±0.2	**2.10**±0.2

Table 5: Significant roosting features selection ratios (*wi*) of Irish bat maternity roosts with standard errors. Values > 1 indicate significant selection of features whilst *wi* < 1 indicate avoidance.

	Brown long-eared	*Common pipistrelle*	*Soprano pipistrelle*	*Lesser horseshoe*	*Leisler's bat*	*Daubenton's bat*	*Whiskered bat*	*Natterer's bat*
No. of roosts	78	27	59	12	22	13	9	10
Building type:								
Farm building	-	-	-	-	-	-	-	-
House	**0.72**±0.1	-	-	**0.49**±0.3	-	**0.63**±0.3	-	-
Church	**1.87**±0.4	-	-	-	-	-	-	-
Ruin	-	-	-	-	-	-	-	-
Other	-	-	-	-	-	-	-	-
Insulation:								
Insulated	-	-	-	-	-	**0.36**±0.3	-	-
Non-insulated	-	-	-	-	-	**1.42**±0.2	-	-
Roof Lining:								
No roof lining	-	-	-	-	-	-	-	**2.27** ±0.7
Felt	-	-	-	-	**2.34**±0.7	-	-	-
Wood	-	-	-	-	-	-	-	-
Other	**0.72**±0.1	-	**1.28**±0.1	-	-	-	-	-
Roof material:								
Tile	-	-	-	-	-	-	-	-
Slate	-	-	-	-	-	-	-	-
Metal	-	-	-	-	-	-	-	-
Other	-	-	-	-	-	-	-	-
None	-	-	-	-	-	-	-	-
Wall lining:								
Brick	-	-	-	-	-	-	-	-
Plaster	-	-	-	-	-	-	-	-
Stone	**1.50**±0.3	-	-	-	-	-	-	-
Wood	-	-	-	-	-	-	-	-
None	-	-	-	-	-	-	-	-
Wall material:								
Brick	**0.12**±0.1	-	**1.37**±0.3	**0.42**±0.1	**0.35**±0.2	**0.26**±0.2	**0.45**±0.3	-
Stone	**1.13**±0.1	**1.69**±0.4	-	**1.29**±0.2	**2.25**±0.4	**2.60**±0.2	**2.06**±0.5	-
Wood	-	-	-	-	-	-	-	-

CONCLUSIONS

Interpreting landscape models

The landscape-based models reveal habitat associations of all bat species that regularly occur in Ireland. These models identify core areas in which species would be expected to occur. The predictive models permit not only informed assessment of an area's likelihood of supporting a particular bat species but also suggest reasons why species may not be present. However, these models should be considered broad generalisations of species' geographical occurrence. Core areas should be considered as those areas where a species is expected and every effort should be made to maintain the favourable status of that area for a species. However, areas outside core area should not be 'discounted' as unimportant. Indeed the occurrence of the species beyond the limits of the core area may be reliant on small fragments of favourable habitat which are particularly vulnerable to environmental change.

The results of landscape, roosting habitat and roosting characteristics are summarised for each species below. The roosting habitat and roost characteristics of soprano pipistrelle and common pipistrelle are summarised together as traditionally these species have been considered to have similar ecology.

*__Note__ to species' summaries: Quadratic associations with particular habitats (i.e. positive relationship with small areas of habitat, followed by a negative relationship as expanse increases, see Figure 1 above) are indicated in Figures 2-10 below by land cover classes followed with a % value in brackets. This percentage value is the area of cover of the land type at the relevant scale before which the likelihood of occurrence declines.

Species' Accounts

Brown long-eared bat

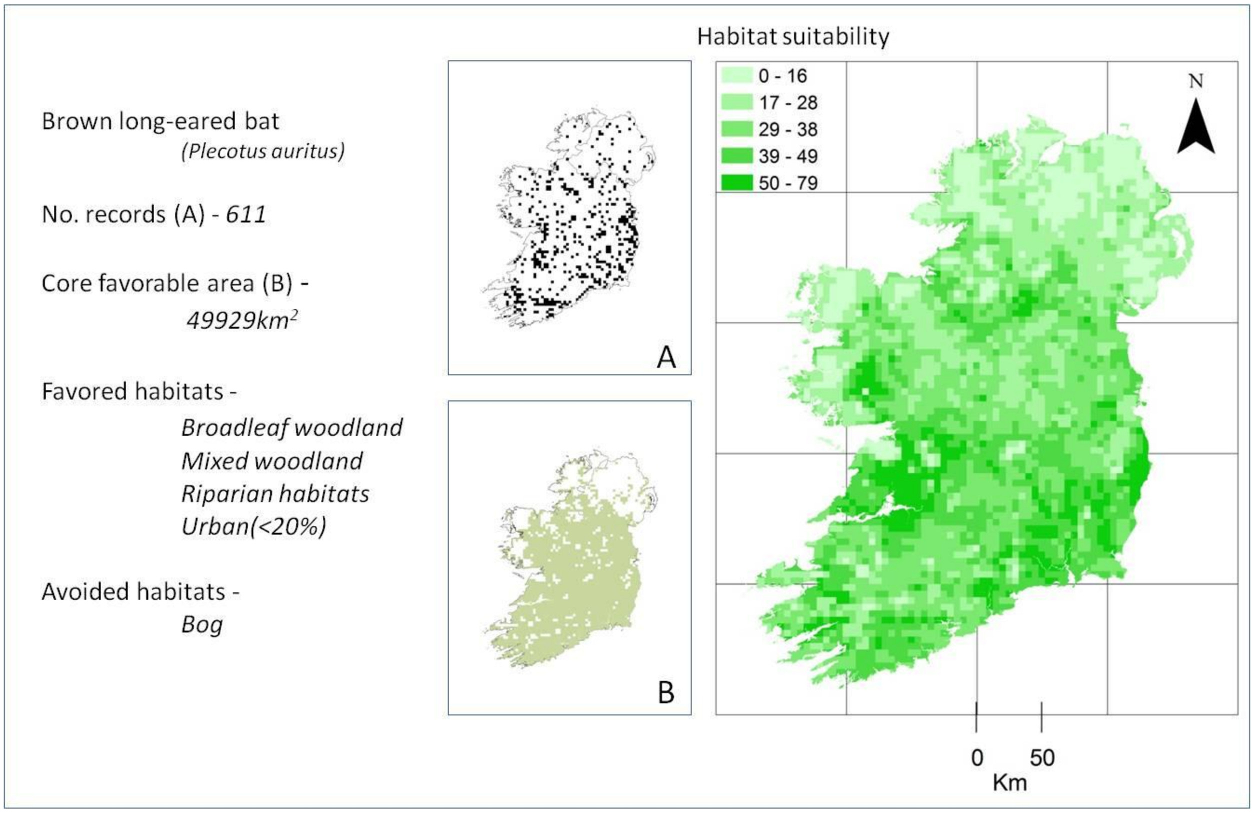


Figure 2: Habitat association summary of brown long-eared bat. Insert A. Shows the distribution of records used to create the landscape model. B. Shows the core area of favourable habitat for the species.

The long-eared bat is known to forage in broad-leaved woodlands, tree lines, scrub, conifer plantations, gardens with mature trees, parkland and orchards (Entwistle *et al.* 1997). The landscape modelling conducted here demonstrates how these associations combine to create a geographic distribution with a southern / eastern bias (Figure 2). This species roosts in close association with foraging habitats but avoids roosting in mixed agricultural areas, bog, marsh and heath and natural grassland. Although important natural habitats in their own right, natural grassland and bog habitats may not provide sufficient cover from predators, in particular, during emergence from roosts. Typical roosts in Ireland are in large open attics where the bats cluster together (McAney 2006). Tree holes, ruins, houses, churches and farm buildings are utilised across its range (Entwistle *et al.* 1997; Marnell and Presetnik 2010). The present analysis of roosting shows selection for stone built, church buildings and avoidance of houses.

Common pipistrelle & Soprano pipistrelle

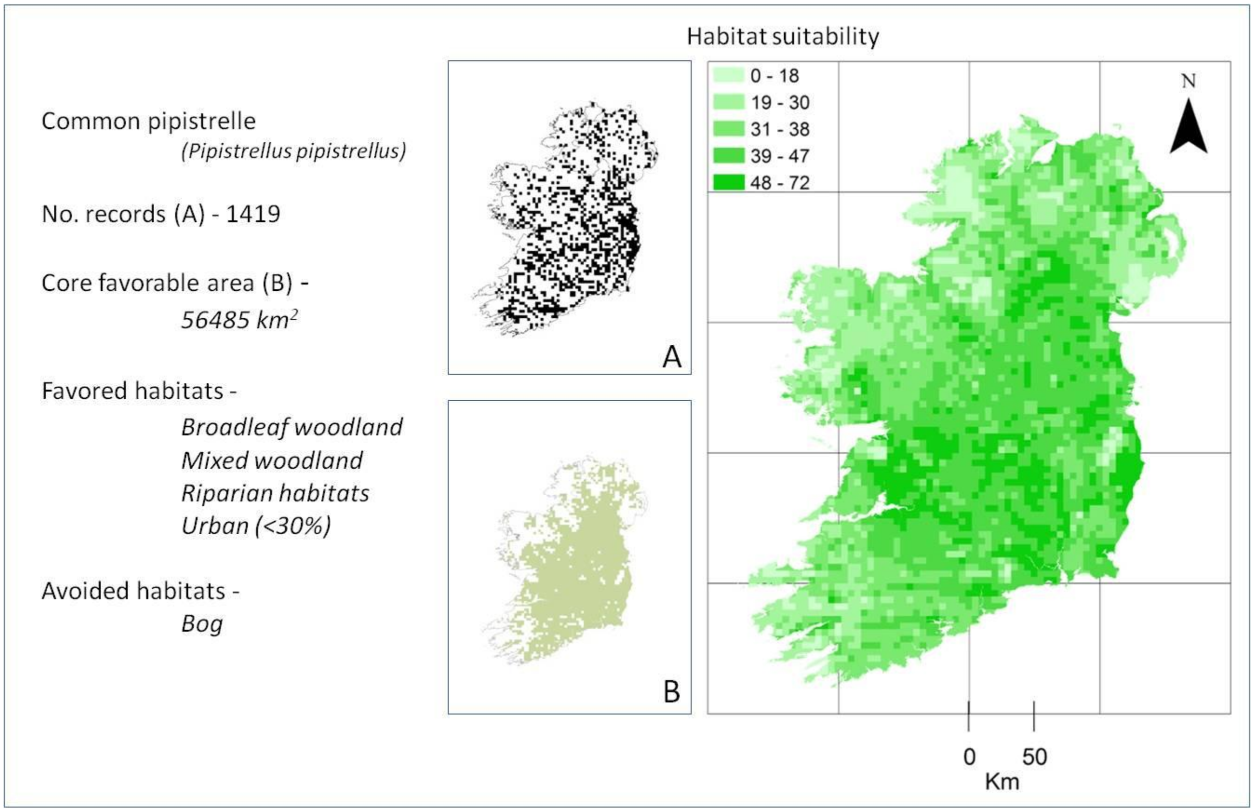


Figure 3: Habitat association summary of common pipistrelle. Insert A. Shows the distribution of records used to create the landscape model. B. Shows the core area of favourable habitat for the species.

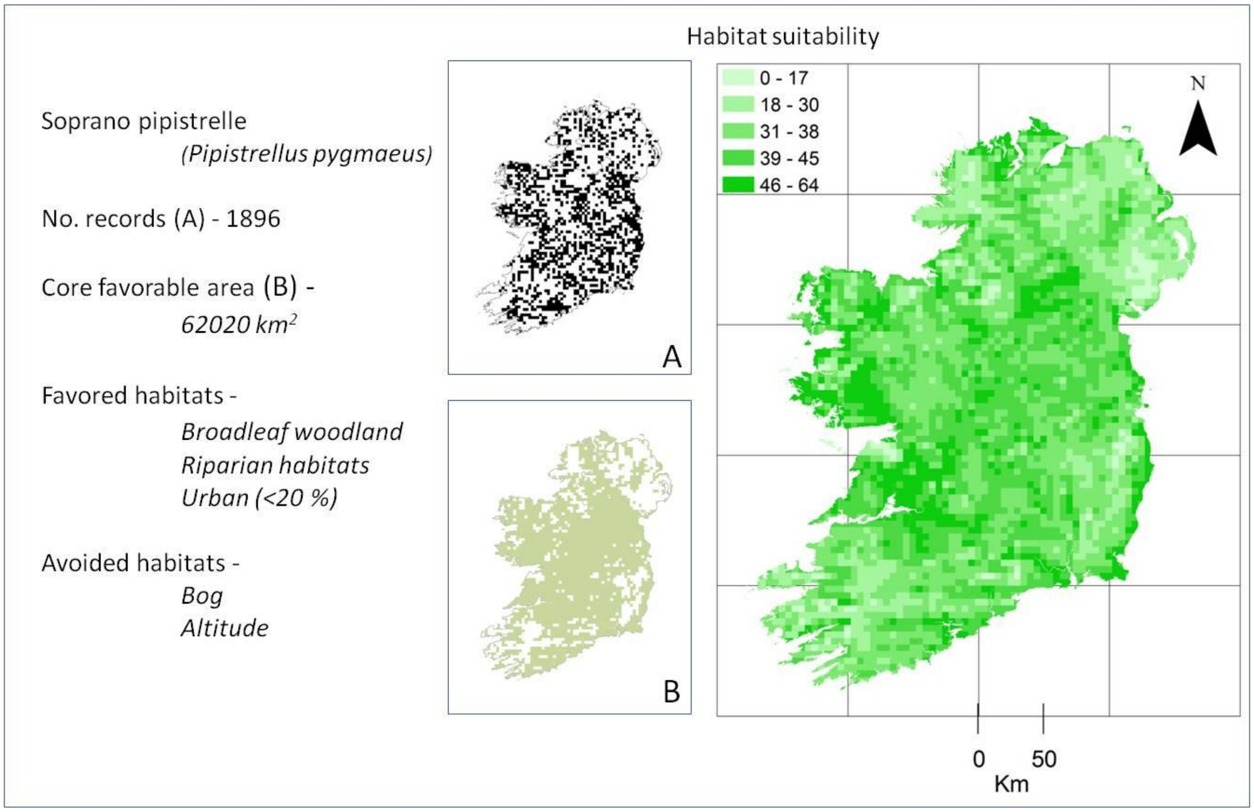


Figure 4: Habitat association summary of soprano pipistrelle. Insert A. Shows the distribution of records used to create the landscape model. B. Shows the core area of favourable habitat for the species.

Common and soprano pipistrelles have broad foraging niches (Russ 1999) which reflect their widespread occurrence in Ireland (Figures 3 & 4). Of all species modelled, these have the largest predicted core areas. Both soprano and common pipistrelle are considered to forage regularly in association with water and other natural land covers (Oakley & Jones 1998; Shiel 1999; Russ & Montgomery 2002). These known associations support the present analyses of habitat selection and landscape modelling (Figures 3 & 4). The soprano pipistrelle roosts in areas with more freshwater and woodland than random, non-roost locations. The common pipistrelle was the only species to have a positive association with the area of pasture close to roosts, although some other species, such as Nathusius' pipistrelle and whiskered bats, have a quadratic relationship with pasture in the general landscape association models.

Summer roosts of *Pipistrellus* spp. are normally in buildings (O'Sullivan 1994) but each species contrasts in roost feature associations with selection for brick built roosts by soprano pipistrelle in comparison to the roosts of most other bat species, whilst the common pipistrelle selects roosts in stone buildings.

Nathusius' pipistrelle

The Nathusius' pipistrelle was regarded as a vagrant in the Ireland and Britain until the 1980's (Stebbings 1988). In 1991, it was afforded the status of migrant winter visitor after a review of the records by (Speakman *et al.* 1991). Following discovery of maternity colonies in Ireland (Russ *et al*. 1998, 2001) and in England (Hutson 1997) it was suggested that Britain and Ireland represent a transitional area where migrating individuals supplement the resident population during the winter (Russ *et al.* 2001). The Nathusius' pipistrelle is associated with natural wetlands and water bodies in its continental range (Arnold & Braun 2002; Sachanowicz *et al.* 2006; Flaquer *et al.* 2009). These associations are reflected in the predicted distribution of the species in Ireland (Figure 5). The core area of the species here is the second smallest of all species modelled, restricted to locations close to large water bodies such as Lough Neagh. The model constructed for Nathusius' pipistrelle had the lowest predictive capability (AUC = 68.4). This is likely to be caused by the small number of known records (n=37). The model provides a good starting point to suggest areas where new records may arise.

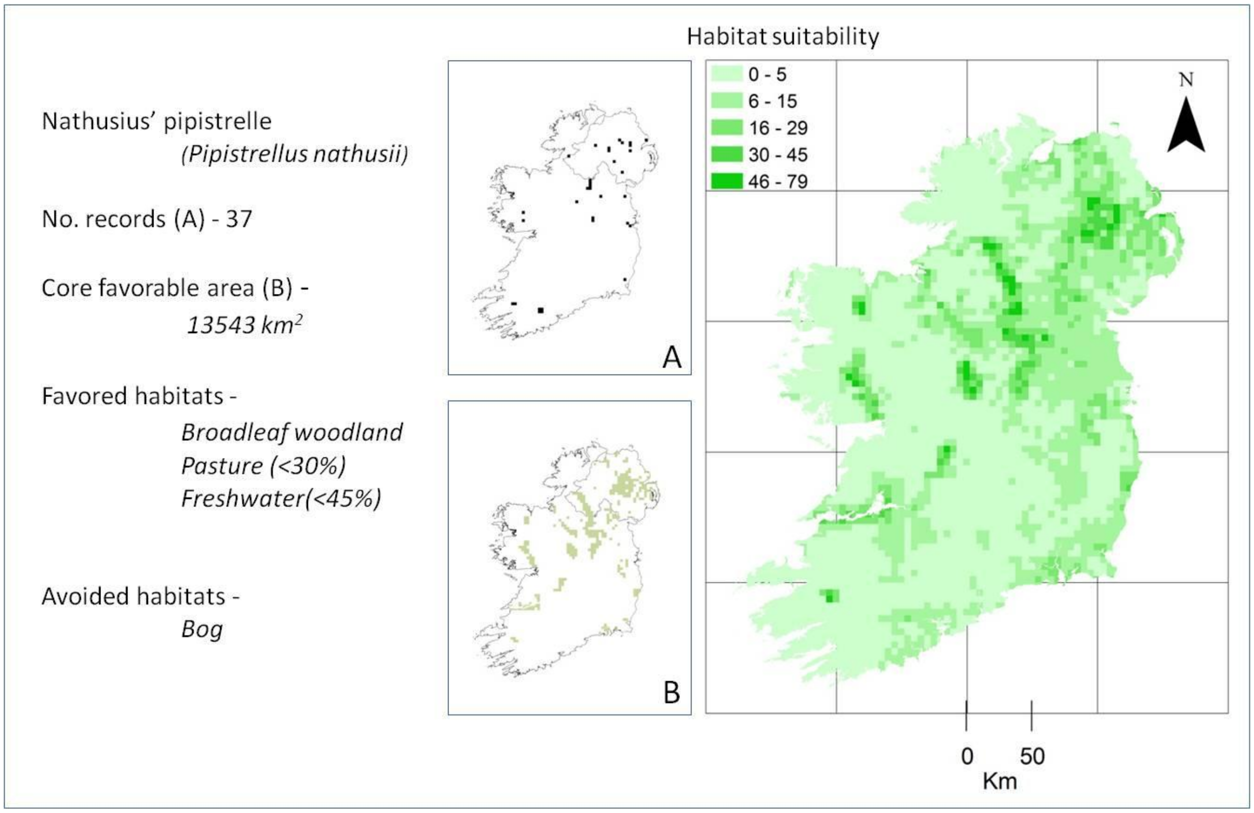


Figure 5: Habitat association summary of Nathusius' pipistrelle. Insert A. Shows the distribution of records used to create the landscape model. B. Shows the core area of favourable habitat for the species.

Currently little is known about the prevalence of maternity roosts of Nathusius' pipistrelles in the Ireland. Historically, maternity roosts of Nathusius' pipistrelle have occurred in Co. Antrim, Northern Ireland, but have been restricted to a small area there (Russ 2008). With increased awareness of the Nathusius' pipistrelle in Ireland it is likely that more records will continue to emerge.

Lesser horseshoe bat

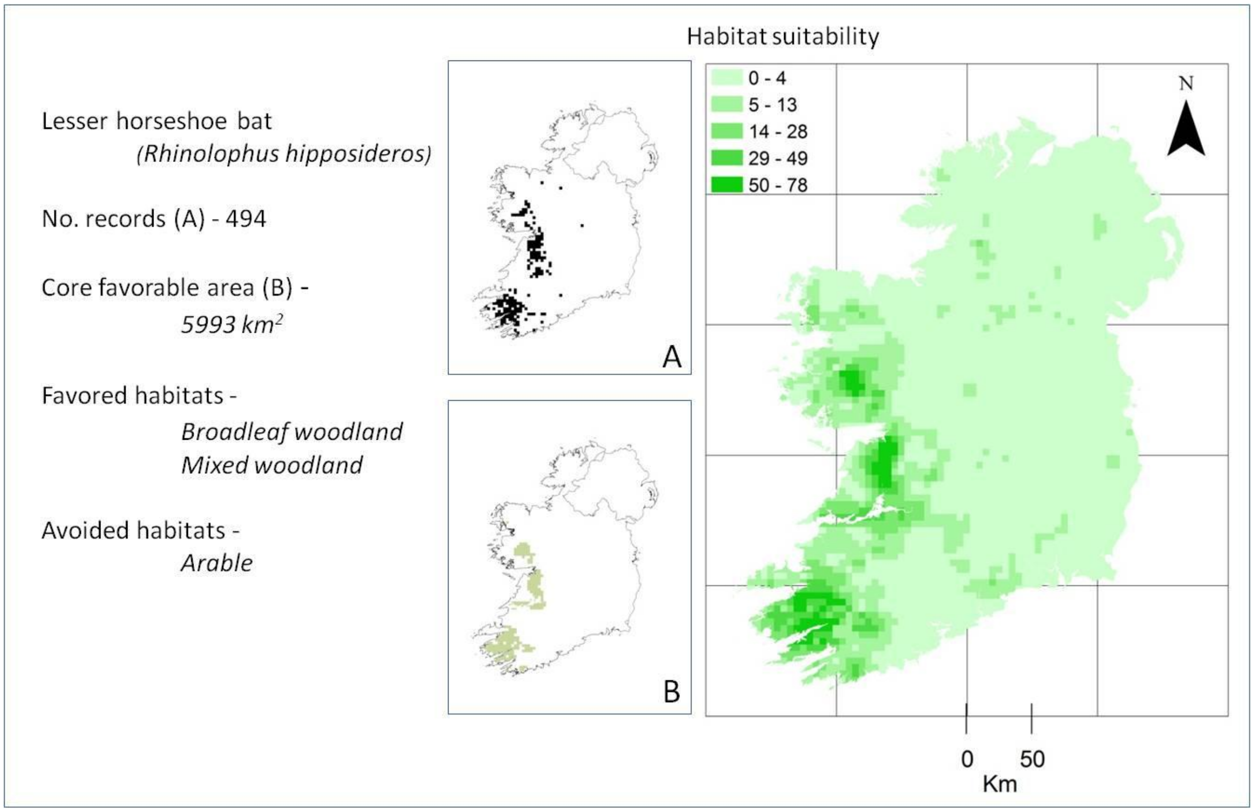


Figure 6: Habitat association summary of the lesser horseshoe bat. Insert A. Shows the distribution of records used to create the landscape model. B. Shows the core area of favourable habitat for the species.

The lesser horseshoe bat forages in deciduous woodland and riparian vegetation normally within a few kilometres of the roost (Bontadina *et al.* 2002). The species is known to rely on linear landscape features to commute from roosts to feeding sites and is reluctant to fly out in the open (Schofield 1996). The lesser horseshoe bat in Ireland is at the most northerly and westerly limits of the species' global distribution (Roche 2001). The core area of the species here is the smallest of all species modelled (5933 Km^2), restricted to karst landscapes of the west of Ireland where caves are utilised frequently as hibernation sites (O' Sullivan 1994). The habitat associations and spatial scales of associations are indicative of this regionally controlled distribution (Figure 6) with a positive association with woodland and avoidance of bog and arable land cover which may not provide enough of the cover that the species requires when commuting from roosts to foraging areas. The predictive capability of the model is the highest of any species (AUC= 94.0). This suggests that the small core area represents the only suitable range for the species in Ireland. Given this small range, significant impacts on the lesser horseshoe may be observed with even small levels of habitat modification or changes in roost availability within this favourable area. It is worth noting that the lesser horseshoe bat avoids areas with mixed agricultural land covers surrounding roosts. This may be important when devising conservation management policies for SAC habitats surrounding important maternity sites.

There are two distinct regions within the core area, one in Kerry / west Cork and one in Clare / Galway. These two areas are divided by marginally favourable habitat in Limerick and north Kerry. Although a marginal area, the continued occurrence of the species in Limerick/north Kerry may have important conservation implications in preventing further fragmentation of the population and allowing movement of individuals between core areas.

Summer roost sites are often in the attics of old or derelict buildings (O' Sullivan 1994). The present analyses of known roosts demonstrate an avoidance of houses, selection for stone buildings and avoidance of brick-constructed buildings.

Leisler's bat

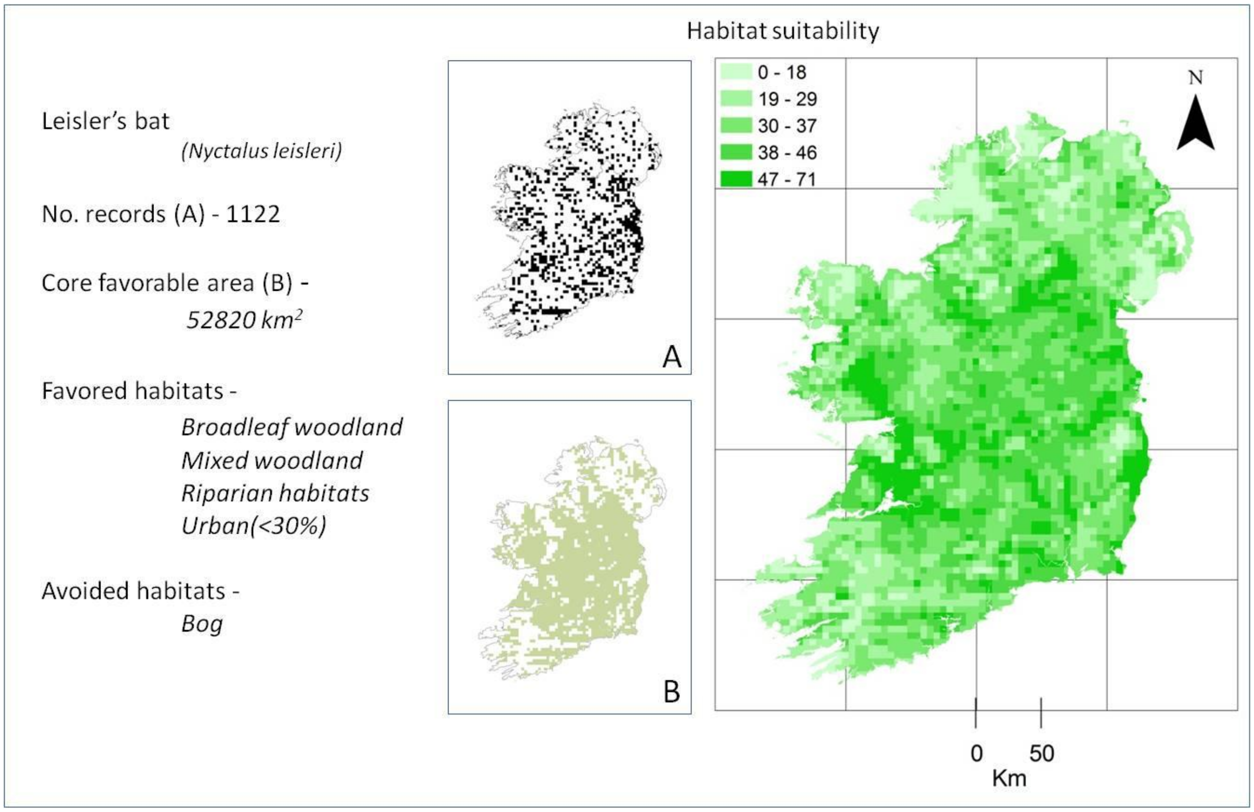


Figure 7: Habitat association summary of Leisler's bat. Insert A. Shows the distribution of records used to create the landscape model. B. Shows the core area of favourable habitat for the species.

Strong habitat associations have been difficult to define for the Leisler's bat in Ireland (Shiel & Fairley 1998; Lundy & Montgomery 2010b). However, radio-tracking has revealed that the species forages in association with pasture or areas of freshwater (Shiel *et al.* 1999). The habitat associations described by the present analyses show an association with riparian habitats but also with areas of woodland (Figure 7). Pasture was not found to be selected or avoided by the present models. Of all the Irish bat species, Leisler's have the most specific roosting habitat selection in terms of the number of land cover classes significantly selected or avoided. The species tends to select roosting habitat with areas of woodland and freshwater, similar to its broad habitat associations. Land cover classes avoided for roosting, however, include mixed agriculture, arable land and conifer woodland and may indicate an avoidance of areas with intensive crop production.

The Leisler's bat is one of the few species that frequently uses tree roosts (Fairley 2001) but nursery roosts tend to be limited to buildings (O'Sullivan 1994). Analysis of maternity roost features shows limited selection for felt lined roofs and stone buildings and avoidance of brick buildings.

Daubenton's bat

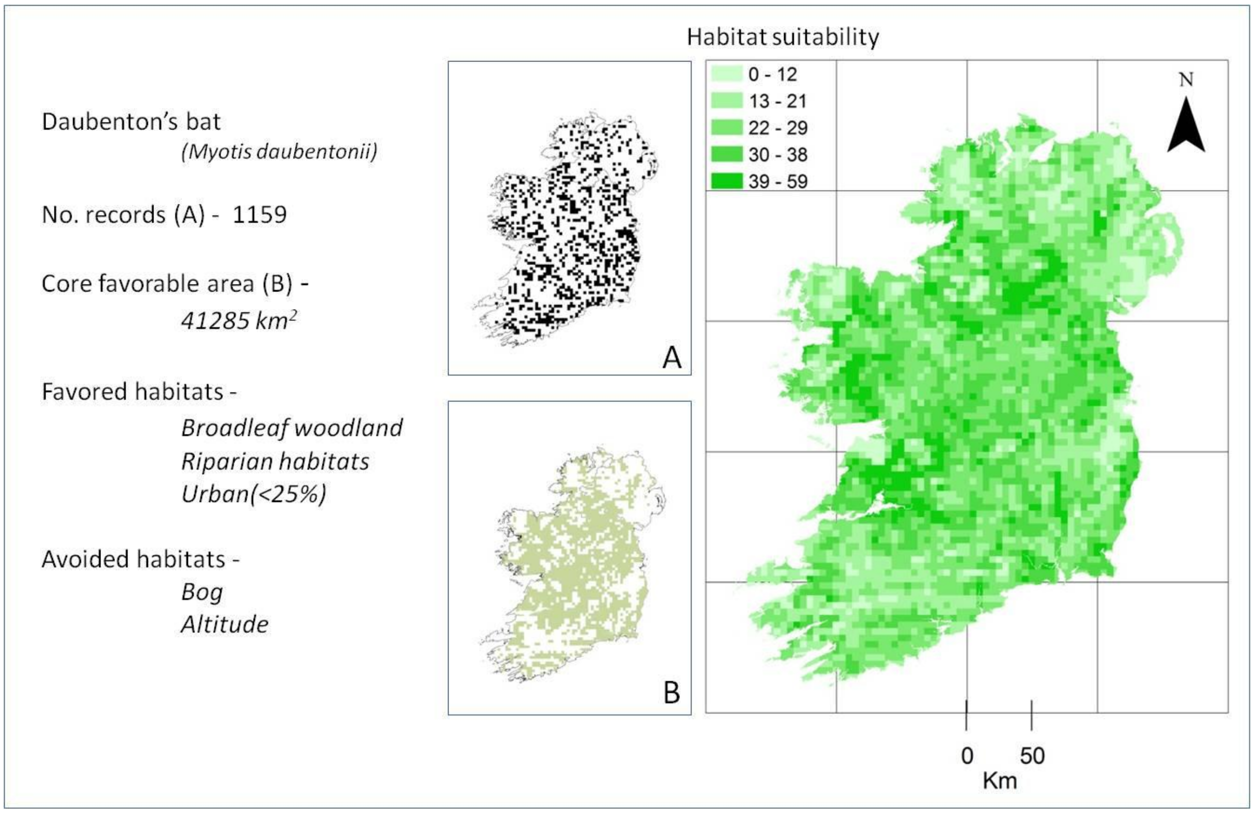


Figure 8: Habitat association summary of Daubenton's bat. Insert A. Shows the distribution of records used to create the landscape model. B. Shows the core area of favourable habitat for the species.

Daubenton's bat is a specialist of freshwater habitats trawling insects from the surface of water (Mackey & Barclay 1989; Racey 1998; Russ & Montgomery 2002). Landscape associations defined here reflect its widespread distribution but high dependence on riparian habitat. The predicted core range of the species has a trend toward central regions (Figure 8). These central lowland areas may provide the slow flowing rivers and abundance of lakes that the species favours for foraging.

Of all the species investigated with respect to roosting associations, only Daubenton's bat selected areas with more bog, marsh and heath coverage than expected at random locations although the general patterns of occurrence were not associated with these land cover classes. This may be because aquatic habitats, its favoured foraging areas, may be linked to this land cover. Indeed, this interaction of fine scale habitat associations and broad landscape associations reflects the complex conservation requirements of some species. The species, similar to others, also avoided roosting in areas with increased agricultural land use.

Roosts of Daubenton's often occur in stone bridges and in buildings during summer (O'Sullivan 1994). The present analysis of roost character selection shows selection for non-insulated stone built roosts whilst avoiding houses.

Whiskered bat

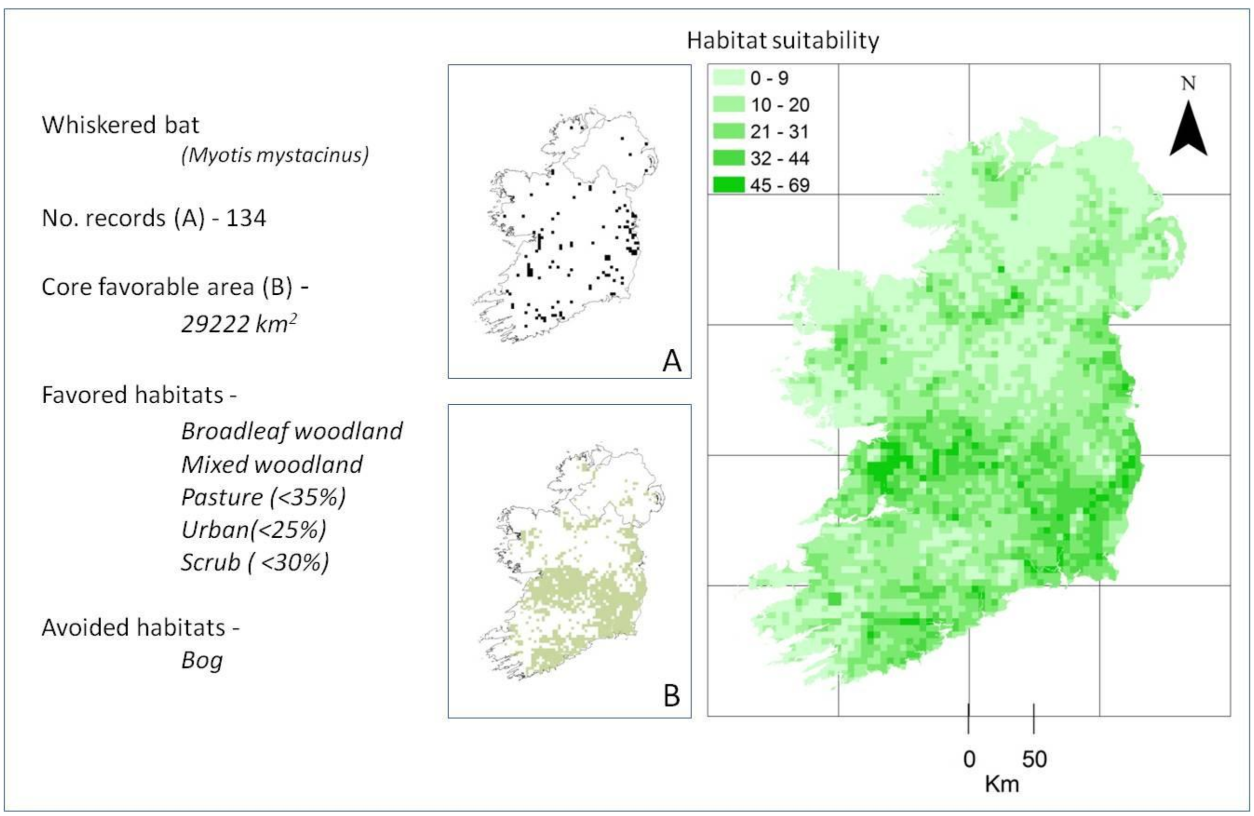


Figure 9: Habitat association summary of whiskered bat. Insert A. Shows the distribution of records used to create the landscape model. B. Shows the core area of favourable habitat for the species.

Highly contrasting habitat associations have been described for whiskered bats; Taake (1984) found an association with agricultural landscapes and riparian habitats surrounding roosts in Germany, whilst Kanuch *et al.* (2008) suggested the whiskered bat to be a woodland generalist with no association with any particular forest type in Slovakia. Berge (2007), in complete contrast, found that it selected pasture with hedgerows in southern England. Recently, radio-tracking whiskered bats in Ireland revealed associations with riparian mixed woodland (CIBR 2010). These broad habitat associations, with the species' presence positively related to woodland cover and small areas of pasture, are reflected in the landscape model of the species (Figure 9). However, the range of the species appears to be restricted, for the most part, to southern and eastern areas of Ireland. Selected roosting habitats include various woodland types (broadleaf/mixed and scrub) in areas surrounding roosts but avoid bog and natural grassland.

Whiskered bats are found in houses during the summer, roosting in small numbers in roof spaces (O'Sullivan 1994; CIBR 2011). The only significant association of any roost feature was selection for stone buildings and avoidance of brick buildings.

Natterer's bat

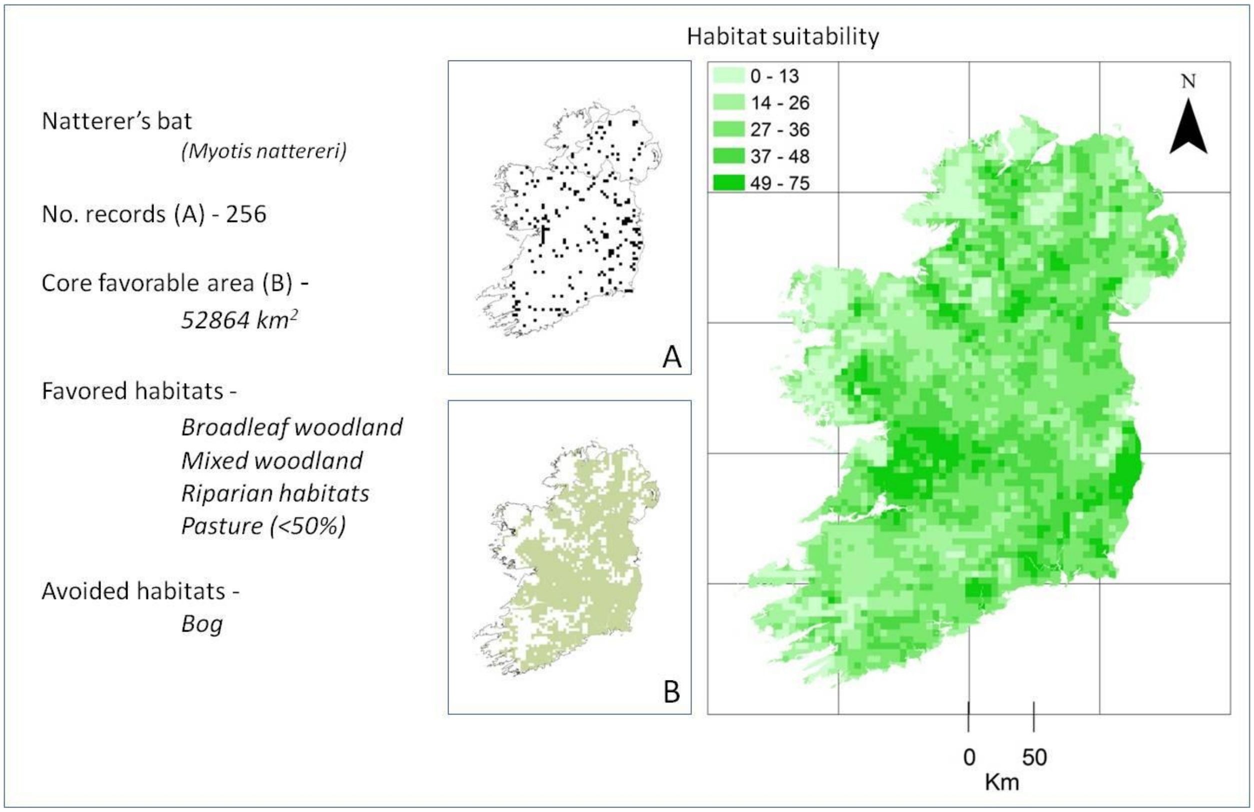


Figure 10: Habitat association summary of Natterer's bat. Insert A. Shows the distribution of records used to create the landscape model. B. Shows the core area of favourable habitat for the species.

Natterer's bats typically forage in a variety of habitats across their European range ranging from meadows, orchards, broadleaf wood to open conifer forest and riparian habitats (Arlettaz 1996; Siemers *et al.* 1999; Siemers & Swift 2006; Smith & Racey 2008). The species is likely to select foraging areas which are rich in horizontal and vertical edges (Siemers *et al.* 1999). The foraging grounds can be up to 4 km from roosts and individuals are faithful to core hunting areas, returning to these on consecutive nights (Siemers *et al.* 1999). Recent radio-tracking of Natterer's bat in Ireland showed that this species forages in pasture but emerges into and utilises woodland during twilight conditions (CIBR 2011). Broadleaf woodland, mixed forests and pasture, which are selected in the MEM reflect these habitat requirements (Figure 10). Roosting habitats avoided include bog and natural grassland while the species selects for various woodland types (broadleaf/mixed and scrub) in areas surrounding roosts.

Colonies of *M. nattereri* are found in buildings during the summer, roosting in small numbers in roof spaces (O'Sullivan 1994). A number of large colonies (>50 bats) have been recorded in churches and other old buildings (McAney 2006; CIBR 2011). The only significant selection defined here is selection for buildings without any roof lining.

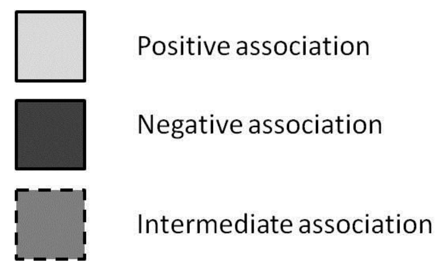
Summary

The results of the present analyses suggest that some associations are universal to the Irish bat community, i.e. positive associations with broadleaf woodland. However, individual species have specific requirements and these combine to produce significantly different distributions for each; the predicted core areas (Table 4) of species range from 5993 km^2 (Lesser horseshoe bat) to 62020km^2 (Soprano pipistrelle). Although the analysis shows lower levels of bat occurrence in mountainous areas, and associated upland land cover, such as bog, this does not mean that these areas are not important for bats. Bats may, in fact, be locally common there and seasonal migrations across mountain ranges may occur in autumn, to swarming sites, and in spring, from hibernacula. Swarming sites or hibernacula may also themselves occur at altitude, in caves or disused mines, but may be hitherto unrecorded.

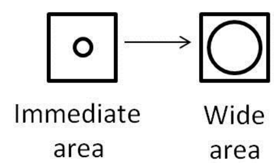
The described associations identify the character of the landscape that makes areas suitable for species. Text Box 1 provides a summary of key land cover associations and the most relevant spatial scale of these associations for each species. The proportion of each species' core area in each county and the proportion of each county which is considered to represent part of the species' core area are provided in Table A1 and Table A2 of the appendix. Within these suitable areas we show how different patterns of roosting habitat / foraging habitat selection combine to create complex patterns for species. These must be considered general patterns of an area's suitability and locations within regions should be assessed on their own merit.

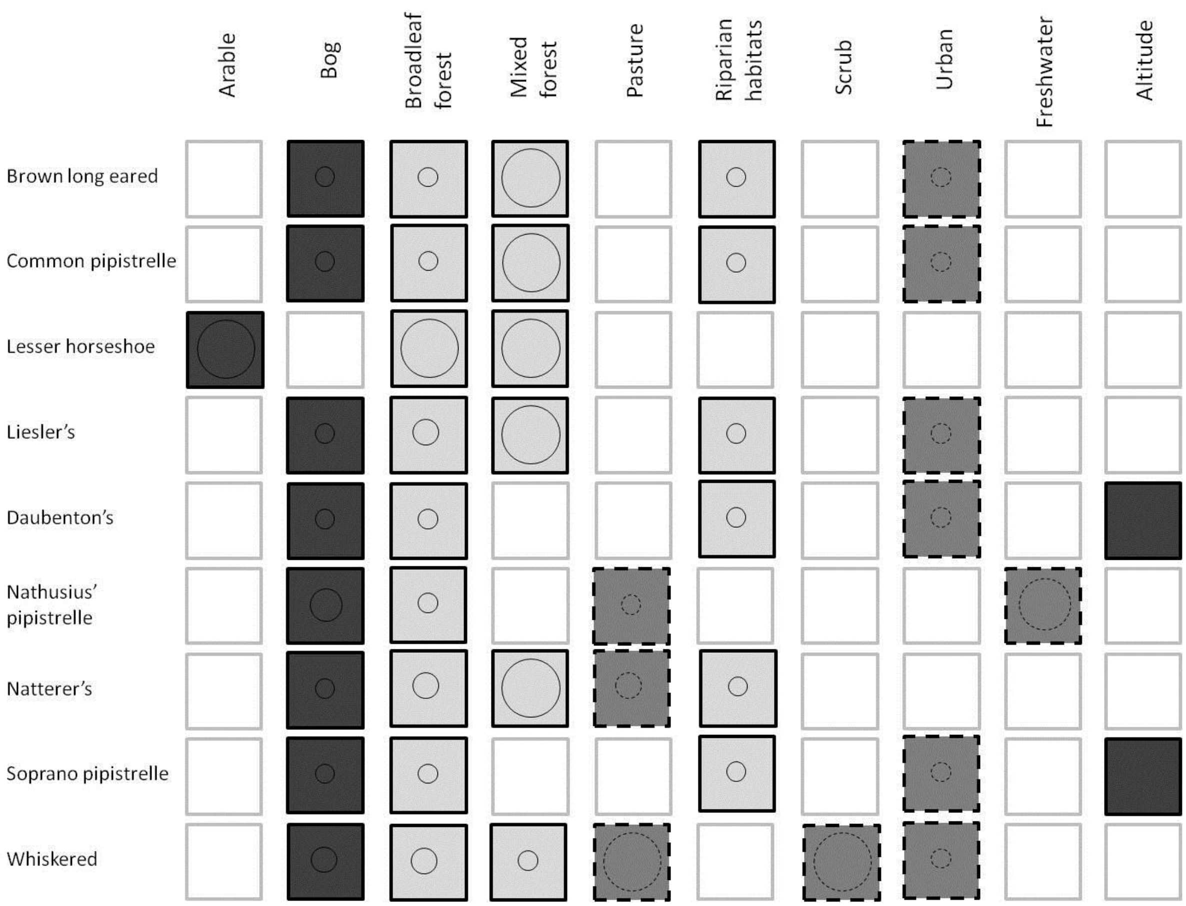
A summary of habitats associations of Irish bats: Two elements of habitat association are identified; direction of association (positive or negative) and scale of association (fine scale or broad scale).

Direction of association: The colour of the box identifies the direction of association. Three relationships are identified; a positive association, a negative association and an intermediate association. An intermediate association reflects that a species is positively associated with a small area of this habitat but as this area increases this association becomes negative. A non-filled box signifies that this habitat is not an important predictor of that species occurring.



Scale of association:
The size of the circle identifies the scale of the habitat that is most important – a small circle identifies that this habitat is important in the immediate area whereas a large circle reflects an association with that habitat at a wider landscape scale.





Text box 1: A summary of the habitat associations of bats.

DEFINITION OF TECHNICAL TERMS

Term	*Definition*
AUC	*Area Under the Curve - a statistic to assess the capability of a model to predict the occurrence of a species across all locations in a region. The value is derived from ROC analysis. The statistic is presented as a percentage of correctly classified areas.*
Core favourable area	*The 'core favourable area' is delineated for species modelled. This area is the suitable area based identified as being above a minimum value of habitat suitability for the species. The minimum value is estimated from the suitability values for the areas that known records occur in.*
GIS	*Geographical Information Systems allow the data management and interpretation of environmental variables across geographic areas.*
Linear response	*A simple straight line response between two variables; these can be positive where both values increase or negative where one value decreases as the other increases*
MaxEnt / MEM	*Maximum Entropy Method modelling commonly applied in the software package MaxEnt allows associations between species occurrence records to be analysed and does not require records where species do not occur. The method defines relationships of occurrence with land cover and other environmental layers to produce a value of suitability based on these predictors. These can be projected on areas where the species' distribution is not known.*
MySQL	*A relational database management system that runs as a server providing multi-user access to a number of databases.*
Quadratic response	*A second-order response between two variables. This response produces a curve where the relationship increases to a point prior to decreasing.*
Recorder 6	*A software tool package for entering, collating and exchanging records of*

	species and habitats.
ROC	*Receiver Operating Characteristic curve is a method to graphically plot the correct classification against the incorrect classification for a predictive model. The graphical plot allows the AUC value to be calculated.*
Selection ratios (wi)	*Selection ratios (wi) provide a measure of the selection / avoidance of habitats / characters by comparing the amount used in ratio to the amount available.*

REFERENCES

Arlettaz R (1996) Foraging behaviour of the gleaning bat *Myotis nattereri* (Chiroptera,Vespertilionidae) in the Swiss alps. Mammalia 60, 181-186

Arnold A, Braun M (2002) Telemetrishe Untersuchungen an Rauhhautfledermausen (*Pipisterllus nathusii*) in den nordbadischen Rheinauen. Schriftenreihe fur Landschaftspflege und Naturschutz 71, 177-189

Bennett AF, Radford J, Haslem N (2006). Properties of land mosaics: Implications for nature conservation in agricultural environments. Biological Conservation 133, 250-264

Berge L (2007) Resource partitioning between the cryptic species Brandt's bat (*Myotis brandtii*) and the whiskered bat (*Myotis mystacinus*). Unpublished PhD. thesis. School of Biological Sciences, University of Bristol.

Bontadina F, Schofield H, Naef-Daenzer B (2002) Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. Journal of Zoology 25, 281-290.

CIBR (2011) *Ecology and genetics of Myotis spp., Natterer's, whiskered and Brandt's bats in Ireland. Centre for Irish Bat Research. NPWS unpublished report*

Entwistle AC, Racey PA, Speakman JR (1997) Roost selection by the brown long-eared bat *Plecotus auritus*. Journal of Applied Ecology 34, 399-408

Fenton MB (1990) The foraging behavior and ecology of animal eating bats. Canadian Journal of Zoology 68, 411- 422

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence / absence models. Environmental Conservation 24, 38 - 49

Flaquer C, Puig-Montserrat X, Francesc UG, Curcó VA, Russo D (2009) Habitat selection in Nathusius' pipistrelle (*Pipistrellus nathusii*): The importance of wetlands. Acta Chiropterologica 11, 149 – 155

Fryxell JM, Wilmshurst JF, Sinclair ARE, Haydon DT, Holt RD, Abrams PA (2005) Landscape scale, heterogeneity, and the viability of Serengeti grazers. Ecology Letters 8, 328–335

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecological Modelling 135, 147-186

Heer M de, Kapos V, Brink BJE ten (2005) Biodiversity trends in Europe: development and testing of a species trend indicator for evaluating progress towards the 2010 target. Proceedings of the philosophical transactions of the Royal Scoiety, series B 360, 397 - 308

Hutson AM (1997) Two species of bat new to the UK. Bat News 46, 2

Jaberg C, Guisan A (2001) Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. Journal of Applied Ecology 38, 1169-1181

Jokimäki J, Huhta E (1996). Effects of landscape matrix and habitat structure on a bird community in northern Finland: A multi-scale approach. Ornis Fennica 73, 97-113

Jones G, Rydell J (1994) Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions of the Royal Society* B: Biological Sciences 346, 445-455

Kanuch P, Danko Š, Celuch M, Krištín A, Pjencák P, Matis Š, Šmídt J (2008) Relating bat species presence to habitat features in natural forests of Slovakia (Central Europe). Mammalian Biology 73, 147-155

Kunz TH, Fenton BM (2003) Bat Ecology. The University of Chicago Press, Chicago

Lourenço S I, JM Palmeirim (2004) Influence in temperature in roost selection by *Pipistrellus pygmaeus* (Chiroptera): relevance for the design of bat boxes. Biological Conservation 119, 237-243

Lundy MG, Montgomery WI (2010a) A multi-scale analysis of the habitat associations of European otter and American mink and the implications for farm scale conservation schemes. Biodiversity and Conservation 19, 3849-3859

Lundy MG, Montgomery WI (2010b) Summer habitat associations of bats between riparian landscapes and within riparian areas. European Journal of Wildlife Research 56, 385-394

Lundy MG, Montgomery WI, Russ J (2010) Climate change linked range expansion of Nathusius' pipistrelle bat, *Pipistrellus nathusii* (Keyserling & Blasius, 1839). Journal of Biogeography 37, 2232–2242

Mackey RL, Barclay RMR, (1989) The influence of physical clutter and noise on the activity of bats over water. Canadian Journal of Zoology 67, 1167-1170

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2003) Resource selection by animals - Statistical design and Analysis for field studies. Second edition, London, Kluwer academic publishers

Marnell F, Presetnik P (2010) Protection of overground roosts for bats (particularly roosts in buildings of cultural heritage importance). EUROBATS Publication Series No. 4. UNEP / EUROBATS Secretariat, Bonn, Germany

McAlpine CA, Rhodes JR, Callaghan JG, Bowen ME, Lunney D, *et al*. (2006) The importance of forest area and configuration relative to local habitat factors for conserving forest mammals: A case study of koalas in Queensland, Australia. Biological Conservation 132, 153-165

McAney K. (2006) A conservation plan for Irish vesper bats. Irish Wildlife Manuals No. 20. NPWS. Ireland

Norberg UM, Rayner JMV (1987) Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of. London. Series B Biological Sciences 316, 335-427

O'Sullivan P (1994) Bats in Ireland. Irish Naturalist Journal; Special Zoological Supplement

Oakley, S.F. & Jones, G. (1998). Habitat around maternity roosts of the 55kHz phonic type of pipistrelle bats (*Pipistrellus pipistrellus*). Journal of Zoology 245, 222-228

Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34, 102–117.

Phillips SJ, Dudik M (2008) Modelling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161-175

Racey PA, Swift SM (1995) Feeding Ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during Pregnancy and Lactation. Journal of Animal Ecology 54, 205-215

Racey, P.A. (1998) The importance of the riparian environment as a habitat for British bats. *Behaviour and ecology of riparian* mammals (eds Dunstone, N. & Gorman, M.L.), pp. 69 – 90, Cambridge University Press, UK

Rebelo H, Tarroso P, Jones G (2010) Predicted impact of climate change on European bats in relation to their biogeographic patterns. Global Change Biology 16, 561-576

Rebelo H, Jones G (2010) Ground validation of presence only modelling with rare species: A case study on barbastelles *Barbastella barbastellus* (Chiroptera: Vespertilionidae). Journal of Applied Ecology 47, 410-420

Roche N (2001) The status of lesser horseshoe bats *Rhinolophus hipposideros* Bechstein in Co. Limerick. Irish Naturalists' Journal 26, 437-48

Russ JM, O' Neill JK, Montgomery WI (1998) Nathusius' pipistrelle bats (*Pipistrellus nathusii*, Keyserling & Blasius 1839) breeding in Ireland. Journal of Zoology 245, 345-349

Russ J (1999) The Bats of Britain and Ireland: Echolocation Calls, Sound Analysis and Species Identification. Alana Ecology, UK

Russ JM, Hutson AM, Montgomery WI, Racey PA, Speakman JR (2001) The status of Nathusius' pipistrelle (*Pipistrellus nathusii* Keyserling & Blasius, 1839) in the British Isles. Journal of Zoology, 254, 91-100

Russ JM, Montgomery WI (2002) Habitat associations of bats in Northern Ireland: Implications for conservation. Biological Conservation 8, 49-58

Russ J (2008) Review of ASSI designation for bats in Northern Ireland. Northern Ireland Environment Agency, Research and Development Series 08/09

Sachanowicz K, Ciechanowski M (2006) First winter record of the migratory bat *Pipistrellus nathusii* (Keyserling & Blasius 1839) (Chiroptera: Vespertilionidae) in Poland: yet more evidence of global warming? Mammalia 70, 168-169

Schofield, H.W. (1996) The ecology and conservation biology of *Rhinolophus hipposideros*, the lesser horseshoe bat. JNCC. UK

Shiel CB, Fairley JS (1998) Activity of Leisler's bat *Nyctalus leisleri* in the field in south-east County Wexford, as revealed by a bat-detector. Biology and Environment 98, 105-112

Shiel CB, Shiel RE, Fairley JS (1999) Seasonal changes in the foraging behaviour of Leisler's bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry. Journal of Zoology. 249: 347-358

Siemers B, Kaipf I, Schnitzler H (1999) The use of day roosts and foraging grounds by Natterer's bats (*Myotis nattereri* Kuhl, 1818) from a colony in southern Germany. Zeitschrift fur Saugetierkunde 64, 241-245

Siemers BM, Swift SM (2006) Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (chiroptera: Vespertilionidae). Behavioral Ecology and Sociobiology 59, 373-380

Smith P, Racey PA (2008) Natterer's bats prefer foraging in broadleaved woodlands and river corridors. Journal of Zoology 275, 314-322

Smith PG, Racey PA (2005) The itinerant Natterer: physical and thermal characteristics of summer roosts of *Myotis nattereri* (Mammalia: Chiroptera). Journal of Zoology, 266, 171-180

Speakman JR, Racey PA, Hutson AM, Webb PI, Burnett AM (1991) Status of Nathusius' Pipistrelle (*Pipistrellus nathusii*) in Britain. Journal of Zoology 225, 685 – 690

Stebbings RE (1988) The conservation of European bats. Christopher Helm Pub Ltd

Taake KH (1984). Strukturelle Unterschiede zwischen den Sommerhabitaten von Kleiner und Grosser Bartfledermaus *Myotis mystacinus* und *Myotis brandtii* in Westfalen. Nyctalus 2, 16-32

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, *et al.* (2004) Extinction risk from climate change. Nature 427, 145-148

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

Veilleux JP, Veilleux SL (2004) Intra-annual and interannual fidelity to summer roost areas by female eastern pipistrelles, *Pipistrellus subflavus*. American Midland Naturalist 152, 196-200

Virkkala R (1991) Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: A multiscale approach. Oikos 62, 59-66

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

Wiens J (1989) Spatial scaling in ecology. Functional Ecology 3, 385-397

Wilson CD, Roberts D (2010) Modelling distributional trends to inform conservation strategies for an endangered species. Diversity and Distributions 17, 182-18

Appendix

Table A1. The percentage area of each county included as part of the core area of species. Values which are above the county mean are marked (*), those counties with significantly higher values, greater than the average plus the standard deviation are marked (**).

	Brown long-eared	*Common pipistrelle*	*Soprano pipistrelle*	*Nathusius' pipistrelle*	*Lesser horseshoe bat*	*Leisler's bat*	*Daubenton's bat*	*Whiskered bat*	*Natterer's bat*
CARLOW	95**	98*	62	3	0	82*	69*	92**	98**
CAVAN	61	86*	90*	55**	0	87*	70*	18	73*
CLARE	84**	80*	88*	13	39**	80*	75**	73*	77*
CORK	83*	67	70	2	11*	45	27	53*	57
DONEGAL	15	18	59	1	0	24	32	7	32
DUBLIN	65	89*	88*	23*	0	92*	35	64*	60
GALWAY	66	75	91*	8	14*	74	65*	40	67
KERRY	67	25	47	4	46**	29	30	17	26
KILDARE	91**	92*	70	14	0	90*	46	51*	74*
KILKENNY	98**	100*	93*	3	0	89*	58*	90**	94**
LAOIS	91*	95*	87*	0	0	92*	58*	82**	98**
LEITRIM	64	40	67	16*	0	59	63*	25	51
LIMERICK	92*	91*	90*	10	14*	82*	69*	29	59
LONGFORD	44	92*	100**	33**	0	87*	48	4	62
LOUTH	78*	95*	95*	8	0	93*	59*	75**	90*
MAYO	41	23	85*	10	8*	54	50	16	27
MEATH	76*	100*	96*	21*	0	97**	78**	28	92**
MONAGHAN	79*	99*	99**	48**	0	99**	84**	12	91*
OFFALY	80*	95*	95*	0	0	95*	71*	59*	81*
ROSCOMMON	51	79	91*	20*	0	78*	57*	16	52
SLIGO	44	44	77	14	0	55	57*	11	45
TIPPERARY NORTH	95**	99*	94*	10	0	90*	65*	81**	97**
TIPPERARY SOUTH	87*	93*	86*	0	0	79*	55	29	58
WATERFORD	89*	83*	74	8	0	80*	59*	68*	81*
WESTMEATH	42	98*	99**	39**	0	97**	67*	3	75*
WEXFORD	96**	95*	61	14	0	72	55	85**	93**
WICKLOW	75*	84*	56	14	0	67	32	68*	77*
Northern Ireland	11	39	33	34	0	29	20	7	50

*Northern Ireland is summarized as one area and is not included in calculation of average values.

Table A2. The percentage of the species' core area in each county. Values which are above the mean are marked (*), those counties with significantly higher contribution to the core area (greater than the average plus the standard deviation) are marked (**).

	Brown long-eared	Common pipistrelle	Soprano pipistrelle	Nathusius' pipistrelle	Lesser horseshoe bat	Leisler's bat	Daubenton's bat	Whiskered bat	Natterer's bat
CARLOW	2	2	1	0	0	1	1	3	2
CAVAN	2	3	3	8**	0	3	3	1	3
CLARE	5*	5*	5*	3	21**	5**	6**	8**	5**
CORK	12**	9**	8**	1	14**	6**	5*	14**	8**
DONEGAL	1	2	5*	0	0	2	4*	1	3
DUBLIN	1	1	1	2	0	2	1	2	1
GALWAY	8**	8**	9**	4*	14**	9**	10**	8**	8**
KERRY	6**	2	4	1	37**	3	3	3	2
KILDARE	3	3	2	2	0	3	2	3	2
KILKENNY	4	4*	3	0	0	3	3	6*	4*
LAOIS	3	3	2	0	0	3	2	5*	3
LEITRIM	2	1	2	2	0	2	2	1	2
LIMERICK	5*	4*	4	2	6*	4*	4*	3	3
LONGFORD	1	2	2	3*	0	2	1	0	1
LOUTH	1	1	1	0	0	1	1	2	1
MAYO	5*	2	8**	4*	7*	6**	7**	3	3
MEATH	4*	4*	4*	4*	0	4*	4*	2	4*
MONAGHAN	2	2	2	5**	0	2	3	1	2
OFFALY	3	3	3	0	0	4*	3	4*	3
ROSCOMMON	3	4*	4*	4*	0	4*	4*	1	3
SLIGO	2	1	2	2	0	2	3	1	2
TIPPERARY NORTH	4*	4*	3	2	0	3	3	6*	4*
TIPPERARY SOUTH	4*	4*	3	0	0	3	3	2	2
WATERFORD	3	3	2	1	0	3	3	4*	3
WESTMEATH	2	3	3	5**	0	3	3	0	3
WEXFORD	5*	4*	2	2	0	3	3	7**	4*
WICKLOW	3	3	2	2	0	3	2	5*	3
Northern Ireland	3	10	7	35	0	8	7	3	13

*Northern Ireland is summarized as one area and is not included in calculation of average values.