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Highlights

▶ We model patterns of habitat selection at multiple scales for a bat species of conservation concern. ▶ Fine scale models were constructed, evaluated and compared with radio-tracking data. ▶ At the broad scale the bats' distribution is mainly limited by climatic conditions. ▶ At the fine scale the bats are strongly associated with unimproved grasslands. ▶ Fine-scale models can be used to identify core foraging areas within species ranges.

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Using multi-scale modelling to predict habitat suitability for species of conservation concern: The grey long-eared bat as a case study

Orly Razgour[a,*], Julia Hanmer[b], Gareth Jones[a]

[a] School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK
[b] Bat Conservation Trust, Quadrant House, 250 Kennington Lane, London SE11 5RD, UK

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ABSTRACT

Although spatial scale is important for understanding ecological processes and guiding conservation planning, studies combining a range of scales are rare. Habitat suitability modelling has been used traditionally to study broad-scale patterns of species distribution but can also be applied to address conservation needs at finer scales. We studied the ability of presence-only species distribution modelling to predict patterns of habitat selection at broad and fine spatial scales for one of the rarest mammals in the UK, the grey long-eared bat (*Plecotus austriacus*). Models were constructed with Maxent using broad-scale distribution data from across the UK (excluding Northern Ireland) and fine-scale radio-tracking data from bats at one colony. Fine-scale model predictions were evaluated with radio-tracking locations from bats from a distant colony, and compared with results of traditional radio-tracking data analysis methods (compositional analysis of habitat selection). Broad-scale models indicated that winter temperature, summer precipitation and land cover were the most important variables limiting the distribution of the grey long-eared bat in the UK. Fine-scale models predicted that proximity to unimproved grasslands and distance to suburban areas determine foraging habitat suitability around maternity colonies, while compositional analysis also identified unimproved grasslands as the most preferred foraging habitat type. This strong association with unimproved lowland grasslands highlights the potential importance of changes in agricultural practices in the past century for wildlife conservation. Hence, multi-scale models offer an important tool for identifying conservation requirements at the fine landscape level that can guide national-level conservation management practices.

1. Introduction

The importance of scale for understanding ecological patterns and processes is widely recognised (Levin, 1992), yet conservation studies and management practices addressing multiple spatial scales are rare (du Toit, 2010). Conservation goals are scale-specific, from identifying national-level priority areas to local site habitat management, and therefore require different conservation planning approaches at different scales (Cabeza et al., 2010). Moreover, because ecosystems or populations cannot be described adequately at a single scale (Levin, 1992) and because the effect of environmental variables is scale-dependent (Collingham et al., 2000), cross-scale studies are necessary for identifying species–habitat relationships and guiding conservation planning (Graf et al., 2005; Lomba et al., 2010).

Mapping the spatial distribution of species is an important aspect of conservation biology, contributing to the management of endangered species, species reintroduction programs, ecosystem restoration, and population viability analysis (Hirzel et al., 2001). Ecological modelling techniques have been mainly used to study broad-scale patterns of species distribution despite their potential to identify fine-scale habitat suitability for endangered species (Fernandez et al., 2003). Only recently have studies applied modelling at multiple-scales to address hierarchical conservation needs within and across species (e.g., Cabeza et al., 2010).

Because absence data are often not available or are unreliable, modelling approaches that require presence-only data are particularly valuable (Hirzel et al., 2002). Recently, Maxent, a presence-only machine learning modelling approach (Phillips et al., 2006), has become the most commonly used species distribution modelling technique because it has been shown repeatedly to outperform other presence-only, as well as presence/absence modelling techniques (Elith et al., 2006; Hernandez et al., 2006). Maxent is especially advantageous when the amount of occurrence data is limited, as is the case with many rare and cryptic species (Wisz et al., 2008).

Predictive distribution modelling is especially relevant for identifying the conservation requirements and potential distribution of

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* Corresponding author. Tel.: +44 0117 9546386; fax: +44 0117 9257374.
E-mail addresses: Orly.Razgour@bristol.ac.uk (O. Razgour), JHanmer@bats.org.uk (J. Hanmer), Gareth.Jones@bristol.ac.uk (G. Jones).

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bats, because their nocturnal nature, wide home ranges, and problems with identification, render it difficult to conduct comprehensive mapping of distributions (Jaberg and Guisan, 2001; Greaves et al., 2006). Despite their high abundance and wide geographic distribution, many bat species have undergone substantial population declines throughout their range in the past century, primarily due to human population expansion and the associated increased demand for land and food (Mickleburgh et al., 2002). However, while bat roosts are protected by law in many European countries, foraging habitats rarely are (Racey, 2009). The drive to maximise food production in the past 60 years has resulted in substantial changes in farming practices with detrimental effects on biodiversity at all trophic levels (Boatman et al., 2007). Bats are likely to be particularly sensitive to the loss of important landscape elements through the removal and degradation of hedgerows and tree lines (Walsh and Harris, 1996; Boughey et al., 2011), habitat fragmentation (Bright, 1993), and the decline of arthropod prey populations as a result of agricultural intensification (Wickramasinghe et al., 2004; Conrad et al., 2006).

We studied the application of species distribution modelling to predicting the availability of suitable habitats for species of conservation concern across spatial scales, from factors that limit distribution at the broad scale to the fine-scale selection of foraging habitats within the potential distribution. Because of the scale-dependent nature of species' responses to ecological parameters, it is important to incorporate the appropriate environmental variables for the specific model scale (Graf et al., 2005). While climatic variables, like average seasonal temperatures and precipitation, vary considerably across broad spatial scales, they do not vary sufficiently at the finer, colony-level, scale to affect patterns of habitat selection. In addition, the resolution of many available eco-geographical maps (like geology and human population density) is too coarse to be included in fine-scale models.

As a case study, we used one of the rarest mammals in the UK, the grey long-eared bat, *Plecotus austriacus* ~~(Fischer, 1829)~~. This locally rare but globally common species is widespread in southern Europe but extremely rare in countries at the northern edge of its distribution (Juste et al., 2008). The UK population is restricted mainly to the southern coast of England and appear to be in decline because several colonies have gone extinct in the past few decades (Harris et al., 1995). Not only is this species rare, but it cannot be adequately detected and identified acoustically due to its low intensity echolocation calls and the presence of a sympatric cryptic species (*Plecotus auritus*) with similar calls (Russo and Jones, 2002). Therefore, the conservation of the grey long-eared bat can especially benefit from the application of ecological modelling techniques. Lack of information on behaviour and ecological requirements has hampered the development of conservation management plans for the grey long-eared bat (Dietz et al., 2009).

This study aims to address this lack of knowledge and develop a method that will allow the identification of potential foraging grounds within the suitable range of populations of conservation concern. Our main objectives are: (1) to determine the effect of environmental variables on species distribution and habitat use at different spatial scales; (2) to evaluate the use of species distribution modelling to identify suitable foraging habitats in unstudied areas; and (3) to identify the conservation requirements of grey long-eared bats across spatial scales.

2. Methods

2.1. Study area

Broad-scale habitat suitability was modelled for the whole of the UK, excluding Northern Ireland (where the species was never recorded). The UK is at the north-western edge of the grey long-eared bat's distribution (Spitzenberger et al., 2006). For the fine-scale foraging habitat suitability study, study sites were located in areas predicted by the broad-scale model as highly suitable. We radio-tracked grey long-eared bats from two maternity colonies located approximately 160 km apart, on the south coast of Devon (50°3′N; 3°3′W) and the Isle of Wight (50°4′N; 1°2′W; Fig. 1). Both study sites were dominated by improved pasture (Devon: 38%, Isle of Wight: 37%) and arable land (22%, 32%), but included also semi-natural habitats including broadleaved woodland (9%, 8%), riparian vegetation (both 3%), and semi-unimproved meadow and marsh (3%, 11%).

2.2. Modelling procedure

We used presence-only species distribution modelling (Maxent) to predict areas that contain suitable habitats for the grey long-eared bat in the UK (broad-scale model, resolution 30 arc seconds, ~1 km^2) and within the maternity colony ranges (fine-scale model, resolution 100 m^2).

2.2.1. Broad spatial scale

For the UK model we used distribution locations with a resolution of 1 km^2, obtained from the National Biodiversity Network (http://data.nbn.org.uk/), Dorset Environmental Records Centre, National Trust, and the Bat Conservation Trust. Only records from the past 30 years (1980–2010) were included in the model. To avoid pseudoreplication we removed duplicate occurrence points, using only one location record per 1 km^2 ($N = 66$). Models were generated using eco-geographical variables that were deemed to be ecologically relevant based on prior knowledge of the biology and annual activity cycle of temperate bats. All variables had a spatial resolution of 1 km^2. The following variables were included in the models: spring, summer and winter temperatures; temperature and precipitation seasonality (Bioclim variables that measure the extent of seasonal variability); annual and summer precipitation; altitude (WorldClim, http://www.worldclim.org); land cover (Land Cover map 2000, Centre of Ecology and Hydrology; reclassified into nine classes; Supplementary 1); geology (British Geological Survey, http://www.bgs.ac.uk/; reclassified into 23 classes); human population density (LandScan 2008 Global Population Database, http://www.ornl.gov/sci/landscan/); and night light pollution (http://www.ngdc.noaa.gov/dmsp/). Only variables that contributed to the model >1% were included in the final model.

2.2.2. Fine spatial scale

Fine-scale foraging habitat models were generated for the two maternity colonies, using the radio-tracking datasets (Section 2.3). Graf et al. (2005) found that the best scale model corresponds to the size of an individual's annual home range. In our study, individual bats could only be radio-tracked for a maximum of two weeks (the battery life of the small transmitters). As a result, the colony range, which includes the combined location fixes of all individual bats radio-tracked throughout the majority of the annual active period (April–September), was used to represent the size of the annual home range.

To obtain presence locations we overlaid in ArcGIS (version 9.2, ESRI) the core foraging areas (Section 2.3) of all radio-tracked bats. The resolution of the model was set at 100 m^2, corresponding to the resolution of the cluster analysis used to generate the core foraging areas. To avoid pseudoreplication we removed duplicate occurrence points resulting from overlapping core foraging areas between bats or several location points from the same bat, selecting one location point from each 100 m^2 cell. To test the ability of species distribution models to identify potential suitable foraging grounds around maternity colony roosts in new locations, only

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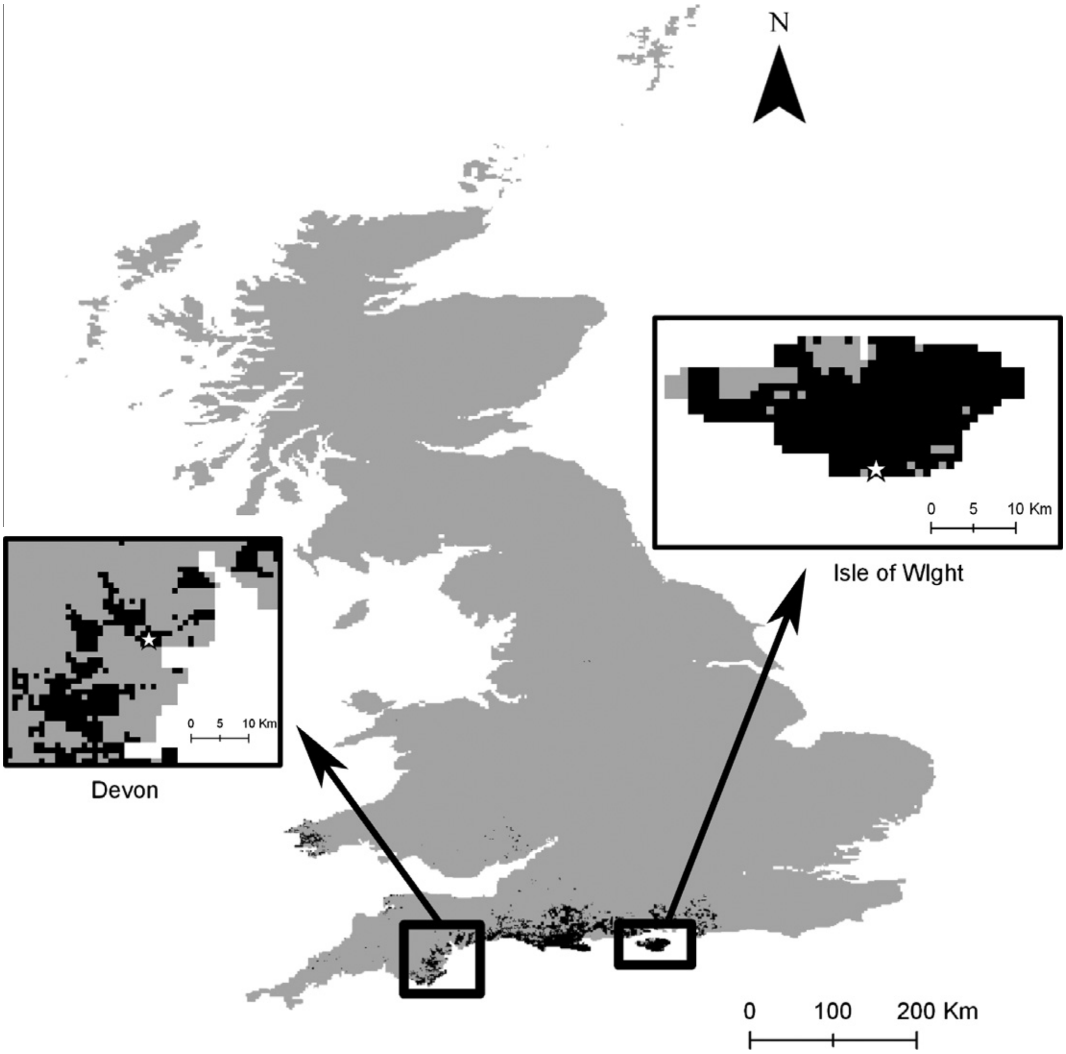

Fig. 1. Habitat suitability map for the grey long-eared bat in the UK based on the Maxent model predictions. Black represents suitable areas and light grey unsuitable. The two study sites (Devon and the Isle of Wight) are enlarged with the colony roost marked with a white star.

presence locations from the Devon colony were used to build the model. The model extrapolation over the Isle of Wight study site was tested using the Isle of Wight core foraging area locations identified through radio-tracking.

Eco-geographical variables were derived from fine-scale habitat studies and aerial photographs (Landmap Spatial Discovery, University of Manchester/University College London), and manipulated in ArcGIS to extract distance measures at a 100 m spatial resolution. The following variables were used: land cover type (Arable, Improved grasslands, Semi-unimproved meadow and marsh, Broadleaved woodland, Conifer plantation, Riparian vegetation, Scrub, Open water, and Suburban) and continuous distance (m) to each land cover type.

2.2.3. Model evaluation

Model fit was evaluated based on the Area Under the Curve (AUC) of the Receiver Operator Characteristics (ROC), which measures the model probability of correctly distinguishing presence from random locations (Phillips et al., 2006). Good model performance was considered when training and test AUC scores were higher than 0.75, indicating reasonable to high model discrimination ability (Pearce and Ferrier, 2000; Elith et al., 2006).

Models were run using the default Maxent settings, with 1000 instead of 500 iterations. We tested for the effect of modifying the regularisation betamultiplier value on model complexity and reducing over-parameterisation by running models with regularisation values ranging between 1 and 10. The regularisation betamultiplier affects the focus or fitting of the output distribution, with larger values giving more generalised, spread out predictions. We used the software ENMtools (version 1.3; Warren et al., 2010; Warren and Seifert, 2011) to select the most parsimonious, best fit model based on Akaike's Information Criterion (AIC) scores. We also used ENMtools to test for multicollinearity in the form of high correlation between model variables. If two variables were found to be highly correlated ($R^2 > 0.75$), the variable that was deemed to be less relevant in an ecological context was removed from the model to test whether multicollinearity affected model predictions.

We ran 20 replications of each model, each time 75% of locations were randomly selected (random seed) to train the model and the remaining 25% to test the model predictions. The 10th percentile (the value above which the model classifies correctly 90% of the training locations) was selected as the threshold value for defining suitable habitats. This is a conservative value that is commonly used in species distribution modelling studies (e.g., Raes et al., 2009; Rebelo and Jones, 2010).

To evaluate the accuracy of the extrapolation of the fine-scale model to new locations, we followed the method suggested by

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Boyce et al. (2002) and modified by Klar et al. (2008). The method relates model predictions to probability of habitat use based on presence only data: in this case, radio-tracking locations from the Isle of Wight that were not used in model generation. Model predictions were plotted on a 100 m^2 grid map of the study area, ranking suitability values into seven categories that covered relatively equal amounts of area. We calculated the proportion of radio-tracking locations within each probability category and divided them by the proportion of available area to obtain area-adjusted use frequencies. These frequencies were correlated with the suitability rank of each category. High positive correlation scores indicate high model accuracy because they suggest that areas with higher suitability based on model predictions are indeed used more often in relation to their availability (Klar et al., 2008).

2.3. Radio-tracking

During April–September 2009 and 2010 we radio-tracked 20 grey long-eared bats (non-reproductive females ($N = 8$), lactating females ($N = 6$), adult males ($N = 4$), and sub-adults ($N = 2$)) from maternity colonies in the Devon and Isle of Wight study areas (Supplementary 2). Bats were captured under license from Natural England and fitted with radio transmitters weighing 0.35 g (PIP3, Biotrack, UK).

Individual bats were radio-tracked throughout the whole night, for an average of three nights (Supplementary 2), using triangulation (Bontadina et al., 2002) and the continuous tracking method (Jones and Morton, 1992) with 'homing in' on a single bat to attain the closest proximity and most accurate location possible. We used Lotek radio-receivers (Models SRX_400, STR_1000, Lotek Engineering, Canada) connected to three-element Yagi antennas (Biotrack, UK) to locate tagged bats. Data on hourly night weather conditions (ambient temperature (T_a), rainfall and wind speed) were obtained from local weather stations within a maximum of 13 km from the study area (Bishopsteignton http://www.canigou.co.uk/bishopsteignton.htm, and Newport weather stations http://www.isleofwightweather.co.uk).

To reduce autocorrelation and lack of independence we only included in the analysis location points recorded at 10–15 min intervals, a sufficient time for most radio-tracked bats to cross their entire home range. Moreover, we omitted poor resolution locations (estimated accuracy range greater than 100 m). Using Ranges 7 (AnaTrack Ltd., UK) we generated 100% Minimum Convex Polygons (MCPs) to represent the seasonal home range of each individual bat and of the colony as a whole. To estimate core foraging areas we used cluster analysis to remove outlying fixes and create 85% clusters in areas where the majority of the night activity was concentrated (Davidson-Watts et al., 2006). To account for potential errors in localisation, a 100 m buffer was added around each location fix when performing the cluster analysis.

To study patterns of fine-scale foraging habitat selection we used compositional analysis (Aebischer et al., 1993) to compare the proportion of habitats used by each bat to habitat availability in the study area. We divided each colony range into the same nine dominant land cover types used in the fine-scale Maxent model (Section 2.2.2).

Linear mixed-effect models (computed in SPSS, version 16, Illinois) were used to analyse the effect of climatic variables and reproductive condition on bat activity (time spent foraging and night roosting per night, and the distance the bat flew throughout the night). Because activity measures did not differ between the two colonies, data for the two colonies were pooled together to increase the sample size. Models were constructed using individual bats as subjects (random factor), radio-tracking nights as the repeated variable, reproductive condition or season as fixed factors, and night weather conditions (T_a, rainfall and wind speed) as the covariates. Data that did not meet the assumptions of normality or homogeneity of variance were square root transformed. The best fit models were selected based on their AIC value.

3. Results

3.1. Broad-scale habitat suitability modelling

The most parsimonious broad-scale habitat suitability model based on AIC scores included the default Maxent regularisation value (betamultiplier = 1). The model had a very good fit (mean $\mathrm{AUC}_{\mathrm{train}} = 0.994$; mean $\mathrm{AUC}_{\mathrm{test}} = 0.984$), but it extrapolated little beyond the current known distribution of the grey long-eared bat in the UK. The majority of predicted suitable areas were on the south coast of England, where most currently known locations occur. An exception is the predicted suitable areas in the southwest tip of Wales, an area where grey long-eared bats have never been recorded (Fig. 1).

Although 12 eco-geographical variables were included in the model, the first three variables (summer precipitation, maximum January temperature, and annual precipitation) contributed together to 68% of the model performance. The most informative variable on its own was maximum January temperature, whereas the variable containing the most unique information was land cover, despite contributing only 6% to the overall model. Based on the model's predictions grey long-eared bats have a high probability of occurring in grassland areas with relatively low summer precipitation (150–180 mm) and high January temperature (>6.5 °C) (Supplementary 3). The same pattern, both in terms of model predictions and contributing variables, was maintained when highly correlated variables ($R^2 > 0.75$; annual precipitation, average spring temperature and altitude) were removed to reduce multicollinearity. However, this model had a lower discrimination ability ($\mathrm{AUC} = 0.991$) and was less parsimonious (higher AIC score) than the original model ($\Delta\mathrm{AIC} = 91.7$).

3.2. Fine-scale activity and habitat selection based on radio-tracking

3.2.1. Factors affecting night activity patterns

The most parsimonious model for all night activity variables, based on the AIC score, was a factorial design including reproductive condition and minimum night T_a. Reproductive condition affected bat foraging time ($F_{2,27} = 4.4$, $P = 0.046$), night roosting time ($F_{2,20} = 9$, $P = 0.0016$) and total night travelling distance ($F_{2,25} = 10.8$, $P < 0.001$). Lactating females foraged for longer, night roosted for longer and travelled further distances than non-reproductive females (pairwise comparisons $P < 0.05$; Table 1). Although only foraging time was affected by T_a ($F_{1,27} = 6.5$, $P = 0.017$), all other variables were affected by the interaction between T_a and reproductive condition. Regression analysis, using one data point per bat (night of minimum T_a) to avoid pseudoreplication, confirms the pronounced positive relationship between bat foraging time and T_a ($R^2 = 0.7$, $F_{1,18} = 41.62$, $P < 0.001$; Fig. 2).

3.2.2. Patterns of foraging habitat selection

Foraging areas were located up to 5 km away from the maternity colony roost. Individual core foraging clusters in both study sites had a significantly different habitat composition from available habitats in individual home ranges and habitat use was not random (Devon: weighted Wilk's Lambda – $\Lambda = 0.01$, $\chi^2 = 50$, $df = 8$, $P < 0.0001$; Isle of Wight: $\Lambda = 0.001$, $\chi^2 = 54$, $df = 6$, $P < 0.0001$). Patterns of foraging habitat selection were remarkably similar between the two study sites. Grey long-eared bats preferred meadows, riparian vegetation and broadleaved woodland, and avoided arable fields, conifer woods and open water (the last

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Table 1
Summary of nocturnal activity and habitat use data for radio tracked grey long-eared bats in Devon and the Isle of Wight. Travel distance is the cumulative distance a bat flew throughout the night (from the day roost to different foraging grounds and back to the day roost), while maximum distance to foraging areas refers to the distance between the colony roost and the furthest core foraging area used by the bat. Data are presented as means (±SD).

Variables	Devon colony	Isle of Wight colony	Non-reproductive females	Lactating females	Males
N	12	8	7	6	4
Emergence (mins after sunset)	32 (±10)	43 (±12)	32 (±5)	36 (±16)	39 (±6)
Foraging time (min)	358 (±104)	341 (±137)	235 (±108)	418 (±44)	364 (±34)
Night roosting (min)	43 (±27)	61 (±36)	30 (±18)	64 (±41)	56 (±30)
Travel distance (km)	8.4 (±4)	11 (±5)	4.3 (±3)	12 (±2)	12.3 (±6)
Maximum distance to foraging areas (km)	3.1 (±1)	3 (±1)	2.1 (±1)	3.3 (±1)	4 (±1)
Home range (km^2)	37.2	17.4	2.2 (±2)	6 (±0.5)	6.1 (±3)

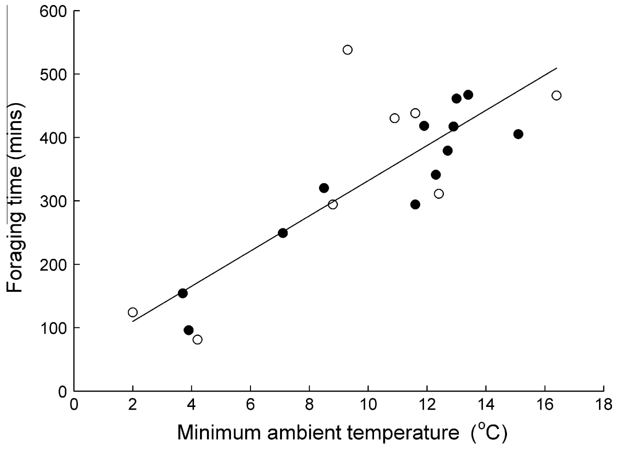

Fig. 2. The increase in grey long-eared bat foraging time with the increase in minimum night ambient temperatures (Foraging time (min) = 54.54 + 27.73 (minimum ambient temperature °C)). Black circles represent bats from the Devon colony (2009) and white circles bats from the Isle of Wight (2010).

two categories were only present in Devon). This is despite the high proportion of arable land within both colony ranges (Devon 22%, Isle of Wight 32%). The two colonies only differed in the selection of suburban areas by Devon bats and the avoidance of improved grassland by Isle of Wight bats (Fig. 3).

3.3. Fine-scale habitat suitability modelling

The model with the best performance based on AIC scores had a mean training AUC value of 0.81 (AUC_{test} = 0.79), and a betamultiplier regularisation value of 2 (and therefore less localised predictions than the default setting model). Of the six habitat variables included in the model, the most important variables were distance to meadows and distance to suburban centres, contributing together 50%. Distance to meadows was also the most informative variable on its own and contained the most information that is absent from other variables. Bats had a high probability of foraging in areas that are less than 200 m away from meadows and are either adjacent to suburban centres or at a distance of 1.3–1.8 km away from them. Of the land cover types, as with the results of the composition analysis, bats used meadows, riparian vegetation and scrub more than expected by chance, but had the lowest probability of occurring in arable land. None of the variables used in the fine-scale model were correlated with one another.

3.3.1. Model evaluation using test radio-tracking data

Both in the Devon and Isle of Wight study sites Maxent predicted additional suitable foraging grounds to those identified through radio-tracking, yet the great majority of radio-tracking core foraging locations fell within areas identified as suitable by the model. Although data from Isle of Wight were not used to generate the model, 74% of core foraging locations identified through radio-tracking were in areas predicted by the model as suitable habitats (Fig. 4). In addition, there was a highly significant positive correlation between ranked model predictions (Supplementary 5) and area adjusted frequency of use based on the Isle of Wight radio-tracking test locations (Spearman Rank Correlation: $R = 0.96$, $N = 7$, $P < 0.001$), which suggests a very high predictive accuracy of the model.

4. Discussion

This study investigated the application of species distribution modelling to predicting patterns of habitat selection at broad and fine spatial scales, using the appropriate eco-geographical variables for the specific model scale and application. We found that at the broad spatial scale the UK distribution of the grey long-eared bat is primarily limited by unsuitable climatic conditions, while at the fine scale, within its potential range, the grey long-eared bat appears to be limited by the availability of its preferred foraging habitats. Similarly, Lomba et al. (2010) showed that while climatic variables determine the potential regional range of a rare plant species, at the local scale land use related variables have a stronger effect on distribution patterns. This corresponds to cross species patterns of rarity, in which climatic variables tend to be the most limiting factor over the entire range of the species, while at finer spatial scales responses to climate are often masked by responses to local environmental variables such as soils, terrain, and habitat type (Gaston, 1994).

4.1. Role of climatic variables

The most important climatic variables limiting the broad-scale distribution of the grey long-eared bat were winter temperature and summer precipitation. Insectivorous bats in the UK arouse frequently from winter hibernation to feed when higher outside temperatures signal increased food availability (Hays et al., 1992; Park et al., 2000). Winter insect activity increases with increasing temperatures (Williams, 1951) because the minimum temperature threshold for flight activity in many insects exceeds 8 °C (Taylor, 1963). It has been suggested previously that the survival of the grey long-eared bat at the northern edge of its range depends on a sufficient supply of flying insects during warm winter evenings to compensate for the depletion of fat stores due to frequent arousals from hibernation (Stebbings, 1970).

Rainfall, on the other hand, has a particularly strong effect on insect activity in the summer, and variation in rainfall and minimum temperature explains more than 66% of the variation in insect activity over summer in England (Williams, 1951). Very wet summer conditions are associated with lower reproductive success in aerial insectivorous bats (Burles et al., 2009) because reduced insect availability can leave lactating females unable to satisfy their increased energetic demands (Kurta et al., 1989). Hence, while

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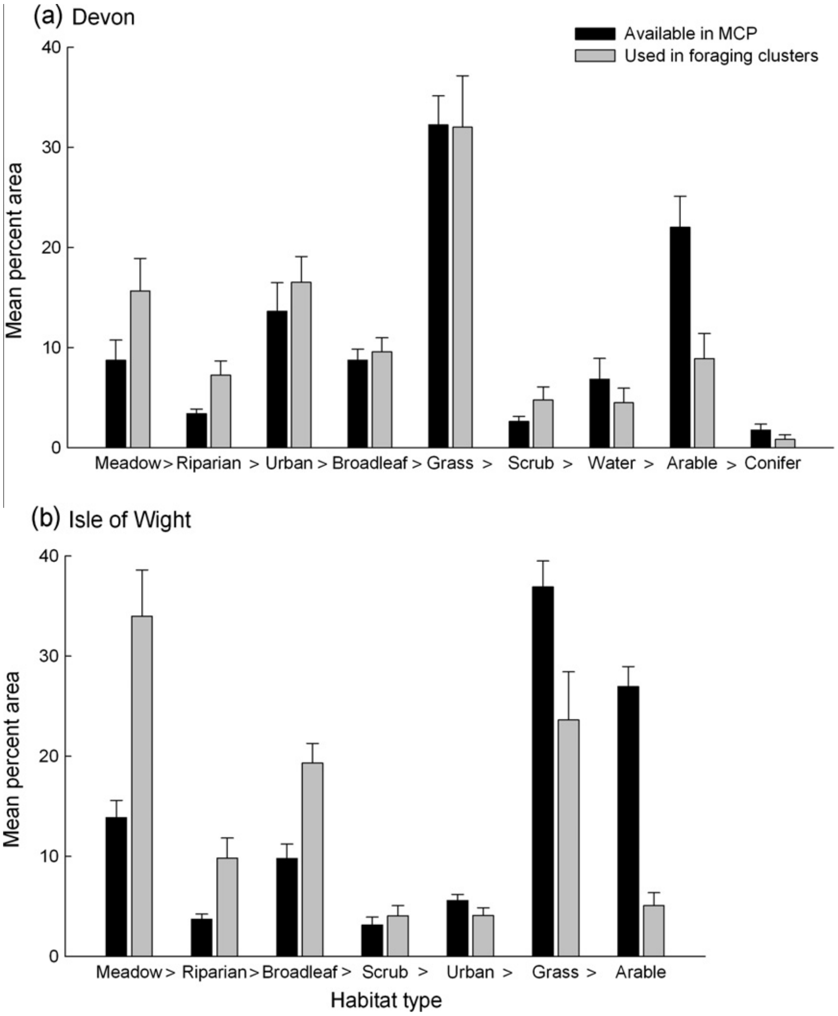

Fig. 3. Selection of core foraging areas by radio-tracked bats in Devon (a) and the Isle of Wight (b) based on habitat composition analysis, comparing available habitats (mean percent area ± SE) within individual bat home ranges (individual bat MCPs) with used habitats (mean percent area ± SE) within individual bat core foraging areas (85% clusters). Habitat types are ranked based on their extent of use relative to availability, from most preferred habitat on the left to least used on the right.

winter temperatures may be a strong determinant of grey long-eared bat overwinter survival, summer precipitation may affect reproductive success.

At the fine scale, climatic factors, and in particular temperature, also strongly affected the nocturnal activity of grey long-eared bats, with foraging activity reduced dramatically as temperatures dropped below 6 °C (Fig. 2). This relationship between foraging time and temperature is probably the result of increased foraging costs with reduced prey availability below 10 °C (Burles et al., 2009). Increased foraging time and night travelling distance in lactating females, despite longer night roosting periods, can be explained by their greater energetic demands (Kurta et al., 1989).

4.2. Role of habitat variables

Land cover was identified as an important variable affecting the broad-scale distribution of the grey long-eared bat. Grassland was the most favoured habitat type both at broad and fine spatial scales. However, only at the finer resolution we were able to distinguish between improved and unimproved grasslands because many unimproved fields are too small to be accurately classified in the coarse 1 km^2 land cover map.

The strong selection of unimproved meadows and marshes probably relates to their high diversity and abundance of Lepidoptera and other insects (Rands and Sotherton, 1986; Di Giulio et al., 2001). In contrast, the avoidance of arable land and conifer woods, when present, may reflect the low abundant and diversity of insect in these habitat types (Winter, 1983; Robinson and Sutherland, 2002). Radio-tracking also allowed the identification of other important foraging habitats, including riparian vegetation and broadleaved woodland, two important foraging habitats for insectivorous bats in general (e.g., Bontadina et al., 2002; Smith and Racey, 2008). However, unlike its sympatric cryptic sister species, the brown long-eared bat, that is primarily associated with deciduous woodlands (Entwistle et al., 1996), the grey long-eared bat only used woodlands extensively when ambient temperatures were low or during heavy rainfall (O. Razgour, personal observations).

The fine-scale Maxent model showed that proximity to unimproved grasslands and distance to suburban areas were the most important variables predicting foraging habitat suitability. Distance to suburban areas followed a bimodal pattern of selection, corresponding on the one hand to the tendency of lactating bats to forage near the vicinity of the maternity roost (Henry et al., 2002), and on the other hand to the selection of more rural foraging habitats away from suburban centres. Semi-natural habitats within urban areas can offer important foraging grounds for bats when the surrounding landscape is dominated by intensive agriculture (Gehrt and Chelsvig, 2003), or in this case also when bats roost in buildings within suburban areas.

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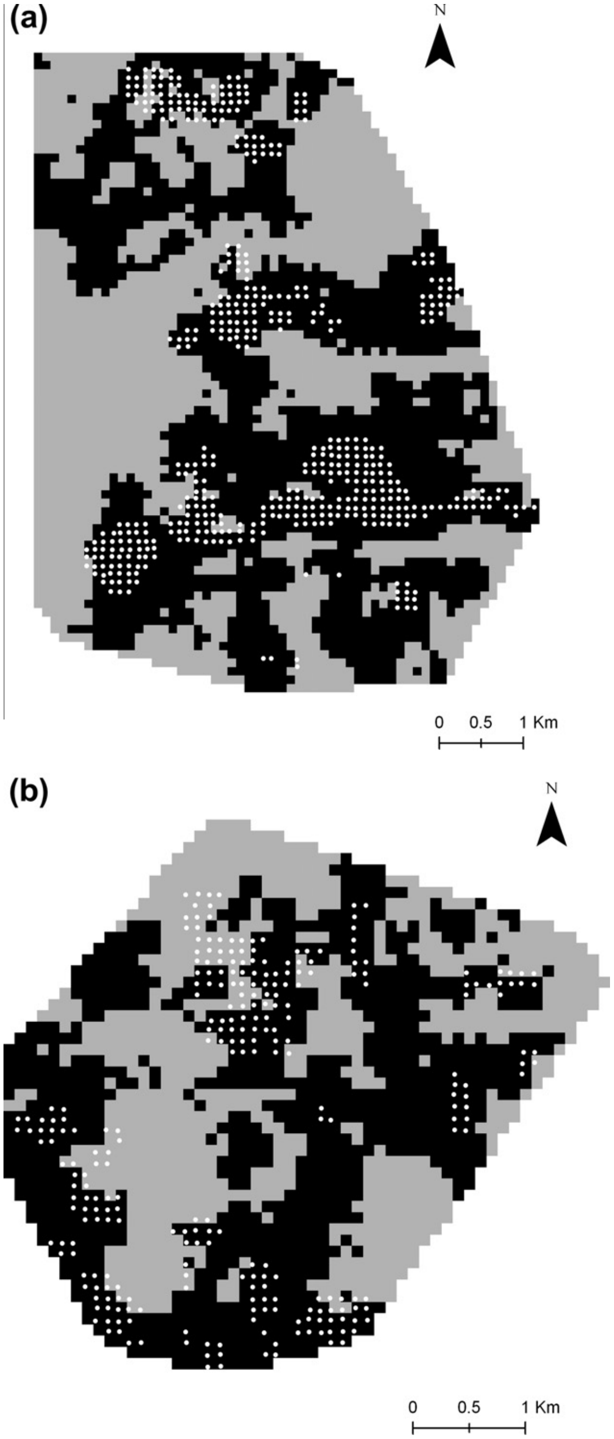

Fig. 4. Habitat suitability maps for grey long-eared bats in the Devon (a) and Isle of Wight (b) study sites based on Maxent model predictions. Location points from the Devon colony were used to construct the model and extrapolate to the Isle of Wight study site, while location points from the Isle of Wight were used to test the model extrapolation in subsequent analysis. Black represents suitable areas and light grey unsuitable. White circles denote core foraging areas identified through radio-tracking.

4.3. Evaluation of modelling approach

Modelling habitat suitability, based on presence only data, may be problematic for species at the edge of their distribution, where environmental conditions represent only a marginal part of the species' fundamental niche, and therefore most individuals live in sub-optimal conditions (Braunisch et al., 2008). Although the UK is at the edge of the grey long-eared bat's distribution, the principal limiting variables identified by the broad-scale Maxent model appear to be relevant across its range. In central and southern Europe the grey long-eared bat is commonly associated with grasslands and open landscapes located in lowlands or lower elevations, which experience higher ambient temperatures (Horáček, 1975; Benda and Ivanova, 2003).

Little extrapolation beyond the currently known distribution may reflect the intensive surveying of bats in the UK, which results in relatively complete distribution maps. Beyond that, lack of location records from south-west Wales may be the result of barriers to colonisation (Rossiter et al., 2000) despite potentially suitable conditions occurring there.

Fine-scale habitat suitability models predicted the location of foraging habitats successfully in the test study site, and revealed similar patterns of foraging habitat selection as traditional methods of radio-tracking data analysis. Beyond the high extrapolation ability, the combined radio-tracking and modelling approach allowed the inclusion of distance variables, which refined patterns of foraging habitat selection. Distance constraints can improve the accuracy of species distribution model predictions because they account for dispersal ability and spatial autocorrelation of environmental variables (Allouche et al., 2008).

4.4. Conservation implications

Grey long-eared bat foraging grounds were located up to 5 km away from the colony roost, and therefore local-scale conservation efforts should focus on enhancing the extent of unimproved grasslands and well-developed riparian vegetation within a 5 km radius around known maternity roosts. Other bat species may require conservation management at wider radii to satisfy their foraging habitat use demands (e.g., Almenar et al., 2009).

Extensive application of inorganic fertilisers, a switch to silage cultivation and increased grazing intensity led to the loss of more than 92% of unimproved lowland grasslands in England (Fuller, 1987; Vickery et al., 2001). This decline is especially concerning given the strong association of grey long-eared bats with meadows and their minimal use of arable fields and improved grasslands. Within the agricultural landscape mosaic, grey long-eared bats tended to use more natural habitats like field margins, hedges, and scattered trees (O. Razgour, personal observations). Non-cropped habitats are an important component of between-field habitat heterogeneity and connectivity, and are associated with the maintenance of farmland biodiversity across trophic levels (Benton et al., 2003). Scattered trees in particular, have been identified as keystone elements in anthropogenically-disturbed landscapes (Manning et al., 2006), and offer important foraging habitats for insectivorous bats ~~(Lumsde and Bennet, 2005).~~ However, Q3 agricultural intensification and mechanisation increases field and farm sizes, resulting in extensive removal of hedgerows and loss of field boundaries (Robinson and Sutherland, 2002).

Less intensive farming practices not only promote semi-unimproved grasslands but also increase the proportion of non-cropped habitat elements in the agricultural landscape (Critchley et al., 2003). Hence, at the broader, national-scale the conservation and long-term survival of grey long-eared bats and other UK bat species may depend on the implementation of such farming practices. This conclusion is supported by studies showing that the activity and species richness of bats and their prey are higher on organic farms (Wickramasinghe et al., 2004), and that the abundance and species richness of moths increases following the implementation of agri-environmental schemes (Taylor and Morecroft, 2009).

The use of multi-scale models allowed us to identify conservation requirements at the fine landscape level that can guide

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national-level conservation management practices. Despite the important role of broad-scale conservation studies in identifying areas in need of conservation investment, they cannot provide sufficient information to direct conservation action (Cabeza et al., 2010). In this study we demonstrated that habitat suitability modelling at both broad and fine spatial scales can be used in combination as important conservation tools, not only to predict potential distribution, but also to identify important foraging grounds for species of conservation concern. This modelling approach is particularly suitable for rare and elusive species that cannot be easily recorded or caught at their foraging grounds.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.08.010.

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