

A survey of high risk bat species across southern Scotland





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COMMISSIONED REPORT

Commissioned Report No. 1008

A survey of high risk bat species across southern Scotland

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COMMISSIONED REPORT

Summary

A survey of high risk bat species across southern Scotland

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Keywords

Bats; Chiroptera; Survey methods; Bat activity; Species distribution; Citizen science; Automated acoustic monitoring.

Background

Our understanding of the status of three species of bat (Leisler's bat *Nyctalus leisleri*, noctule *Nyctalus noctula* and Nathusius' pipistrelle *Pipistrellus nathusii*) in southern Scotland is inadequate to inform policy relevant conservation. This study aims to collect baseline data for all species of bats in the region, with focused analyses on the three bat species to:

- Identify “hotspots” for the three species for advising on future wind energy development.
- Discuss the significance of the three species at wind farms in relation to the survey findings.
- Produce revised population estimates for the three target species.
- To identify any noteworthy local bat species assemblages (all species).

Main findings

- 715 different 1 km squares (3.4% of the survey area) were surveyed for bats in 2016. This sample comprised 1,537 complete nights of recording in 1,422 different recording locations. 667,755 recordings were collected which, following analyses and validation, were found to include 399,242 bat recordings.
- The ranges occupied by noctule, Leisler's bat and Nathusius' pipistrelle in southern Scotland are restricted with little overlap between species. For the two *Nyctalus* species, there is a clear east–west split, with Leisler's bat occurring in the west and noctule mainly in the east. For both Leisler's bat and noctule, occupancy and activity patterns were particularly aggregated, with a comparatively small number of 1 km squares contributing a large proportion of the recorded distribution and activity. Nathusius' pipistrelle was recorded at few sites, dispersed across the survey area, with some clustering of records in the southwest and the north of the region.
- We estimate that 16% and 24% of the populations of the three high risk species are exposed to existing and approved wind farms, with 50% of this exposure at just 10% of wind farms. Whilst wind farms tended to be located at higher elevation than the three high-risk bat species most commonly occur, there was still significant spatial overlap. Because there is little overlap in the ranges of the three high risk bat species, any steps

taken to reduce the risk posed by wind farms at a local scale are most likely to benefit a single species, rather than having broader benefits for the three high risk species.

- It is likely that the true population estimates for the two *Nyctalus* species are likely to far exceed the current published estimates of a few hundred individuals for the whole of Scotland. Considering that the 715 1 km squares surveyed in 2016 comprised just 3.4% of the survey area, and that there were 4,327 recordings of Leisler's bat from 224 1 km squares, and 2,101 recordings of noctule from 152 1 km squares, it is likely that the minimum population sizes of Leisler's bat and noctule for the whole of Scotland are in the thousands. Indications from the survey are that Nathusius' pipistrelle was much less abundant than the two *Nyctalus* species in southern Scotland, with just 185 recordings from 23 1 km squares. Considering the migratory status of Nathusius' pipistrelle it is likely that some records of this species in this survey, particularly at coastal locations, were of migrants. However at one site close to Stranraer (Dumfries and Galloway) in the southwest of the survey area, male advertisement calls were recorded, which may suggest the possibility of breeding in this area. It is expected that the minimum population size of Nathusius' pipistrelle in Scotland is likely to be in the hundreds.

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Stuart Newson, Mark Wilson and Rob Raynor conceived the ideas and designed the methodology; Hazel Evans, David Jarrett and Mark Wilson coordinated distribution of equipment and data collection from volunteers; David Jarrett and Mark Wilson carried out professional fieldwork; Stuart Newson analysed the data with support from Simon Gillings and Stuart Newson led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

1. INTRODUCTION

Worldwide efforts to develop sustainable methods of energy production have led to an increase in the use of renewable sources, with particular emphasis on wind energy. Despite clear environmental benefits associated with this type of technology, many studies have identified bat fatalities at wind farms, which raise concerns about the effects of wind turbines on bat populations (e.g. Rodrigues *et al.*, 2015; Lintott *et al.*, 2016). To minimise the impact of future wind farm development on bats, it is necessary to identify key areas for bats. This requires surveys and analyses that are able to provide a robust understanding of large-scale patterns in species' distributions and abundance (Pereira & Cooper, 2006; Jones, 2011).

Provision of the necessary data is particularly challenging for bats, because most species are nocturnal, wide ranging and difficult to identify. As a consequence, the majority of published spatial modelling studies on bats have used presence-only data (i.e. where there is no direct information collected about either real absence or non-detection), collected through unstructured opportunistic sampling (reviewed in Razgour *et al.*, 2016). This is despite there being considerable literature on the value of random or representative sampling, and of prioritising the collection and analysis of presence-absence data (strictly detection / non-detection data) (e.g. Brotons *et al.*, 2004; Ward *et al.*, 2009). With developments in passive bat detectors, software to aid the analysis of sound files and improving knowledge of species identification (Barataud, 2015), it is now possible to conduct large-scale representative acoustic assessment of bat species' distributions using presence-absence data and information on activity as a measure of abundance (e.g. Newson *et al.*, 2015). This can be achieved with non-professional volunteers, where the use of autonomous recording devices and standardised protocols for deploying detectors has proven potential to provide data that is comparable in quality to that collected by bat specialists, but at a fraction of the cost (Newson *et al.*, 2015).

This study capitalises on the enthusiasm of volunteers to participate in biodiversity monitoring to collect systematic bat distribution and activity data throughout southern Scotland. This is an area which has one of the highest densities of wind farms in Britain (The Wind Power 2015), and for which there is a particular paucity of relevant information on bats to guide decision making. The aim of this study was to collect data on all species of bats in the region to identify noteworthy local bat species assemblages, but to carry out focused analyses on three bat species (Leisler's bat *Nyctalus leisleri*, noctule *Nyctalus noctula* and Nathusius' pipistrelle *Pipistrellus nathusii*) that are currently considered to be at highest risk from wind turbine development in southern Scotland (Natural England, 2014; Rodrigues *et al.*, 2015). This study examines the likelihood of the three species being present at wind farms in the region. All three of these species have previously been reported in pre-construction surveys at existing and proposed wind farm sites in the region (R. Raynor, pers. comm.). In some of these surveys, patterns of activity suggested regular foraging in the survey area, or the presence of a nearby roost. Current understanding of the status of all three of these species of bats in Scotland is poor. Existing population estimates for the two *Nyctalus* species are 20 years old and based on expert opinion (Harris *et al.*, 1995), and suggest that Scottish populations may be limited to a few hundred of each species. More recent unpublished information suggests that the population sizes for these species are larger than this, but there is a persistent belief that these species are rare and occupy restricted ranges in Scotland. There is no published Scottish population estimate for Nathusius' pipistrelle, although it has been suggested that the total British population may be around 4,000 individuals (Battersby, 2005). In practice, it is not straightforward to estimate absolute abundance (often referred to as true abundance) from passive bat detector data because bats cannot be individually identified from recordings. To date no published peer-reviewed study has attempted to do this for any species of bat. As a consequence, we focus discussion on population size on what the data can tell us about likely minimum estimates rather than a formal analysis of population size.

2. METHODS

2.1 Southern Scotland Bat Survey protocol

The project focused on a survey area of 21,033 km², roughly comprising the southern third of Scotland (Fig. 1). This region is dominated by semi-natural and improved grassland, with extensive areas of moorland, heath and bog, coniferous woodland and arable, and ranging from sea-level to over 800 m. Although there has been little in the way of extensive or systematic bat recording in this area, local studies and *ad hoc* recording have recorded 10 species to date, (Table 1) including records assigned to a pair of species (whiskered bat *Myotis mystacinus* and Brandt's bat *M. brandtii*) which are difficult to separate acoustically. It should be noted that Brandt's bat has only recently been confirmed as being present in Scotland based on DNA analyses of a single dropping, with all other recent records of the species pair being confirmed as whiskered bat.

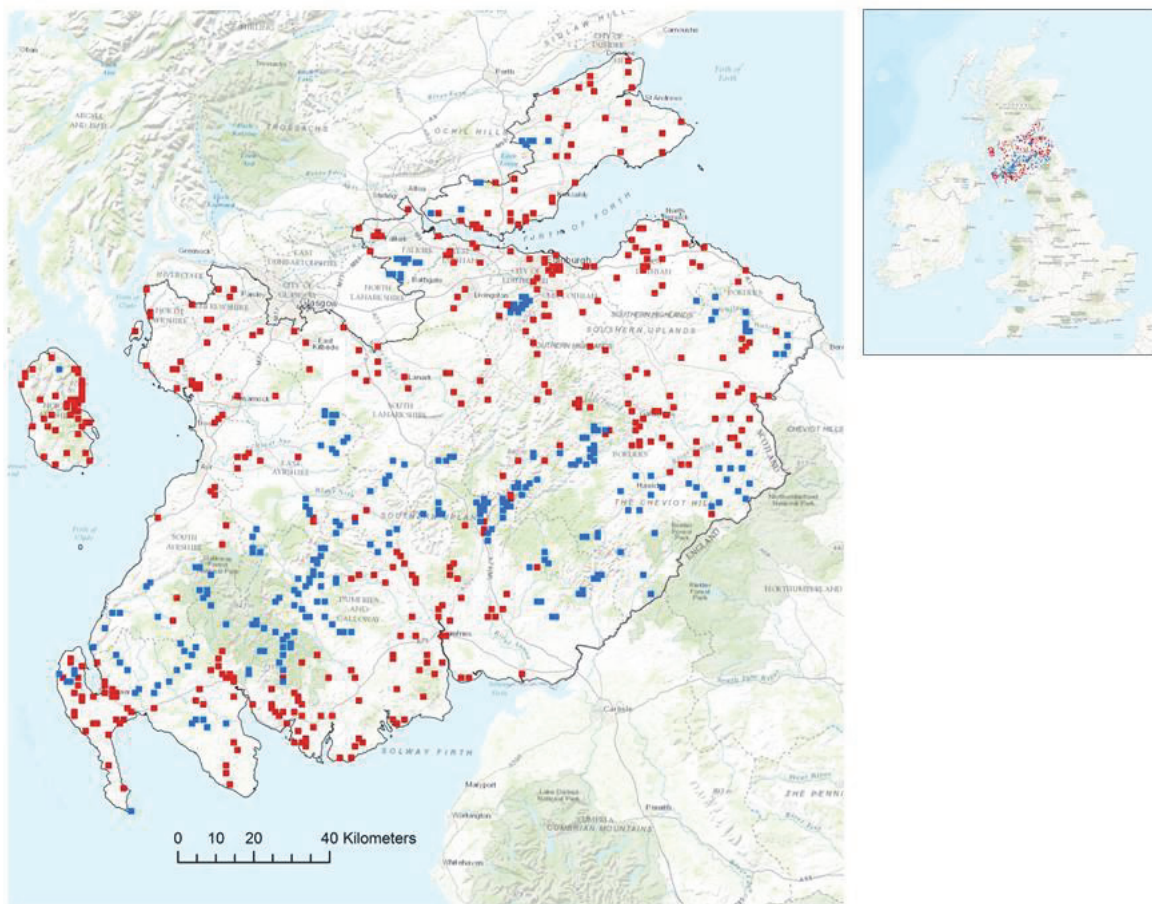


Figure 1. Distribution of 1 km squares surveyed through the Southern Scotland Bat Survey and location in relation to Great Britain (inset). Red squares were surveyed by volunteers, blue squares by project fieldworkers.

The fieldwork was undertaken under the auspices of the Southern Scotland Bat Survey (<http://www.batsurvey.org/scotland/>) which ran from May until the beginning of October 2016 to cover the main period of bat activity. Collaborating with several organisations and local libraries, this project set up 16 “Bat Monitoring Centres” at locations already open to and used by the public, from which anyone could borrow a passive real-time bat detector for a few days. For more information on the Bat Monitoring Centres and how they were chosen see Annex 1. The detectors were Wildlife Acoustics SM2Bat+ detectors, which record in full-

spectrum at 384 kHz (Waters & Barlow, 2013) and automatically trigger by calls of passing bats. A high pass filter of 4 kHz was used to define the lower threshold of the frequencies of interest for the triggering mechanism. Recording was set to continue until no trigger was detected for a two second period. The National Trust for Scotland, Royal Society for the Protection of Birds and Forestry Commission also borrowed multiple bat detectors for extended periods, and two paid fieldworkers deployed detectors in areas and habitats where volunteer uptake during the season was low. This was done by monitoring volunteer uptake during the season, and using an adaptive approach to deploy paid fieldworker effort in a strategic gap-filling manner.

Detectors were typically deployed at c.6pm and left to record until the following morning. Microphones were mounted on 3 m poles to avoid ground noise and reduce recordings of reflected calls. Guidance was given to avoid surveying bats in persistent heavy rain, strong wind or if the nightly temperature was predicted to fall well below 7°C, and on the placement of microphones which should be deployed at least 1.5 meters in any direction from vegetation, water or other obstructions. See www.batsurvey.org/scotland/resources/ for a copy of survey instructions provided to volunteers and field recording sheet. At the end of a recording session, the memory card was returned to the British Trust for Ornithology (BTO) for analyses, along with a completed recording form giving the dates and grid references at which the detector was used.

Between one and three nights of recordings were collected in each sampled 1 km square with locations for different nights of recordings being separated by at least 200 m. Volunteers were encouraged to preferentially select one or more 1 km square to survey from 1000 'priority' squares. These squares were randomly selected, prior to the start of the survey season, from all 1 km squares in the survey area that were not associated with human habitation, as defined as not containing the Centre for Ecology and Hydrology (CEH) 2007 land cover category 'built up areas and gardens' (Morton *et al.*, 2011). The study adopted this approach following a similar, smaller project in Norfolk (Newson *et al.* 2015) which found that 1 km squares chosen by volunteers tended to be biased towards areas with high human population (i.e. close to where volunteers live). Where selecting a random priority square was not feasible, volunteers were given the opportunity to select an alternative square of their choice for surveying, on the understanding that the study would need to test for and potentially correct for bias.

Publicity via BTO members and surveyors, various blogs, social media and e-newsletters directed people to an online sign-up tool, showing survey coverage, available squares, and enabling volunteers to sign up. The survey map was updated throughout the survey season; recordings were analysed and preliminary feedback on species recorded given to volunteers during the project rather than at the end of the season. The sign-up map was linked to an online detector booking system, to help coordinate the booking out of detectors.

2.2 Semi-automated acoustic identification of bats

Automated passive real-time detectors are triggered when they detect sound within a certain frequency range. Monitoring on this scale can generate a very large volume of recordings, efficient processing of which is greatly aided by a semi-automated approach for assigning recordings to species. In this study an acoustic classifier *TADARIDA* (a Toolbox for Animal Detection in Acoustic Recordings Integrating Discriminant Analysis; Bas, 2016) was used. All recordings from the Southern Scotland Bat Survey were passed through the *TADARIDA* random forest classifier (Step 1). This entailed extraction of 150 measures of call characteristics from each recording (Annex 2, Bas & Bas, 2016), and a comparison of these against measurements taken from an extensive reference library of manually identified ultrasound recordings.

The classifier allows up to four different “identities” to be assigned to a single recording, according to probability distributions between detected and classified sound events. From these, species identities are assigned by the classifier, along with an estimated probability of correct classification (as compared with the underlying training database) on a scale of 0–1. For common *Pipistrellus pipistrellus* and soprano pipistrelle *Pipistrellus pygmaeus*, which accounted for >95% of all bat recordings made during the survey, *TADARIDA* identifications of these species for which the estimated probability of correct classification was high (≥ 0.8), were taken as being accurate. The call shape (similar to a hockey-stick) and frequencies of common and soprano pipistrelle are sufficiently characteristic to allow reliable classification of these species by the classifier.

Manual checking (Step 2) of spectrograms using software SonoBat (<http://sonobat.com/>) was used as an independent check of the original species identities assigned by the *TADARIDA* classifier. Using the output from Step 1, manual checks were carried out on a random sample of 1,000 recordings each of common and soprano pipistrelle, to verify that classifier identification of these species was accurate. For the other species, all recordings were inspected with SonoBat regardless of the associated probability of correct classification. Species identities were checked (and re-classified if necessary) based on call parameters defined in Russ (2012) and Barataud (2015). For a summary of important call parameters used in Step 2 see Annex 3.

Once species identities had been checked by looking at individual recordings in isolation, calls assigned to species whose calls had the most potential to be confused with those of other species (e.g. bats in the genus *Myotis* and *Nyctalus*) were re-examined in SonoBat, comparing them to other recordings potentially of the same bat made from the same location on the same night at neighbouring points in time (Step 3). All subsequent analyses use final identities upon completion of the above inspection and (where necessary) correction steps.

2.3 Elevation and habitat bias

Allowing participants some flexibility in their choice of survey squares, as described above, could bias geographical coverage, particularly towards areas of human habitation. Because environmental bias in datasets can be very influential when predicting spatial patterns of distribution and activity (e.g. Leitão *et al.*, 2011), the study evaluated the extent to which the habitat composition of surveyed 1 km squares deviated from a random sample using habitat summarised at a 1 km square resolution and derived from Centre for Ecology and Hydrology Land cover Map 2007 data (Morton *et al.*, 2011). The availability of each of nine broad habitat types (human, arable, semi-natural grassland, improved grassland, coniferous woodland, broad-leaved woodland, moorland, heath and bog, coastal and inland water) was summarised across all 1 km squares in the survey area (showing that, for example, 13% of the survey area was coniferous woodland). For each habitat, the study determined whether the 1 km squares sampled for bats were biased by comparing overall availability of the habitat with the extent of habitat within the surveyed 1 km squares. The expected margin of error (i.e. the range of differences between overall availability and extent of a habitat in surveyed squares that one would expect to see in the absence of biased sampling) was determined by repeated random sampling of N squares, where N was the number of squares surveyed. Sampling was repeated 1,000 times and the 25th and 975th ranked values of the availability of each habitat across the random samples were expressed as a percentage of the actual habitat availability values. If the extent of a habitat within surveyed squares was above or below these 95% confidence limits, this indicates that it was over- or under-represented, respectively (i.e. survey square selection was biased towards, or against the habitat in question). Sampling bias was evaluated with respect to elevation in a similar way, by comparing mean elevations of surveyed 1 km squares with those of 1 km squares across the whole the survey area. Mean elevations at a 1 km resolution were derived from a 90m resolution digital elevation model (Jarvis *et al.*, 2008).

2.4 Nightly patterns of bat activity

Important for considering mitigation measures, such as reducing wind farm operation during hours of peak bat activity, the study examined how bat activity varied by time of night and by season. Nightly activity was determined for each half-month period and presented according to the percentage of sample squares on which each bat species was detected. Where sample squares were surveyed more than once in a period, the study combined data across visits. Activity through the night was analysed by first converting all bat pass times to time since sunset (sunset times from <http://data.gov.uk/dataset/uk-sunrise-sunset>) and then assessing the frequency distribution of passes relative to sunset for the whole season and in half-month periods.

2.5 Spatial models of bat distribution and activity

To assess the value of the data collected here for informing our understanding of bat activity and species distributions at a large spatial scale, it was necessary to consider the data in a spatial modelling framework.

The study here used Generalised Boosted Regression, which is an ensemble implementation of Regression Trees that estimates the form of the relationship between a response variable and its predictors without *a priori* specification of a data model (Elith *et al.*, 2008). This technique estimates a large number of simple models, which are combined to form a final model optimized for prediction, using cross-validation for model building. Models were produced using the R package gbm (Ridgeway 2013) and using the gbm.step function of Elith & Leathwick (2011) to find the appropriate learning rate and number of trees, for each model. Following analyses of similar data in Newson *et al.* (2015), we used a tree complexity parameter of 10 and started with a learning rate of 0.001. We then changed the learning rate to find a value that was slow enough to result in an initial steep decline in prediction error followed by a gradual approach to the minimum, and where the number of trees at the minimum point was as close to 1,000 as possible based on the rules of thumb in Elith *et al.* (2008). Models were trained with 10-fold cross validation with a bagging fraction of 0.5 and assessed for predictive performance using either the area under the ROC curve (AUC) for occurrence models or the correlation coefficient between observed and predicted value for bat activity. For evaluation of AUC values, the study used the approach recommended by Swets (1988): excellent AUC > 0.90; good 0.80-0.90; fair 0.70-0.80; poor 0.60-0.70; and fail 0.50-0.60 although it is accepted that these divisions are fairly arbitrary. For occurrence models it was assumed a Bernoulli distribution for the response variable and for activity models, a Poisson distribution.

Before analysis, the bat data used in the models had to be standardised because bat detectors operated all night, and night length varied by a factor of two over the season. This had implications for species detection probabilities and the number of passes recorded. Based on patterns of activity with respect to sunset time, the core activity of all species of bats occurred in the first six hours after sunset (see Results), all data were standardised by considering only bat passes up to six hours after sunset. The shortest night length in the survey area is 6 hours and 40 minutes. Detectors were usually in position and recording before sunset. Some species (e.g. noctule) were recorded before sunset only in a very small minority of recordings (only 0.3% of detected bat passes were before sunset). Within this approximate six hour operating window the study determined presence-absence, and the total number of detected passes by each species of bat, for each visit.

To generalise the recordings at sample locations to the rest of the region, it was necessary to include factors in the model that are likely to influence bat presence and activity. Weather conditions affect the activity of bats at a given location (e.g. Barlow *et al.*, 2015). For each 1 km square in the survey area, hourly minimum temperature, precipitation and wind speed

recorded at the closest weather station were extracted (MIDAS Land and Marine Surface Stations Data – available from <http://catalogue.ceda.ac.uk/uuid/220a65615218d5c9cc9e4785a3234bd0>) and then summarised these for the six hour recording window of each visit (minimum temperature, mean wind speed, total precipitation).

Some bat species have precise feeding and roosting requirements, so habitat in and around the sampling location is likely to affect the species present. Habitat was summarised at a 1 km square resolution from CEH land cover data containing the percentage of nine broad habitat types (detailed above), and mean elevation derived from a 90 m resolution digital elevation model (CGIAR-CSI, 2008). In addition, habitat availability and elevation in the wider landscape were quantified because bats forage over a wider area than a 1 km square. For this the study determined the area of each habitat and mean elevation across the 1 km square of interest and its immediate neighbours (9 km²). Two further larger landscape extents were considered (16 km² and 25 km²) at the beginning of the study, but because land cover and elevation were strongly correlated across landscape scales ($r > 0.90$), the study chose to use a single landscape scale that best fitted known home range sizes. Because bat distribution and activity may vary seasonally, week number was also included as a covariate. This means that 26 predictor variables were included in each model (easting, northing, nine habitat variables and elevation at two spatial scales, three weather variables and week number).

The study focuses here on ten species of bat known to occur in Scotland. These include whiskered and Brandt's bats, which are difficult to distinguish acoustically and are, therefore treated together as a species pair. Once models had been built, mid-season (corresponding to the 27th week of the year) predictions of occurrence probability and activity (pass frequency) were made for each species in every 1 km square, using habitat data for each square and under normal (mean) weather conditions for that time of year. For presentation purposes, activity predictions of less than 0.5 passes per night (strictly for data from the first six hours of the night) were removed and the study only presents maps for species where at least 100 grid squares remained. All probability of occurrence maps use the same colour scale, ranging from >0 to 1 in increments of 0.1. Bat activity maps use a 10-colour scale, where grid cells are placed into bands according to the 10 equal divisions of predicted activity. Gini coefficients, which quantify the degree of aggregation among a set of values, were used to assess the degree to which bat occupancy and activity were uniform (the coefficient tends to 0) or aggregated (the coefficient tends to 1) among 1km squares. Gini coefficients were calculated using the *ineq* package in R (Zeileis, 2014).

2.6 High risk bat species at wind farms

For the three bat species considered to be a highest risk from wind farms (noctule, Leisler's bat and Nathusius' pipistrelle), 1 km square level predictions of activity and probability of occurrence derived through the spatial modelling above were ordered from highest to lowest, and the top 1%, 5% and 10% of squares determined for each species. A single composite map for the three species, which reflects the highest threshold level (top 1%, 5% or 10%) recorded for each 1 km square across the six maps, was produced to assist decision making in relation to future wind turbine construction.

The likely overlap of noctule, Leisler's bat and Nathusius' pipistrelle populations with existing and approved wind farms was quantified for each species by calculating the sum of the predictions from the occurrence and activity models that fell within the average maximum foraging radius for each species around each wind farm. In the absence of more detailed spatial data on the footprint of each wind farm, the study used a point location dataset of existing and approved wind farm locations (The Wind Power, 2015). Based on existing information (Bat Conservation Trust, 2015) a cautious approach was taken and used a 4 km

average maximum foraging radius for noctule and 3 km for Leisler's bat and Nathusius' pipistrelle.

2.7 Identifying important local bat assemblages

A map showing the combined distributions of all bats species was produced to highlight areas with noteworthy local bat species assemblages. The approach taken here was to sum the estimates of probability of occurrence for each 1 km square in southern Scotland. High probability of occurrence and many species contribute to make an area being more important in terms of its species assemblage.

3. RESULTS

3.1 Survey coverage

714 different 1 km squares (3.4% of the survey area) were surveyed for bats in 2016. This sample comprised 1,537 complete nights of recording in 1,422 different recording locations. 667,755 recordings were collected which, following analyses and validation, were found to include 399,242 bat recordings (Fig. 1, Table 1). 275 volunteers took part in the project, each of whom borrowed either a single detector from a hosting centre or multiple detectors for an extended period. These volunteers surveyed 375 1 km squares, with two paid fieldworkers surveying a further 339 1 km squares. Maps of bat activity showing the number of recordings of each species per night are presented in Annex 5. Manual checking of 1,000 randomly selected recordings each of common and soprano pipistrelle suggested that less than 1% of recordings were incorrectly assigned (in most of these cases to the other species) which was deemed an acceptable error rate for these highly abundant and geographically widespread species.

Table 1. Bat species detected by the Southern Scotland Bat Survey, number of recordings of each species following validation and a summary of the scale of recording.

Species	Species code	No. of recordings following validation	No. of different 1-km squares (% of total)
Daubenton's bat, <i>Myotis daubentonii</i>	Mdau	12,913	291 (41%)
whiskered / Brandt's bats, <i>Myotis mystacinus</i> / <i>M. brandtii</i>	Mmys/Mbra	1,130	150 (21%)
Natterer's bat, <i>Myotis nattereri</i>	Mnat	2,306	363 (51%)
noctule, <i>Nyctalus noctula</i>	Nnoc	2,101	152 (22%)
Leisler's bat, <i>Nyctalus leisleri</i>	Nlei	4,327	224 (32%)
common pipistrelle, <i>Pipistrellus pipistrellus</i>	Ppip	99,058	624 (88%)
soprano pipistrelle, <i>Pipistrellus pygmaeus</i>	Ppyg	240,532	635 (90%)
Nathusius' pipistrelle, <i>Pipistrellus nathusii</i>	Pnat	185	23 (3%)
brown long-eared bat, <i>Plecotus auritus</i>	Paur	960	238 (34%)
Unidentified <i>Myotis</i> species	Myotis	2,718	320 (45%)
Unidentified <i>Pipistrellus</i> species	Pipspp	32,965	582 (82%)
Unidentified <i>Nyctalus</i> species	Noclei	47	36 (5%)

3.2 Habitat and elevation bias

The availability of each habitat type was summarised across all 1 km squares in the survey area, showing that, for example, 24.8% of the area was semi-natural grassland (neutral, calcareous or acid grassland). To determine whether, and to what extent, habitat composition in our sample of surveyed 1 km squares was biased, the study compared the mean cover of each habitat in surveyed squares to the 95% confidence limits for this habitat derived from random sampling. Habitat availability in surveyed squares did not significantly differ from that in the whole survey area for the five most common habitats, which were arable, semi-natural grassland, improved grassland, coniferous woodland and moorland, heath and bog (Fig. 2). Together, these habitats comprised about 90% of the survey area. Three rarer habitats (human habitat, broadleaved woodland and inland water) were over-sampled (Fig. 2). However, although the amount of human habitat, broadleaved woodland and inland water sampled was significantly higher than would be expected in a random sample, the extent of this over-sampling contributed less than 2% more human habitat, broadleaved woodland and inland water to the overall sample.

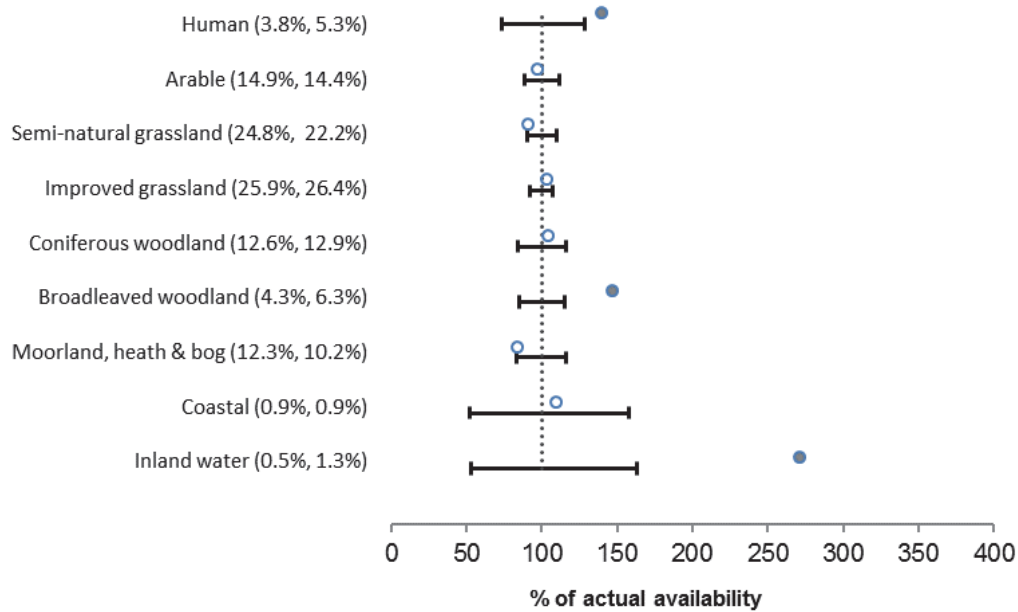


Figure 2. Testing for bias in the coverage of different habitat types by the Southern Scotland Bat Survey. Dots show the observed coverage of each habitat type as a percentage of the actual proportional cover of the habitat type (the actual value is given as the first value in brackets). The bar shows the range of values expected from a random sample of the same size achieved by the survey. Filled circles highlight habitats that were significantly over or under-sampled.

In relation to elevation, the sample was skewed towards greater coverage of lowland 1 km squares of between zero and 150 metres (Fig. 3) with mean elevation falling outside the 95% confidence interval. Nevertheless, the survey sampled across the range of elevations present in the survey area, which has positive and important implications for modelling of species distributions and activity. Previous work in Norfolk controlled for pronounced under-sampling of arable habitat by including a weighting in the subsequent analyses (Newson *et al.* 2015). With these data, where the sample was very close to a random sample, the inclusion of comparable weighting resulted in negligible improvement in the representativeness of the dataset and was not considered further.

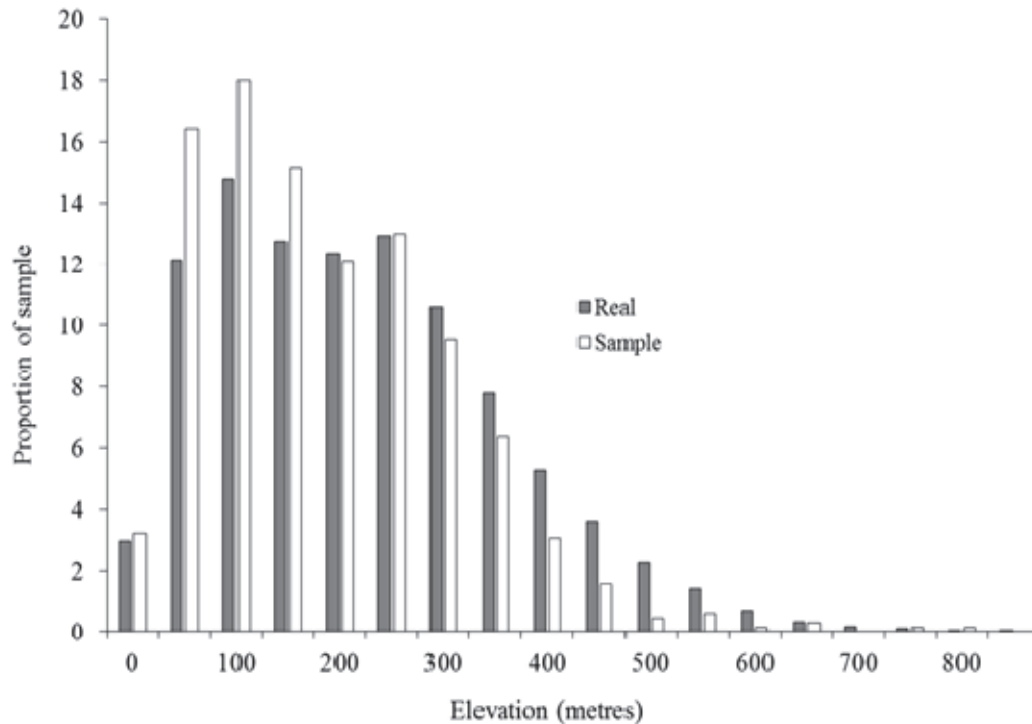


Figure 3. Coverage of the elevational range achieved by the Southern Scotland Bat Survey in relation to the availability of elevation strata in the survey area.

3.3 Nightly variation in bat occurrence and activity

Examining the nightly activity of bats through the season with respect to sunset time, found that the core activity of bats occurred in the first six hours after sunset, irrespective of time of year, length of night and species (Fig 4). However, most species exhibited low levels of activity later in the night, particularly late in the season (Fig. 4), highlighting the need to standardise data prior to analysis when considering nights of variable length. There were large differences between species in the timing of activity. For example, brown long-eared bat *Plecotus auritus* showed little change in activity between one and six hours after sunset, whilst common and soprano pipistrelle were most active shortly after sunset with activity falling thereafter (Fig 5). Noctule and to a lesser degree Leisler's bat, showed a characteristic activity peak in the first two hours after sunset, during which 55% and 43% of the total activity for these two species was recorded (Fig. 5).

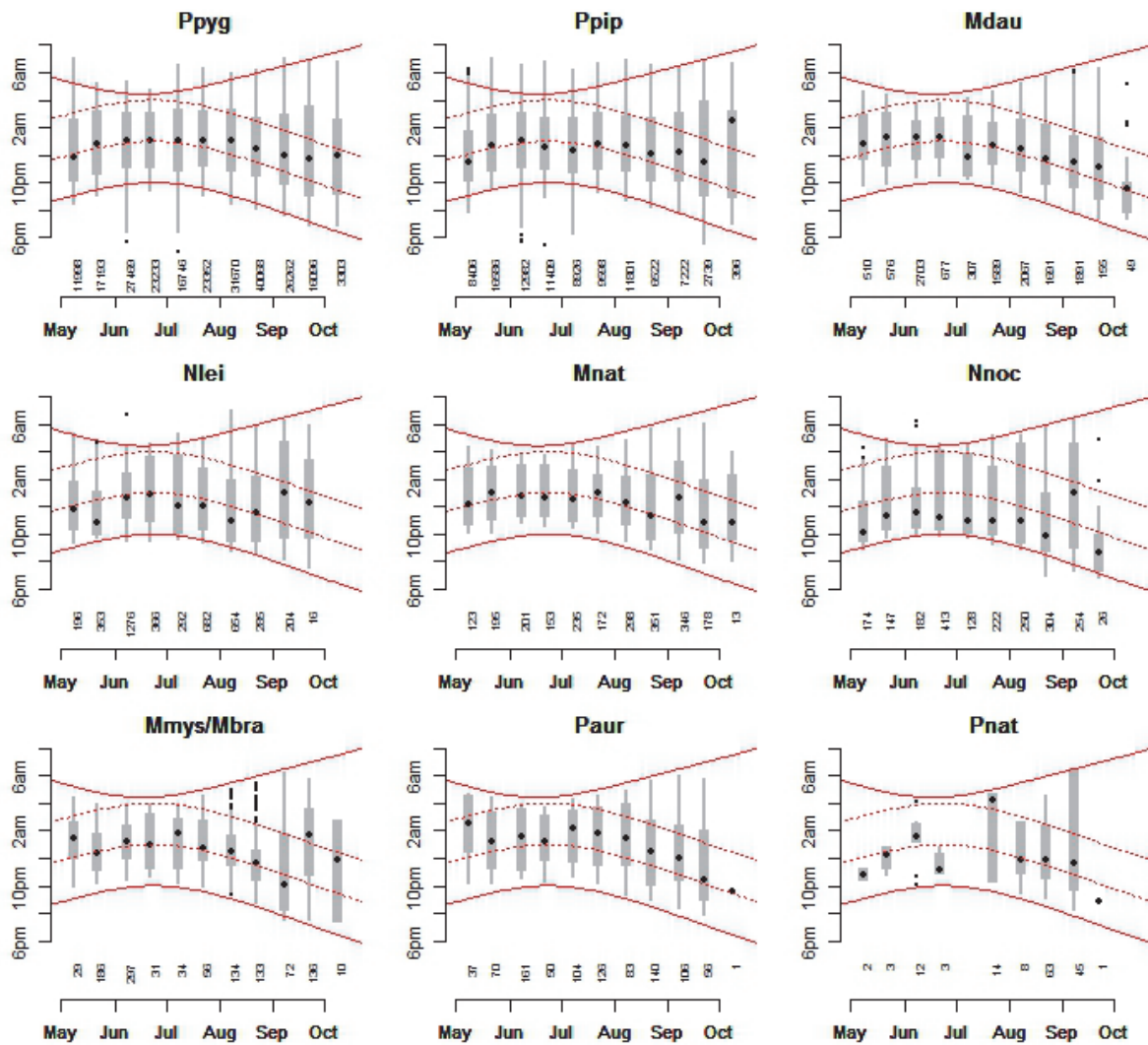


Figure 4. Patterns of nightly activity through the season with respect to sunset time. Individual box plots summarise the timing of bat passes during half-month periods. The solid red lines show sunset and sunrise times and the two dashed lines indicate 3 hours and 6 hours after sunset. For box plots, wide bars show quartiles, lines extend up to 1.5 times the interquartile range, large dots show the median and small dots show outliers. Numbers give the total number of recordings in each period.

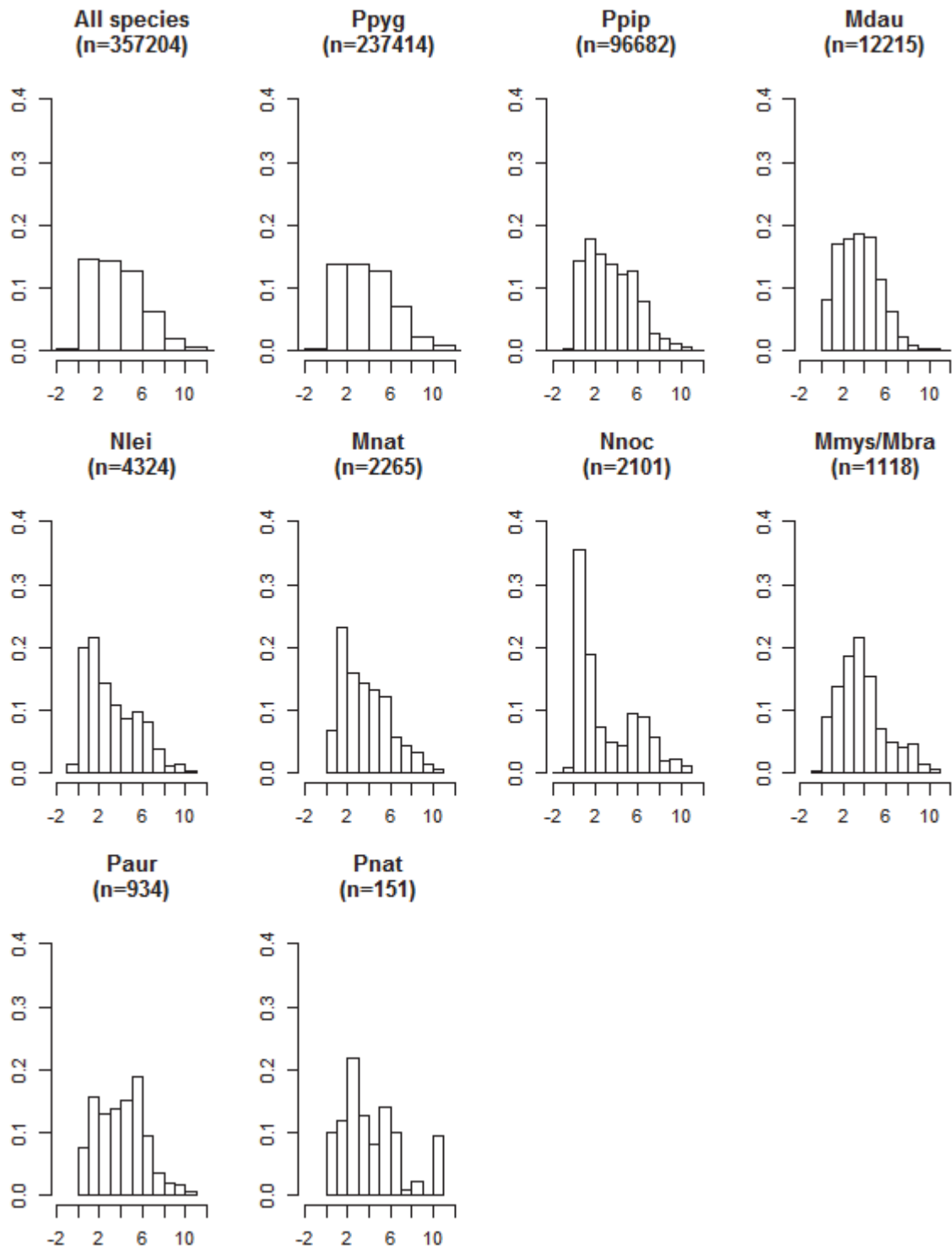


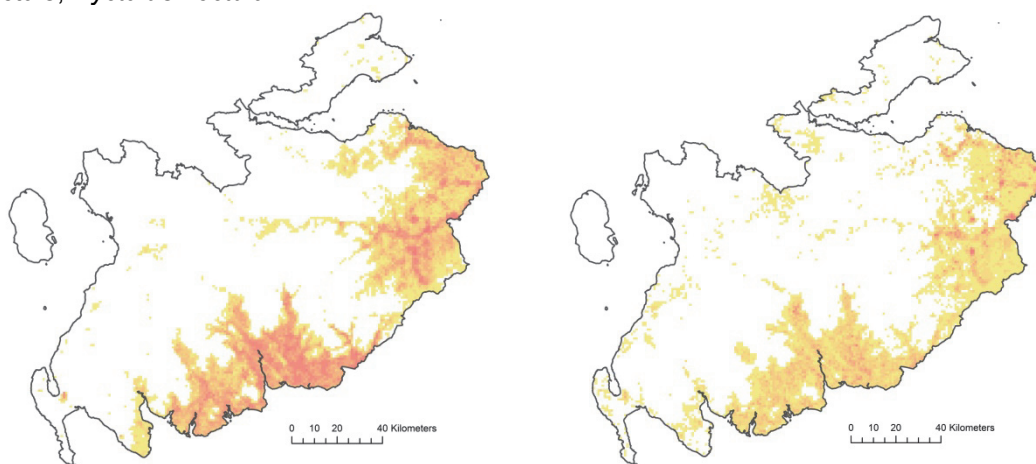
Figure 5. Frequency distributions of the number of bat recordings with time (hours) since sunset calculated over the whole season. Negative times indicate passes prior to sunset and accounted for 0.3% of all bat recordings.

3.4 Spatial patterns of distribution and activity

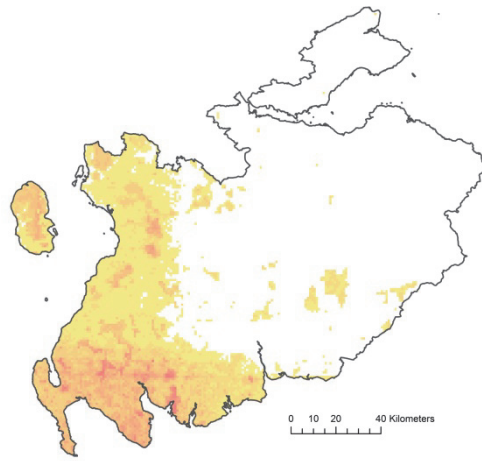
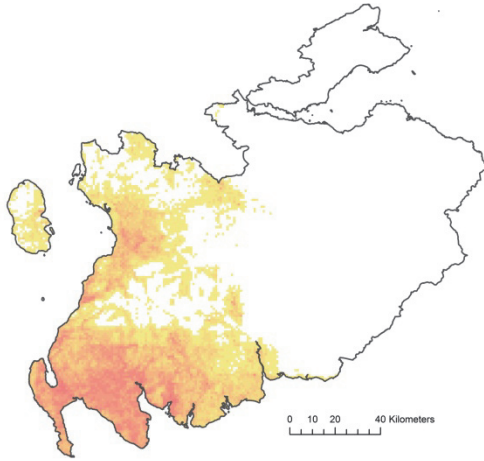
Models of bat distribution and activity were produced for all species (Fig. 6), but maps of activity for whiskered / Brandt's bats and Nathusius' pipistrelle are not shown because the majority of predictions were less than 0.5 passes per night. The learning rate used for each model, number of trees on which the final model was based and model performance statistics (AUC values for distribution modelling and correlation coefficient between observed and predicted values for bat activity) are shown in Table 2. On average, models validated using occurrence data showed fair AUC values (0.70–0.80) with noctule good (0.90) and Leisler's bat excellent (0.94). For bat activity, the correlation coefficients averaged 0.28, and ranged from 0.12 for Daubenton's bat to 0.57 for noctule. These values are fairly low, but are comparable or higher than published elsewhere for other analyses of abundance type information, and are likely to reflect the influence of stochasticity on the survey data (e.g. Johnston *et al.* 2013).

Considering the distribution and activity of noctule and Leisler's bat, there was little overlap in range, with a clear east- west split, with Leisler's bat occurring in the west and noctule mainly in the east (Fig. 6). Using Gini coefficients to assess the degree to which numbers of recordings were uniform or aggregated, noctule and Leisler's bat had the highest Gini coefficients for distribution of over 0.60 reflecting their restricted ranges. Gini coefficients of activity for noctule and Leisler's bat were also high, highlighting that comparatively few 1 km squares contribute a large proportion of the recorded activity (Table 2). For Nathusius' pipistrelle, for which there was perhaps some clustering of records in the north (Fife) and south-west (around Stranraer) of the region, had a relatively high Gini coefficient for distribution of 0.36. However, a lower Gini coefficient for activity of 0.28 reflects a number of sites at which a small number of recordings of Nathusius' pipistrelle were made. Most other bat species showed Gini coefficients for distribution of 0.22–0.26 (Table 2), with those of common and soprano pipistrelle close to zero reflecting their widespread distribution. Whilst common and soprano pipistrelle are widespread in distribution terms, there were some differences in spatial patterns of activity, with soprano pipistrelle having a comparatively high Gini coefficient for activity of 0.34, highlighting spatial clustering in activity, with noticeably greater levels of activity in lowland river valleys, and noticeable lower activity in upland areas and on the island of Arran (Fig. 6).

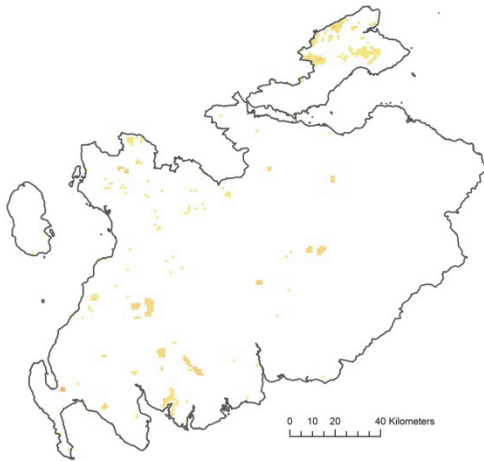
noctule, *Nyctalus noctula*



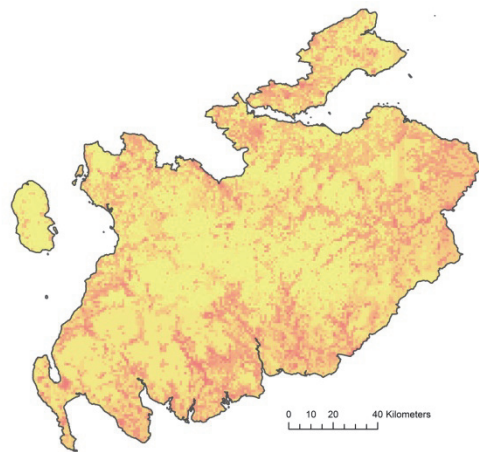
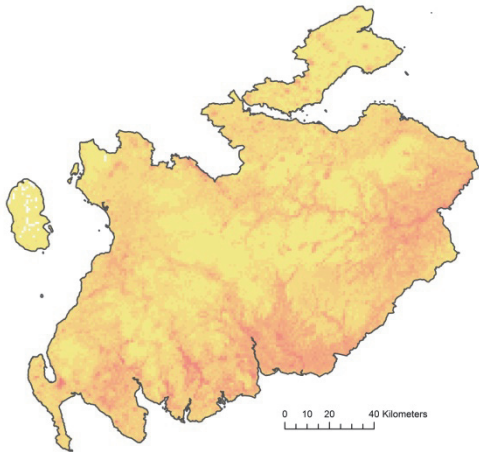
Leisler's, *Nyctalus leisleri*



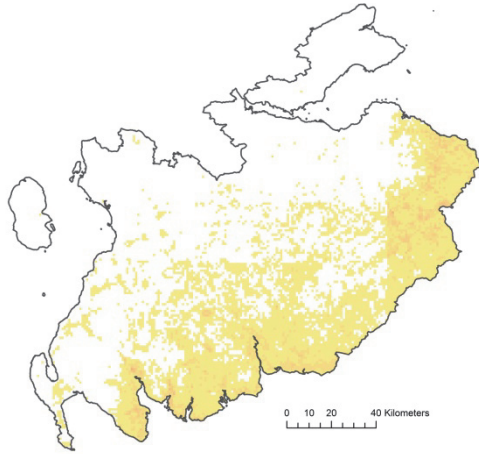
Nathusius' pipistrelle, *Pipistrellus nathusii*



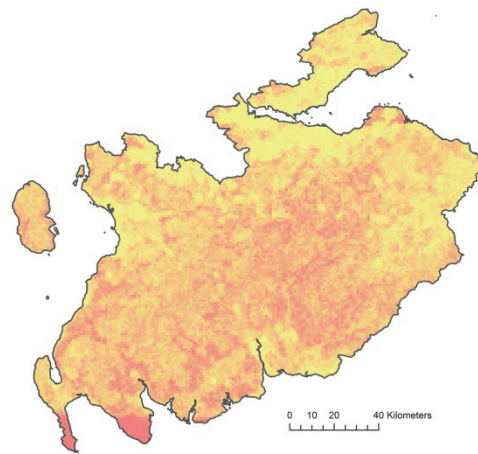
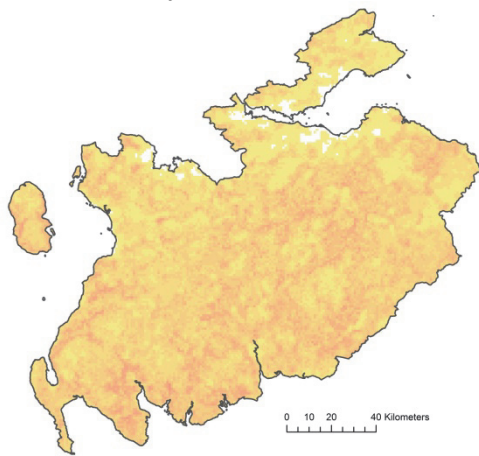
Daubenton's bat, *Myotis daubentonii*



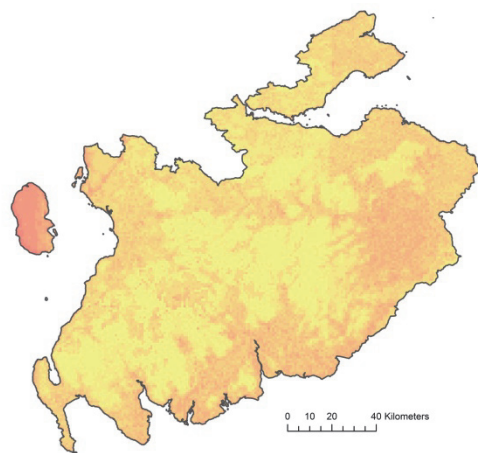
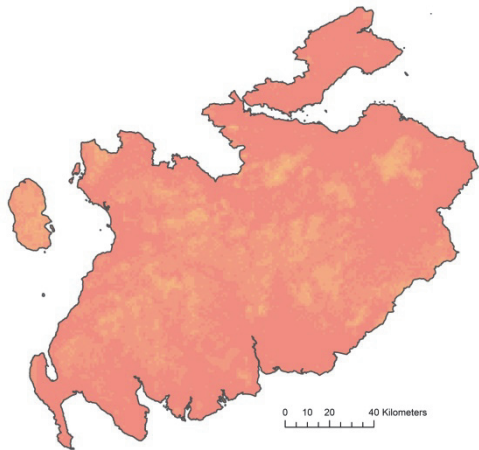
whiskered / Brandt's bat, *M. mystacinus / brandtii*



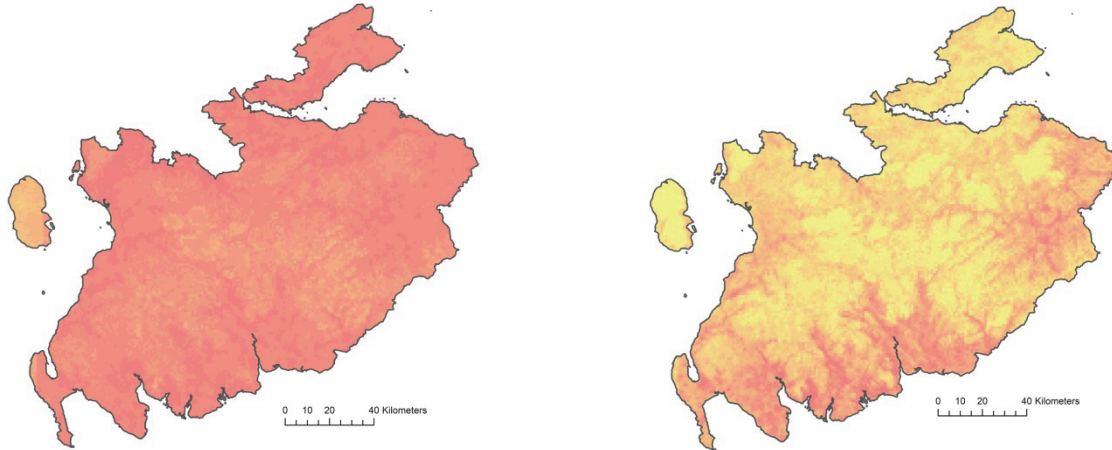
Natterer's bat, *Myotis nattereri*



common pipistrelle, *Pipistrellus pipistrellus*



soprano pipistrelle, *Pipistrellus pygmaeus*



brown long-eared bat, *Plecotus auritus*

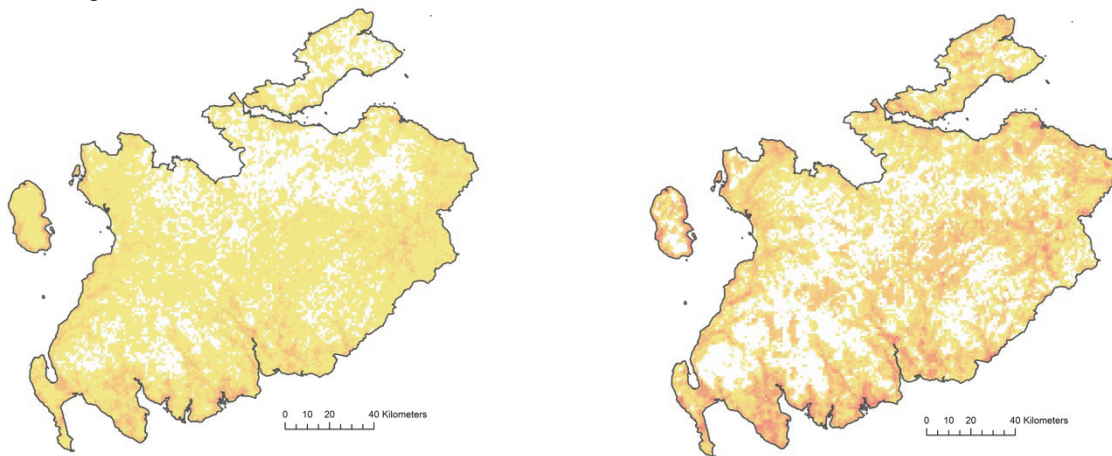


Figure 6. Maps of predicted occurrence probability (left) and predicted activity (right; a proxy for abundance) for bats in southern Scotland. Activity maps are only shown for species with predictions of at least 0.5 recordings per 6-hours in at least 100 1-km squares. Darker tones indicate higher probability of occurrence or higher activity. Occurrence maps share the same scale (probability in increments of 0.1 from 0 to 1). The scale for activity maps varies among species although in each case the darkest colour represents the top 10% of locations for that species.

Table 2. Results of generalised boosted regression models to predict patterns of bat occurrence and activity. *lr* is the learning rate used for each model and *nt* is the number of trees on which the final model was based. Model performance was assessed by cross-validation and quantified using area under the receiver-operator curve (AUC) for occurrence models and the correlation coefficient between observed and predicted values for relative abundance. Gini coefficients measure the level of aggregation in predicted occurrence or activity.

Species	Predicted Occurrence				Predicted Activity			
	<i>lr</i>	<i>nt</i>	AUC	Gini	<i>lr</i>	<i>nt</i>	<i>r</i>	Gini
Daubenton's bat	0.004	1,150	0.75	0.26	0.0002	1,200	0.12	0.04
whiskered / Brandt's bat	0.0017	1,200	0.77	0.26	0.0005	1,000	0.13	0.09
Natterer's bat	0.002	1,250	0.71	0.22	0.002	1,150	0.15	0.15
noctule	0.004	1,150	0.90	0.62	0.0085	1,150	0.57	0.67
Leisler's bat	0.0053	1,000	0.94	0.67	0.0079	1,400	0.55	0.76
common pipistrelle	0.0018	1,100	0.72	0.04	0.001	1,400	0.16	0.14
soprano pipistrelle	0.0016	1,250	0.80	0.05	0.003	1,100	0.38	0.34
Nathusius' pipistrelle	0.0015	1,200	0.77	0.36	0.0015	1,200	0.15	0.28
brown long-eared bat	0.003	1,000	0.73	0.24	0.002	1,050	0.27	0.28

3.5 Current and future risk of wind farms to priority bat species

Because the three species considered to be at highest risk from wind farms, noctule, Leisler's bat and Nathusius' pipistrelle, had quite different spatial patterns of distribution and activity (Fig. 6), there was little overlap in the core areas (top 1%, 5% and 10% of squares, ranked by probability of occurrence or activity) (Annex 6). The composite map that combines the core areas across the three species (Fig. 7) identified 5,753 1 km squares (26% of 1 km squares) as being priority areas where the three species are likely to be at highest risk from wind farm development. Within this area, 892 squares (4% of area) were flagged as being in the top 1% of highest priority and were concentrated in the southern and eastern parts of the region.

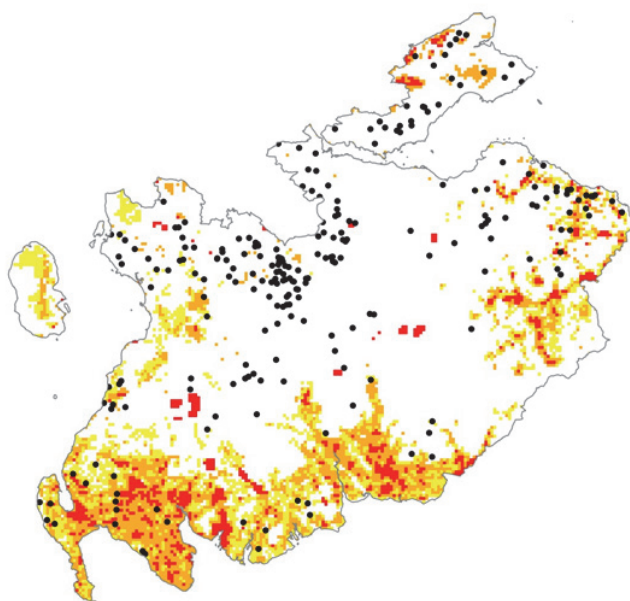


Figure 7. Composite map identifying the top 1%, 5% and 10% (red, orange and yellow) 1 km squares in the survey area for noctule, Leisler's bat and Nathusius' pipistrelle based on the highest ranking across occurrence and activity maps in Annex 6. The distribution of existing and planned wind farms are shown as black dots.

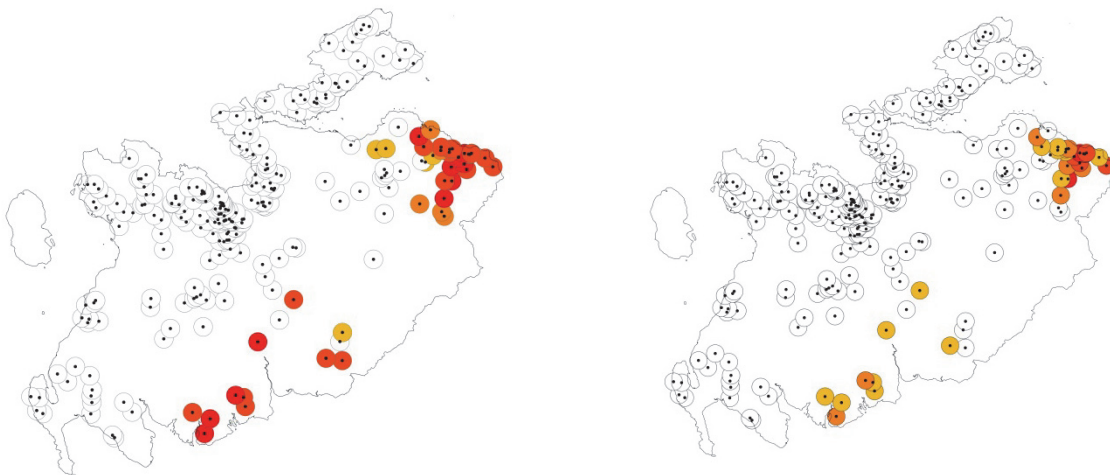
The likely exposure of noctule, Leisler's bat and Nathusius' pipistrelle populations based on the sum of the predictions from the occurrence and activity models that fell within the average maximum foraging radius for each species around each wind farm (Fig. 8), found that for occurrence and activity, 16% and 24% of the populations of these species are likely to be exposed to existing or approved wind farms (Table 3). For each species, about 50% of this exposure is at just 10% of wind farms. Whilst wind farms tended to be located a higher elevation than the three high-risk bat species most commonly occur, there was still significant spatial overlap (Fig. 9).

Table 3. Exposure of noctule, Leisler's bat and Nathusius' pipistrelle distribution and activity (as a proxy for abundance) to existing and planned wind farms. Exposure is calculated as the sum of the predictions from the occurrence or activity models that fall within the average maximum foraging distance of the species.

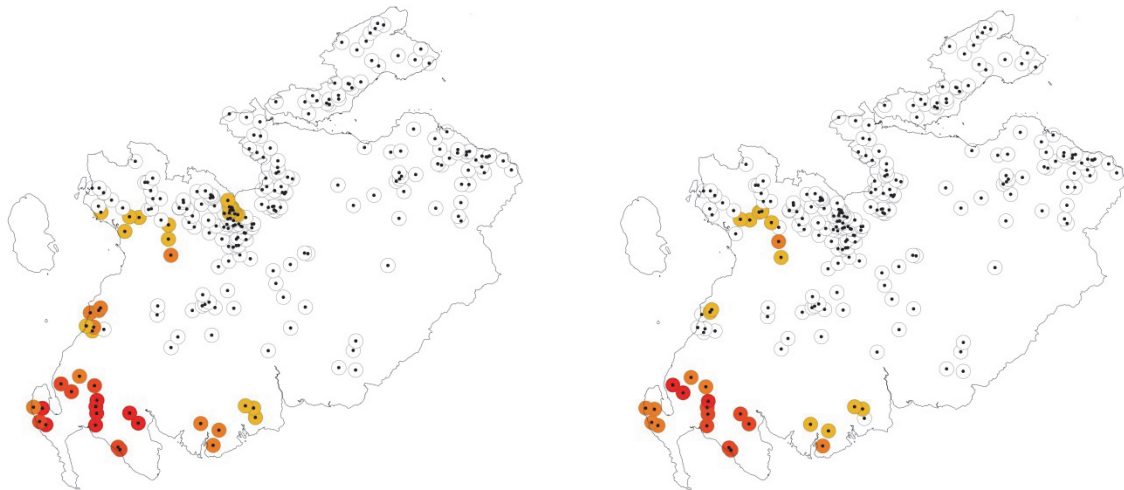
Species	Average maximum foraging distance (km) ¹	Exposure (% of the range or overall activity levels)		Sum of predicted values within wind farm footprint of top 10% (% of sum of total survey area).	
		Distribution	Activity	Distribution	Activity
noctule	4	660.8 (22%)	3,771.7 (24%)	320.9 (11%)	2,026.2 (13%)
Leisler's bat	3	539.4 (18%)	4,324.6 (16%)	305.8 (10%)	2,944.1 (11%)
Nathusius' pipistrelle	3	41.4 (20%)	-	33.63 (16%)	-

¹ Source: Bat Conservation Trust (2016)

noctule, *Nyctalus noctula*



Leisler's bat, *Nyctalus leisleri*



Nathusius' pipistrelle, *Pipistrellus nathusii*

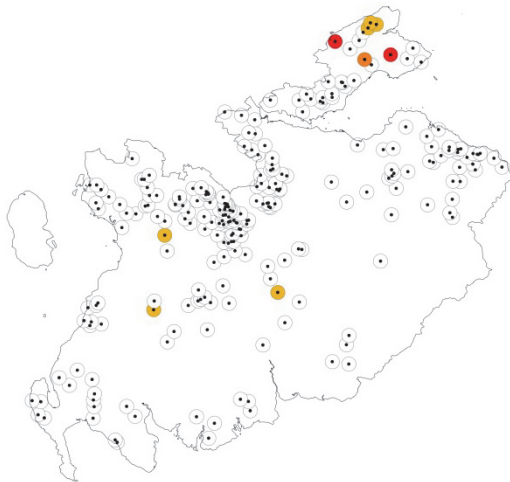
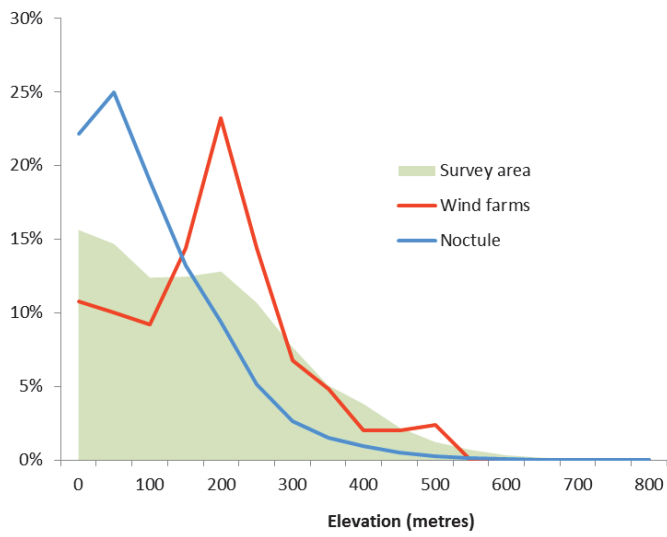
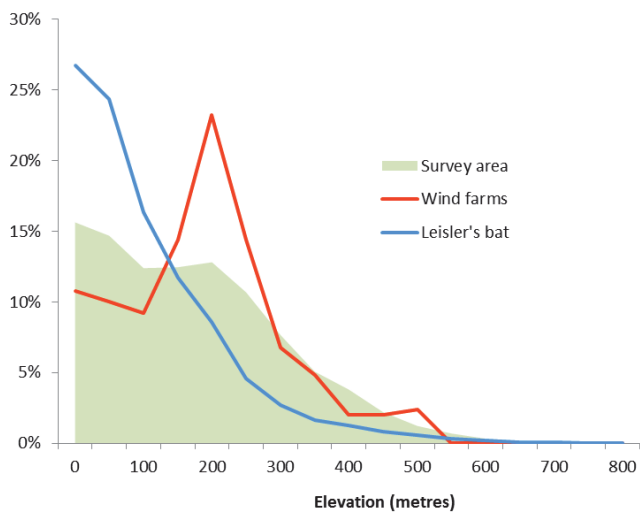


Figure 8. Maps showing the likely exposure of noctule, Leisler's bat and Nathusius' pipistrelle distribution (left) and activity (right) to existing and planned wind farms. Exposure is calculated as the sum of the predictions from the occurrence and activity models that falls within the average maximum foraging radius of each species around wind farms and ordered into five equal bands ranked from lowest (white) to highest exposure (red).

noctule, *Nyctalus noctula*



Leisler's bat, *Nyctalus leisleri*



Nathusius' pipistrelle, *Pipistrellus nathusii*

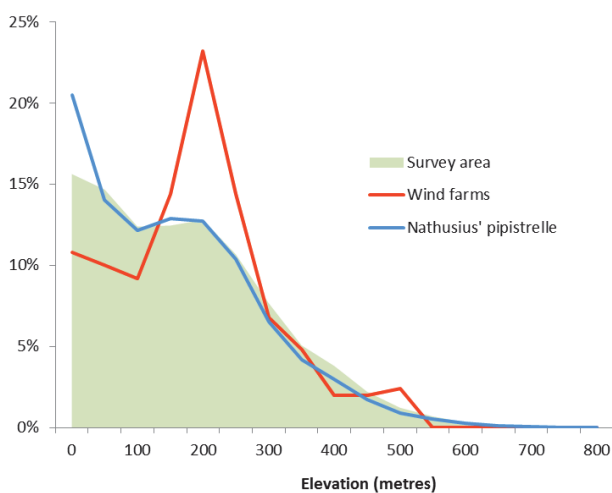


Figure 9. Elevation of existing and approved wind farms at a 1 km square level in relation to occupancy (model predictions) as a proportion of the total for the three high risk species across the survey area.

3.6 Identifying noteworthy local bat assemblages

By combining model predictions of occurrence across all bat species, it is possible to look at the relative importance of different areas in terms of its species assemblage. Through Fig. 10, individual species are allowed to contribute equally to the production of a species assemblage map. This highlights prior expectations of broader species assemblages in lowland areas in the south and east of the region.

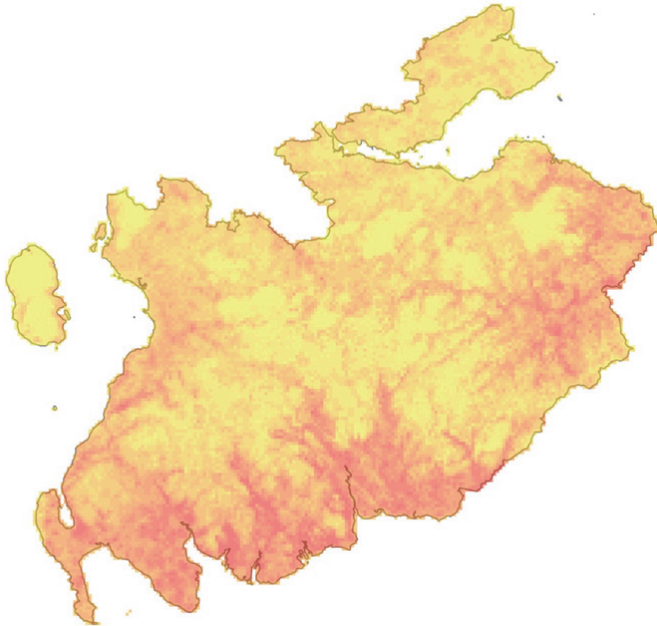


Figure 10. Map showing spatial variation in the importance of different areas for their bat assemblages. High probability of occurrence and many species contribute to make an area more important in terms of its species assemblage. The darkest colour represents the top 10% of locations.

4. DISCUSSION

Our large-scale deployment of static real-time bat detectors has produced realistic spatial patterns of bat occurrence and activity throughout southern Scotland, enabling production of objective risk maps for the region's wind farms. The dataset of close to 400,000 bat recordings, produced in collaboration with the region's citizen scientists, has improved our understanding of all bat species in the region. It has been particularly valuable, however, for defining patterns of occurrence and activity for Leisler's bat, noctule and Nathusius' pipistrelle, for which the risk of wind turbine collision is believed to be particularly high. The ranges occupied by each of the three species in southern Scotland are restricted with little overlap between species. For the two *Nyctalus* species, noctule and Leisler's bat, there is a clear east-west split, with Leisler's bat occurring in the west and noctule mainly in the east. For both Leisler's bat and noctule, occupancy and activity patterns were particularly aggregated, with a comparatively small number of 1 km squares contributing a large proportion of the recorded distribution and activity. The latter can be viewed as a proxy for abundance, with high levels of activity typically occurring where a species is most abundant. Nathusius' pipistrelle was recorded at few sites, dispersed across the survey area, with some clustering of records in the southwest and the north of the region.

4.1 Risk of wind farms to priority bat species

Exploring the likelihood of Leisler's bat, noctule and Nathusius' pipistrelle being present at different wind farms in the region, the study estimates that individually between 16% and 24% of the populations of the three high risk species overlap with existing and approved wind farms, with 50% of this overlap at just 10% of wind farms. This underlines the importance of wind farm placement in determining the likely impact of wind farms on bats, and the disproportionate impact that a small number of wind energy developments could have on these species. The study identified the top 1%, 5% and 10% of the region as being the most sensitive areas; information that can be used in decision making in relation to future wind farm construction. It should be noted that because there is little overlap in the ranges of the three high risk bat species, any steps taken to reduce the risk posed by wind farms at a local scale are most likely to benefit a single species, rather than having broader benefits for the three high risk species.

This study focuses here on making predictions at a 1 km square level using broad-scale habitat, elevation and weather variables. However, because the study has the point locations at which bat detectors were left out to record, an extension to this work could be to consider how bats use the landscape at a finer scale. Connectivity analyses and identification of commuting corridors has been looked at in Roscioni *et al.* (2014) in relation to wind farms, but reliable inference was limited in that study by the availability of data (distribution modelling with just 19 presence-only records). The identification of commuting corridors may be particularly important for guiding finer-scale wind farm placement. Reducing wind farm operation during hours of peak bat activity in high risk areas could also limit the potential for wind farm collision. Noctule and Leisler's bat showed high activity in the first two hours after sunset, after which collision risk would be reduced.

4.2 Insights into bat status in Scotland

Considering the current understanding of the status of the three bat species, for which there are Scottish population estimates for the two *Nyctalus* species only, it is likely that the true populations of these species far exceed the current published estimates in Harris *et al.* (1995) of a few hundred individuals for the whole of Scotland. It is not straightforward to estimate absolute abundance (often referred to as true abundance) from bat recordings, because bats cannot be individually identified from these recordings. However, considering that the 715 1 km squares surveyed in 2016 comprised just 3.4% of the survey area, and that there were 4,327 recordings of Leisler's bat from 224 1 km squares, and 2,101

recordings of noctule from 152 1 km squares, it is likely that the minimum population sizes of Leisler's bat and noctule for the whole of Scotland are in the thousands. This revision holds even if it were assumed that the survey area encompassed the entire Scottish range of the two *Nyctalus* species. Whilst we would not want to infer outside the area for which we have data ourselves, it has been noted that with Leisler's bat recorded on the island of Arran and in adjacent Ayrshire (and nearby Northern Ireland), there is the possibility that this species is also present on the adjacent Kintyre peninsula. In addition, with the distribution of Leisler's bat (in the west of the region) extending to northern-most limit of our survey area, it is very possible, that the distribution of this species extends further north.

Because detection probability is likely to vary markedly between species, differences in the number of recordings between species cannot be straightforwardly interpreted as differences in abundance. For example, using detection distance tables for the Wildlife Acoustics microphone used here at 20°C and relative humidity of 50% (Agranat, 2014), and given an estimate of how loud each species is (Sound Pressure Level in db), we expect that the detection distance of Nathusius' pipistrelle will be about 20 m compared with noctule, which would be detected up to about 40 m. However, indications from the survey data are that Nathusius' pipistrelle was much less abundant than the two *Nyctalus* species, with just 185 recordings from 23 1 km squares. It is likely, considering the migratory status of Nathusius' pipistrelle (Russ *et al.*, 2001) that some records of this species in this survey, particularly at coastal locations, were of migrants. However, at one site close to Stranraer (Dumfries and Galloway) in the southwest of the survey area, male advertisement calls were recorded. These are often given in close proximity to a maternity roost, and suggest the possibility of breeding in this area. It is expected that the minimum whole of Scotland population size of Nathusius' pipistrelle is in the hundreds and, considering the scarcity of male advertisement calls, there are likely to be few maternity colonies in the southern Scotland survey area at least. Because additional records outside the survey area suggest that this species is more widespread in the rest of Scotland than the two *Nyctalus* species (www.bats.org.uk/pages/uk_bats.html#Resident), the abundance of this species is very likely to be higher than the minimum estimate here.

Whilst this work provides support for revising upwards the population estimates for Leisler's bat, noctule and Nathusius' pipistrelle, it does not contradict the original belief that these species are restricted in range, and that a comparatively small area of southern Scotland supports a large part of the populations of each of these species. As such, the findings of this study should not influence the perceived vulnerability of these species, but do indicate that they may be more exposed to wind farms than previously assumed.

4.3 Survey recommendations and limitations

This study made use of an acoustic classifier developed for us by colleagues at Muséum National d'Histoire Naturelle in Paris to help in the processing of large volumes of recordings and to enable an initial assignment of species identities. In order for citizen science projects that generate a large volume of data to operate efficiently it is essential that a large proportion of data processing is automated (Digby *et al.*, 2013). Provided that automatic classifiers consistently discriminate identity, they can remove the influence of variation in volunteer experience and skill, which can have a bearing on detection and identification of some species. This can have particularly serious consequences for analyses of spatial or temporal trends, since volunteer skill may vary in space and / or time. In this study, all recordings were manually inspected (bar those of the two widely recorded pipistrelle species, for which a sample of recordings were checked) regardless of the associated probability of correct classification. These automated classification techniques are still relatively new, so there is currently a need to take a cautionary approach in their use (Russo & Voigt, 2016). Only by critical evaluations of classifiers in real world scenarios, as done here (and see Newson *et al.*, 2015, 2017), will it be possible to improve our understanding of

their limitations, enabling us to make improvements that ultimately, will allow them to be used in a more unsupervised manner. For the long-term monitoring of bats, it will be important to curate datasets of raw recordings in such a way that they can be re-analysed following significant advances in automatic identification, while maintaining links to expert validation to ensure consistency in the semi-automated process.

Whilst the focus of this study has been to provide baseline information relevant to assessment and mitigation of the risks to bats posed by wind farm development, there is clearly an opportunity to maintain and develop the infrastructure and volunteer-base. The value of the data for addressing questions relating to wind farm construction would likely increase, as coverage within the survey area improved, and data collected from repeat visits to the same sites would enable the detection of changes in bat populations, which in turn would feed into an ongoing assessment and conservation priorities for this taxon. More generally this would make a substantial and cost-effective contribution to long-term, large-scale bat monitoring, with the potential to put these data to a wider range of uses than the survey was designed to address. Similar data have been used to describe ecological patterns for a number of bat species and at a variety of spatial scales, including studies of spatial variation in relative abundance, habitat selection, phenology of seasonal and nocturnal activity (e.g. Azam *et al.*, 2015; Millon *et al.*, 2015; Newson *et al.*, 2015; Border *et al.*, 2017). Such a contribution to our understanding of bats would be particularly valuable in Scotland, where levels of volunteer participation in the UK National Bat Monitoring Programme survey are, for most species, insufficient to produce statistically robust country trends (Bat Conservation Trust, 2015). Some of the most remote parts of southern Scotland included in the 2016 survey were covered by paid fieldworkers, and it may be necessary to repeat surveys in at least a subset of these areas, to ensure that future datasets remain representative of the wider survey area.

4.4 Conclusions

As well as contributing to our understanding of bat distribution and activity in southern Scotland, this study illustrates that it is possible to collect presence-absence data at a large spatial scale to provide large-scale representative data to be used for spatial modelling. Increased reliance on presence-absence data generated by this kind of sampling will lead to an improvement in the quality of bat data, and in the reliability of the conclusions drawn from them. This is particularly important when these conclusions feed into conservation management and regulation, as these can impact not only on the conservation status of bats but also on decisions made about economic development and the attitude of society towards conservation.

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ANNEX 1. REQUIREMENTS OF CENTRES HOSTING BAT DETECTORS

1. Evenly spaced, close to main roads, and areas with people / potential volunteers. Ideally away from the edge of the target area to maximise accessibility and the number of potential volunteers from the surrounding area (originally looked for 15 centres).

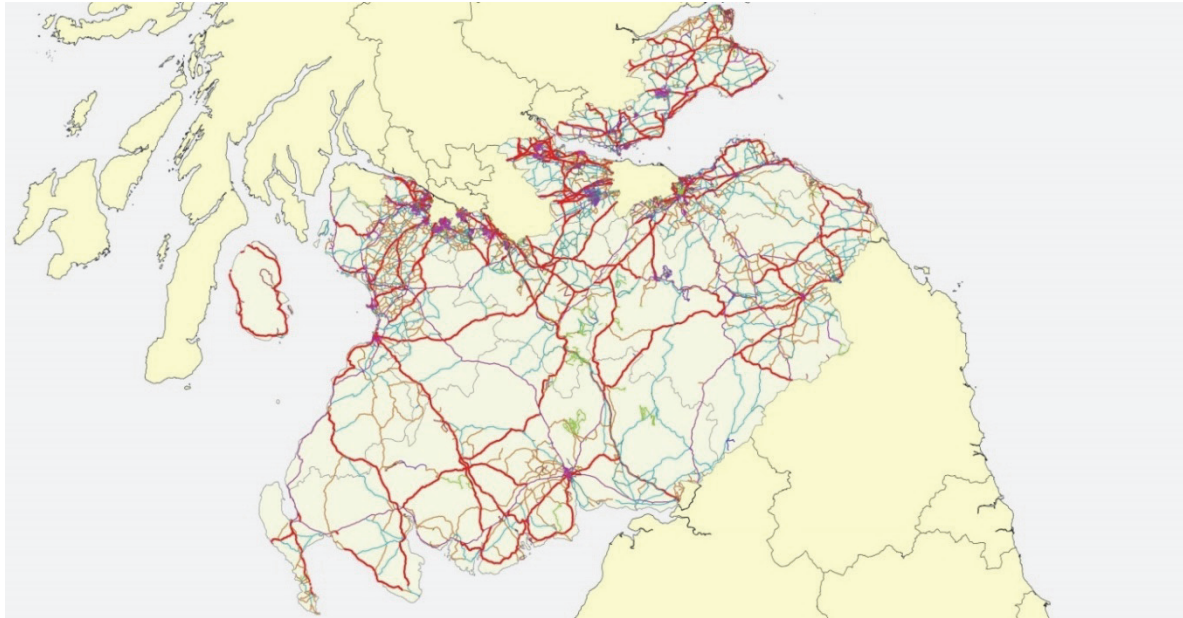


Figure 1a. Road network where thicker lines denote primary roads or motorways.

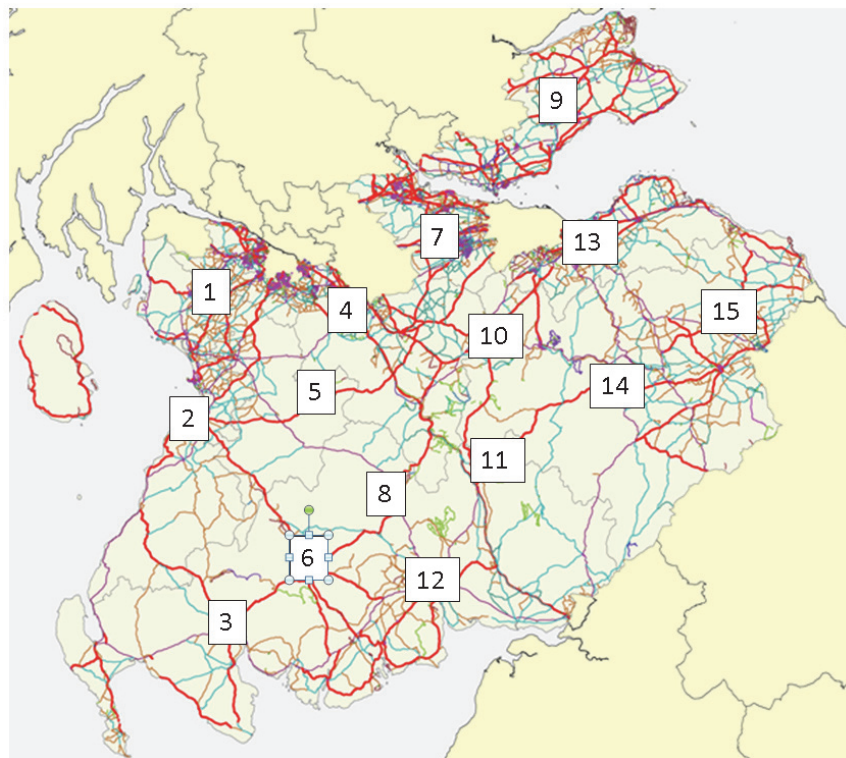


Figure 1b. Road network and the first attempt to approximately locate 15 centres based on road network only.

- Ideally centres hosting a detector should be open to the public six or seven days a week with good opening hours. Priority was given to centres where staff, volunteers or members would be interested in using the equipment themselves / promoting the project, and ideally include a range of organisations and local libraries.**

Note: to give an idea of the maximum target level of uptake possible - if a detector were to be fully booked out from a centre for the whole season (May to September), it would be possible to survey about 40 1km squares.

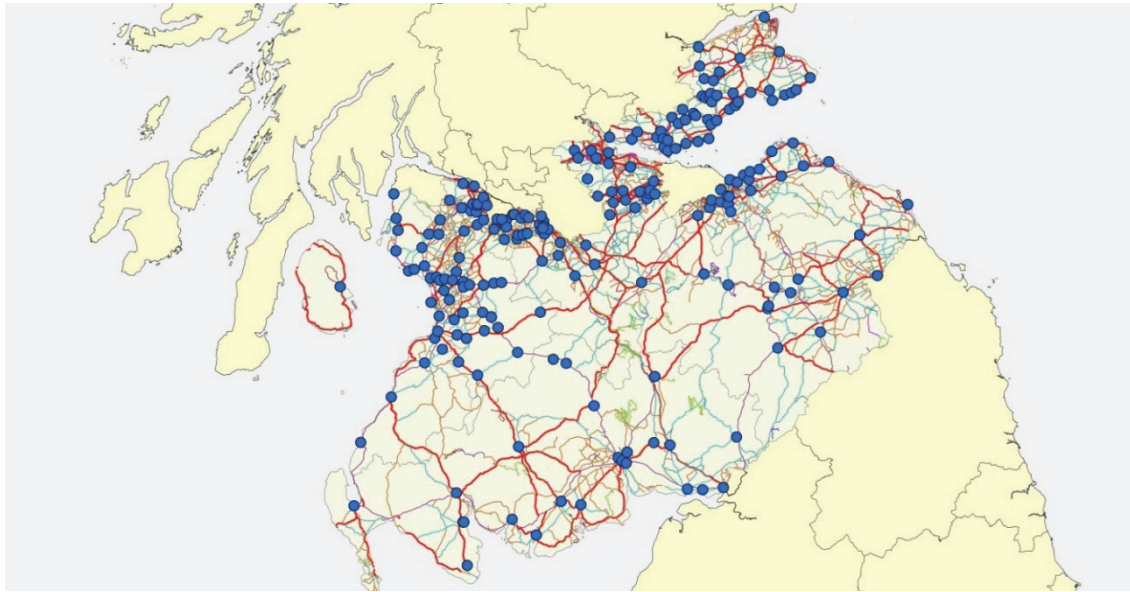


Figure 1c. Potential centres - local libraries (not all have good opening times and days).

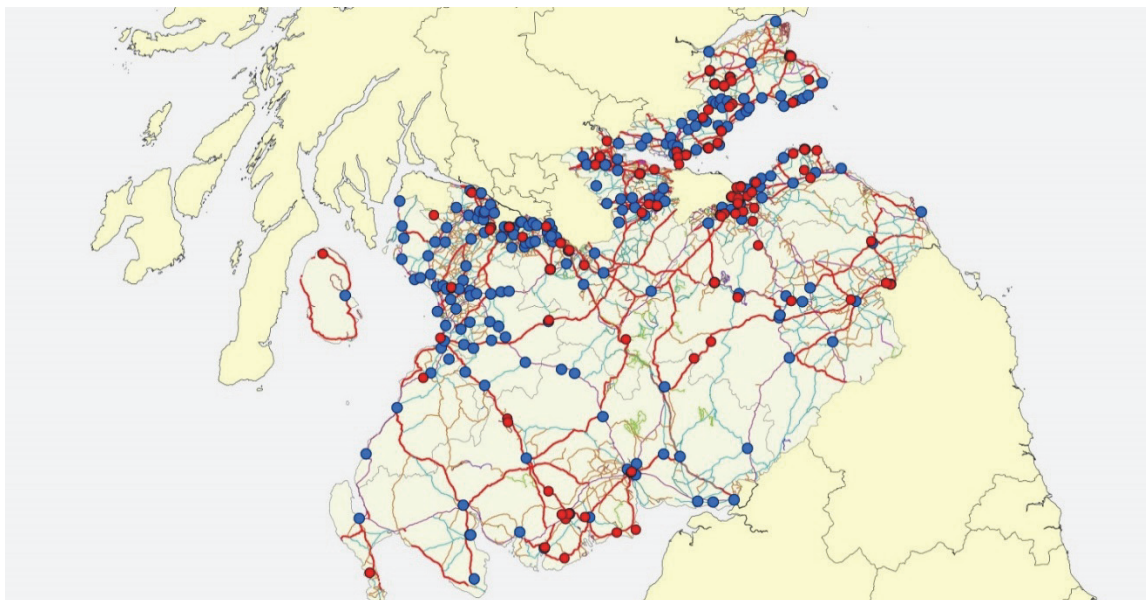
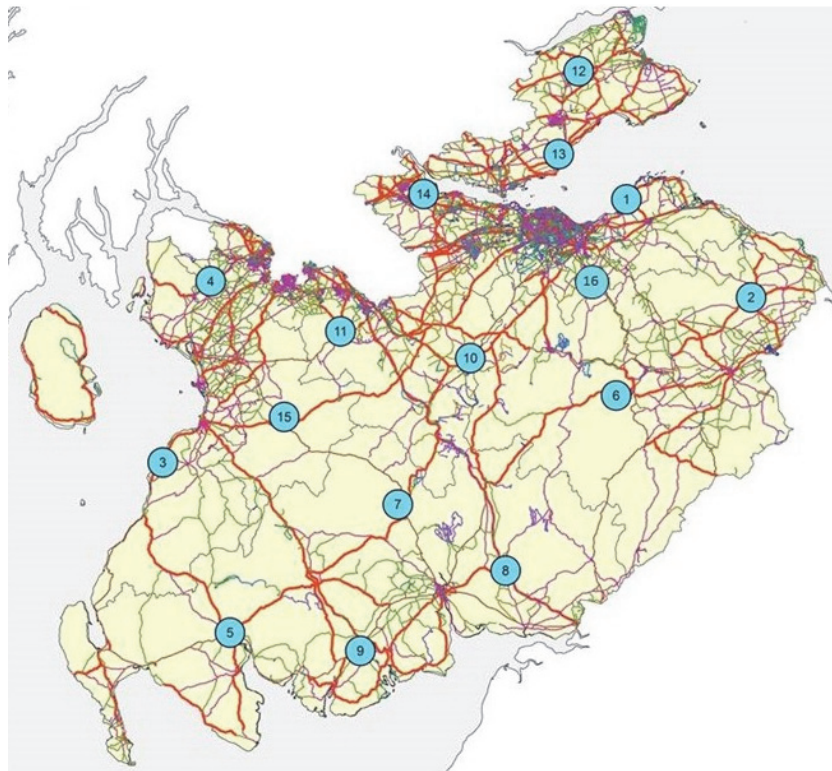


Figure 1d. Potential centres – (NTS properties, castles, museums, community centres etc.- unlikely to be exhaustive in term of possibilities).



1. SOC, Aberlady
2. Duns library
3. NTS, Culzean Castle
4. RSPB, Lochwinnoch
5. Newton Stewart library
6. Bowhill House
7. Drumlanrig Castle
8. Lockerbie library
9. NTS, Threave Castle
10. Biggar Museum
11. Strathaven library
12. Scottish Deer Centre
13. Stranraer library
14. SWT, Urban Wildlife Cent
15. Cumnock library
16. TWIC, Vogrie

Figure 1e. The final choice of Bat Monitoring Centres in southern Scotland (www.batsurvey.org/bat-monitoring-centres/). This is a network of centres from which anyone could borrow a passive detector for a few days.

ANNEX 2. BAT CALL MEASUREMENTS

Call measurements extracted and used by the random forest classifier in Step 1 of the recording validation process are shown below. Measurements with the prefix CM, CS, CN, CO and CO2 relate to linear descriptors of each detected sound event (DSE), and correspond to the elements that contain the maximum amplitude within each time window, the starting edge of the DSE, the upper frequency edge of the DSE, the lower frequency edge of the DSE and the first elements forming a local amplitude maximum on each frequency band respectively. The call measurements are described in more detail in Bas & Bas (2016) Tadarida-L GitHub repository https://github.com/YvesBas/Tadarida-L/blob/master/Manual_Tadarida-L.odt

Measurement	Description of call measurement
Amp1	Average amplitude among time windows within 1st quarter of DSE
Amp2	Average amplitude among time windows within 2nd quarter of DSE
Amp3	Average amplitude among time windows within 3rd quarter of DSE
Amp4	Average amplitude among time windows within last quarter of DSE
BW	Maximum frequency - minimum frequency
CM_5dBBW	Frequency of farthest point before frequency of maximum amplitude and less than 5 dB below peak amplitude
CM_5dBDur	Time difference between 5dBBF point and 5dBAF point
CM_ELB2POS	The same as ELBPOS, but bend id determined by global slopes before and after bend
CM_ELB2SB	Slope of the part of the line ending at the first bend identified by global slopes (ELB2POS)
CM_ELBPOS	Duration of line to the point where the line makes a "bend" divided by the duration of the line before the first eventual ascent of the line. A "bend" is defined as the first element x where the slope ratio between 3 elements before and 3 elements after x is under 0.6
CM_ELBSB	Slope of the part of the line ending at the first bend determined by local slopes (ELBPOS)
CM_EnSI	End Slope
CM_FIF	Frequency of the flattest part of the line (calculated on 5 consecutive time windows). If several frequencies get a 0 slope, FIF takes the value of longest null slope.
CM_FISI	Slope at the FIF point
CM_LoSI	Slope of the lower part of the line (below HCF - frequency of the point of maximum change of slope before frequency of flattest part of the line)
CM_RAFE	Ratio of time windows average frequency before the master point and after + ratio of the time windows average amplitude before master point and after
CM_RAFFP3	Ratio of the sums of time windows average amplitude weighted by amplitude (of the point of the line), before and after master point
CM_SAMP	Slope between the master point and the end of the line
CM_SBAR	SBMP/SAMP
CM_SBMP	Slope between the beginning of the line and the master point
CM_SDCL	Cumulated changes in frequency slope of the part of the line before the first eventual ascent succeeding the master point
CM_SDCLOP	Cumulated changes in frequency slope of the "main slope" of line. The "main slope" is defined as the part of the line which contains the master point and has no change of slope direction.
CM_SDCLR_DNP	SDCL divided by the number of changes of direction of the line (positive / negative) / Dur
CM_SDCLROP	SDCLOP / Dur
CM_SDCLRWB	SDCLWB / Dur
CM_SDCLRXYOP	SDCLWB divided (a second time) by duration
WB	
CM_SDCR	Cumulated changes in frequency slope / Dur
CM_SDCRXY	(SDCR / BW) / Dur
CM_Slope	Modulation Slope

CM_StSI	Start Slope
CM_THCF	Time of the point which gave "HCF", where HCF is the frequency of the point of maximum change of slope over/before FIF (in fraction of line duration)
CM_UpSI	Slope of the upper part of the line (over HCF)
CN_EnSI	End Slope
CN_FIF	Frequency of the flattest part of the line (calculated on 5 consecutive time windows). If several frequencies get a 0 slope, FIF takes the value of longest null slope.
CN_FPSI	Slope at the point of maximum amplitude
CN_LoSI	Slope of the lower part of the line (below HCF)
CN_SDCR	SDC / Dur
CN_Slope	Modulation Slope
CN_StSI	Start Slope
CN_THCF	Time of the point which gives "HCF" (in fraction of line duration)
CN_UpSI	Slope of the upper part of the line (over HCF)
CO_EnSI	End Slope
CO_FPSI	Slope at the point of maximum amplitude
CO_LoSI	Slope of the lower part of the line (below HCF)
CO_SDCR	SDC / Dur
CO_Slope	Modulation Slope
CO_StSI	Start Slope
CO_THCF	Time of the point which gives "HCF" (in fraction of line duration)
CO_UpSI	Slope of the upper part of the line (over HCF)
CO2_5dBBW	Difference between 5dBBF and 5dBAF
CO2_5dBDur	Time difference between 5dBBF point and 5dBAF point
CO2_EnSI	End Slope
CO2_FISI	Slope at the FIF point
CO2_FPkD	Difference of _FPk with previous detected sound event
CO2_ISlope	1/Slope
CO2_LoSI	Slope of the lower part of the line (below HCF)
CO2_SDCR	SDC / Dur
CO2_Slope	Modulation Slope
CO2_StSI	Start Slope
CO2_THCF	Time of the point which gives "HCF" (in fraction of line duration)
CO2_TPk	Time of amplitude peak (in fraction of line duration)
CO2_UpSI	Slope of the upper part of the line (over HCF)
CS_ELB2POS	The same as ELBPOS, but the bend id determined by the global slopes before and after the bend
CS_ELB2SB	Slope of the part of the line ending at the first bend identified by global slopes (ELB2POS)
CS_ELBPOS	Duration of line to the moment where the line makes a "bend" divided by the duration of the line before the first eventual ascent of the line. A "bend" is defined as the first element x where the slope ratio between 3 elements before and 3 elements after x is under 0.6
CS_ELB2SB	Slope of the part of the line ending at the first bend determined by local slopes (ELBPOS)
CS_EnSI	End Slope
CS_FIF	Frequency of the flattest part of the line (calculated on 5 consecutive time windows). If several frequencies get a 0 slope, FIF takes the value of longest null slope.
CS_FPSI	Slope at the point of maximum amplitude
CS_LoSI	Slope of the lower part of the line (below HCF)
CS_SDCLOP	Cumulated changes in frequency slope of the "main slope" of the line. The "main slope" is defined as the part of the line which contains the master point and has no change of slope direction.
CS_SDCLR_DNP	SDCL_DNP / Dur
CS_SDCLR0P	SDCL0P / Dur
CS_SDCLRY_DNP	SDCLR_DNP divided by frequency amplitude
CS_SDCLRY0P	SDCL0P divided by frequency amplitude of the pan

CS_SDCLWB	Cumulated changes in frequency slope of the part of the line between the middle between start and master point and the first eventual ascent after master point
CS_SDCR	SDC / Dur
CS_SDCRXY	SDCRY / Dur
CS_Slope	Modulation Slope
CS_StSl	Start Slope
CS_THCF	Time of the point which gives "HCF" (in fraction of line duration)
CS_UpSl	Slope of the upper part of the line (over HCF)
CVamp	Coefficient of variation of Amp1, Amp2, Amp3 and Amp4.
Dbl8	Amplitude difference between the detected sound event and low-frequency noise (=everything below 8kHz)
Dur	detected sound event duration
EnStabLg	Average change of amplitude between adjacent elements on a square of 21 x 21 elements around the master point (~6 ms - ~11kHz)
EnStabSm	Average change of amplitude between adjacent elements on a square of 7 x 7 elements around the master point (~2 ms - ~5kHz)
FileDur	File duration
FMin	Minimum frequency
HeiEM	Number of time windows within the detected sound event, whose mean amplitude exceeds 80% of the mean amplitude of the master point time window
HeiEMT	Number of time windows, after master point and within the detected sound event, whose mean amplitude exceeds 80% of the mean amplitude of the master point time window
HeiET	Number of time windows within the detected sound event, whose cumulated amplitude exceeds 80% of the cumulated amplitude of the master point time window
HeiRM	HeiEM divided by total number of time windows
HeiRMT	HeiEMT divided by total number of time windows
HeiRT	HeiET divided by total number of time windows
HeiRTT	HeiETT divided by total number of time windows
HetCMC	Proportion of consecutive time windows where average amplitude slope changes
HetCMD	Average difference of average amplitude between each pair of consecutive time windows
HetCMfP	Density of local average amplitude maxima among time windows
HetCTC	Proportion of consecutive time windows where cumulated amplitude slope changes
HetCTD	Average difference of cumulated amplitude between each pair of consecutive time windows
HetCTfP	Density of local cumulated amplitude maxima among time windows
HetPicsMABD	3rd quartile of intervals between local average amplitude maxima among time windows
HetPicsMALD	1st quartile of intervals between local average amplitude maxima among time windows
HetPicsMRBLD	HetPicsMABD / HetPicsMALD
HetPicsTABD	3rd quartile of intervals between local cumulated amplitude maxima among time windows
HetPicsTRLBD	HetPicsTABD / HetPicsTALD
HetX	Proportion of change of amplitude slope, among each set of 3 consecutive elements along the time axis.
HetYr	Idem HetY but restricted to the 7 time windows around the master point.
Hlo_Ampdif	Same parameters for potential lower harmonic
Hlo_PosEn	Same parameters for potential lower harmonic
Hup_AmpDif	Amplitude difference between the detected sound event and its potential upper harmonic
Hup_RFMP	Ratio of FreqMP between "potential harmonic" (see definition above) and the detected sound event
Int25	1st quartile of intervals between detected sound events of similar frequency

	bands (i.e. whose master point is within +/- 2 frequency bands around the current detected sound event master point, corresponding to an approx. 3 kHz interval)
Int75	3rd quartile of intervals between detected sound events of similar frequency bands (i.e. whose master point is within +/- 2 frequency bands around the current detected sound event master point, corresponding to an approx. 3 kHz interval)
LgIntDev	Median deviation from Int75 among the half largest "similar frequency" (see Int75 above) intervals
NextMP1	Time difference between master points of the detected sound event and the next one
NextMP2	Time difference between master points of the detected sound event and the next one whose master point is between FMax and FMin, and conversely its FMin-FMax interval contains FreqMP of the current detected sound event
NoiseDown	Average amplitude among the elements neighbouring the detected sound event on the top on a 3-element width (approx. 2 kHz above)
NoiseNext	Average amplitude among the elements neighbouring the detected sound event on the right on a 3-element width (approx. 1 ms after)
NoisePrev	Average amplitude among the elements neighbouring the detected sound event on the left on a 3-element width (approx. 1 ms before)
NoiseUp	Average energy among the elements neighbouring the detected sound event on the bottom on a 3-element width (approx. 2 kHz below)
PosMP	Time Position of the master point (in fraction of the detected sound event duration)
PrevMP1	Time difference between master points of the detected sound event and the previous one
PrevMP2	Time difference between master points of the detected sound event and the previous one whose master point is between FMax and FMin, and conversely its FMin-FMax interval contains FreqMP of the current detected sound event
PrevSt	Time difference between starts of the detected sound event and the previous one
RAHE4	Ratio of average amplitude between the first quarter of the detected sound event and the following. The first six time windows are more weighted. For the second part, only the part not exceeding the quarter of the length of the first part after master point is counted
Ramp_1_2	The same for half frequency
Ramp_2_1	Ratio of average amplitude between the elements whose frequency is twice that of the detected sound event and those of the current detected sound event
Ramp_2_3	The same for frequency multiplied by 2/3
Ramp_3_1	The same for triple frequency
Ramp_3_2	The same for frequency multiplied by 1.5
RAN_1_2	The same for half frequency
RAN_2_1	Ratio of cumulated energy between the elements surrounding (3 elements width) those whose
RAN_2_3	The same for frequency multiplied by 2/3
RAN_3_1	The same for frequency multiplied by 3
RAN_3_2	The same for frequency multiplied by 1.5
RAN_4_3	The same for frequency multiplied by 4/3
RInt1	Int75 / Int25
RIntDev1	LgIntDev/SmlntDev
SmlntDev	Median deviation from Int25 among the half smallest "similar frequency" (see Int25 above) intervals
Stab	An index of amplitude stability around the master point: average amplitude change between neighbouring elements within the detected sound event, inversely weighted by distance from Master Point
StTime	Start time of the detected sound event (detected sound event)
VarInt	IntDev/MedInt
VarLgInt	LgIntDev/Int75

VarSmInt	SmIntDev/Int25
VBDPPicsM	VBDPicsM / HetPicsMABD
VBDPPicsT	VBDPicsM / HetPicsMABD
VLDPPicsM	VLDPicsM / HetPicsMALD
VLDPPicsT	VLDPicsT / HetPicsMALD

ANNEX 3. VALIDATION OF BAT RECORDINGS

Important call parameters used in Step 3 of the recording validation process to manually check species identity based on call parameters in Russ (2012) and Barataud (2015) and adapted from Newson et al. (2015). For some species (e.g. brown long-eared bat) identification is more straightforward, whilst for other species, (e.g. the *Myotis* bats), there is overlap, such that a high proportion of recordings are assigned to genus only.

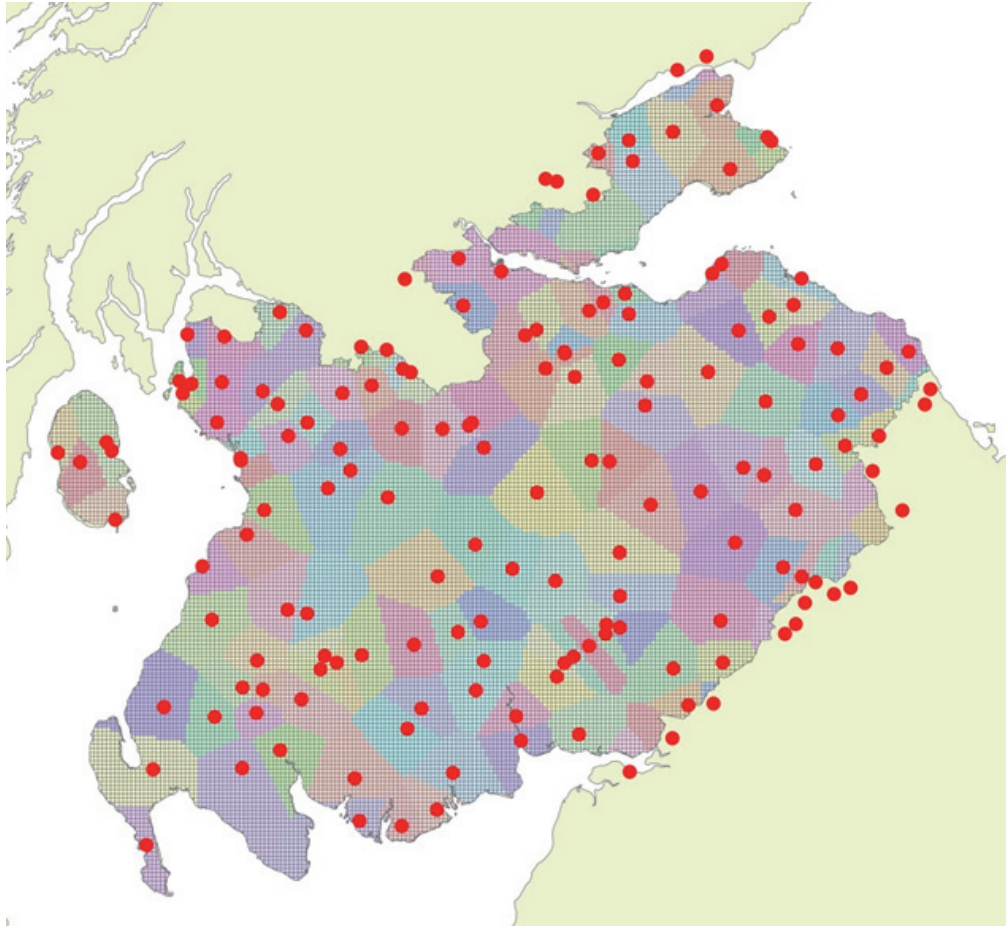
Species	Species code	Main confusion species	Most important call parameters for species identification ¹
Daubenton's bat, <i>Myotis daubentonii</i>	Mdau	Mmys /Mbra (and Mnat)	Calls often sigmoidal in shape Start frequency (rarely) >100 kHz End frequency (typically) about 25 kHz Often slight kink or bend at heel of call at about 40 kHz
whiskered / Brandt's bats, <i>Myotis mystacinus</i> / <i>M. brandtii</i>	Mmys/Mbra	Mdau (and Mnat)	Start frequency (commonly) >100 kHz End frequency (typically) > 30 kHz Sometimes slight kink at knee of call at >35 kHz In open areas calls can be similar to Mdau
Natterer's bat, <i>Myotis nattereri</i>	Mnat	Other <i>Myotis</i> bats	Most distinctive <i>Myotis</i> in study area Very high bandwidth End frequency (often) <20 kHz Short duration calls – (often) over 100 kHz change in frequency over 1 ms No kink at knee or heel of call in closed or semi-closed habitat is distinctive
noctule, <i>Nyctalus noctula</i>	Nnoc	Nlei (and Eser)	Two main call types: an FM / qCF ² call and qCF call. FM / qCF call peak frequency of about 24 kHz, call duration about 14 ms qCF call peak frequency of about 19 kHz, call duration about 22 ms Call types (often) produced alternatively
Leisler's bat, <i>Nyctalus leisleri</i>	Nlei	Nnoc (and Eser)	As noctule two main call types FM / qCF call peak frequency of about 27 kHz, call duration about 8 ms qCF call peak frequency of about 23 kHz, call duration about 17 ms Calls types (often) produced alternatively
Nathusius' pipistrelle, <i>Pipistrellus nathusii</i>	Pnat	Ppip	Typical hockey-stick shaped <i>Pipistrellus</i> call End frequency of all calls <40 kHz
brown long-eared bat, <i>Plecotus auritus</i>	Paur	None (<i>Pipistrellus</i> social calls – but not regular series of calls)	Normally distinctive with two harmonics, the first starts around 55 kHz and ends about 24 kHz and second starts around 73 kHz and ends about 33 kHz

¹ See Russ (2012) and Barataud (2015) for a more detailed description and comparison of call parameters.

² FM = frequency modulated, qCF quasi-constant frequency (see Russ 2012, section 2.3.3 for a full description of call types).

ANNEX 4. DISTRIBUTION OF WEATHER STATIONS

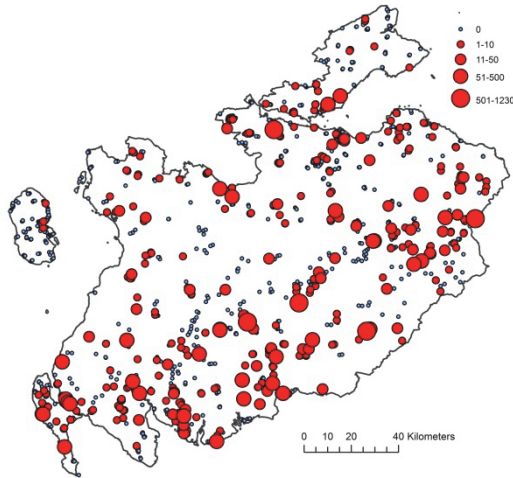
Distribution of weather stations and how 1 km squares in southern Scotland are assigned to the closest weather station. Hourly minimum temperature, precipitation and wind speed recorded were extracted (MIDAS Land and Marine Surface Stations Data – available from <http://catalogue.ceda.ac.uk/uuid/220a65615218d5c9cc9e4785a3234bd0>).



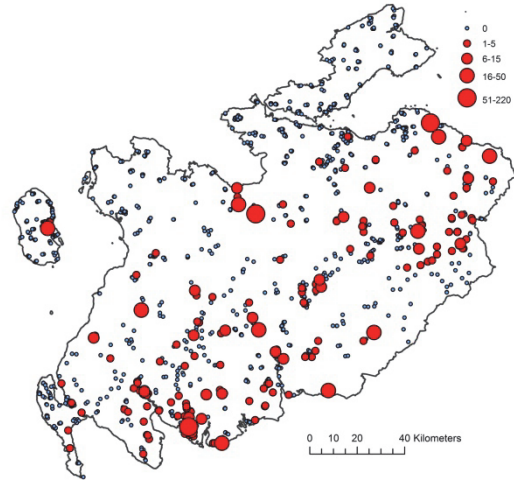
ANNEX 5. MAPS OF BAT ACTIVITY

Number of recordings / night) as a proxy for abundance.

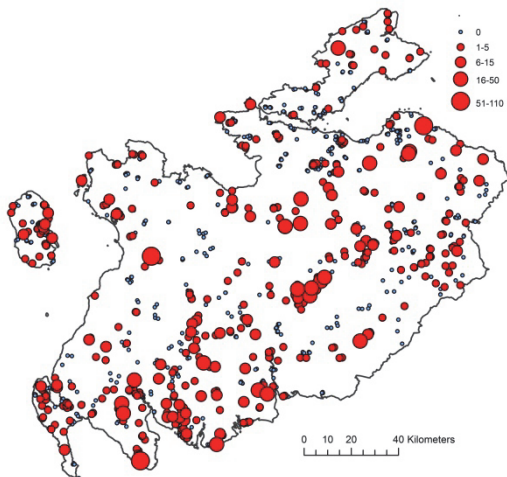
Daubenton's bat, *Myotis daubentonii*



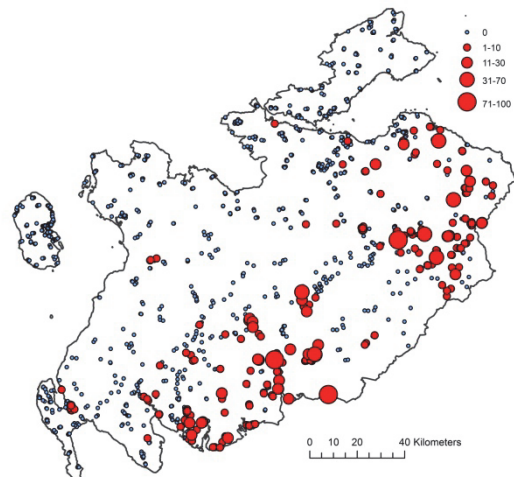
whiskered / Brandt's bats, *Myotis mystacinus* / *M. brandtii*



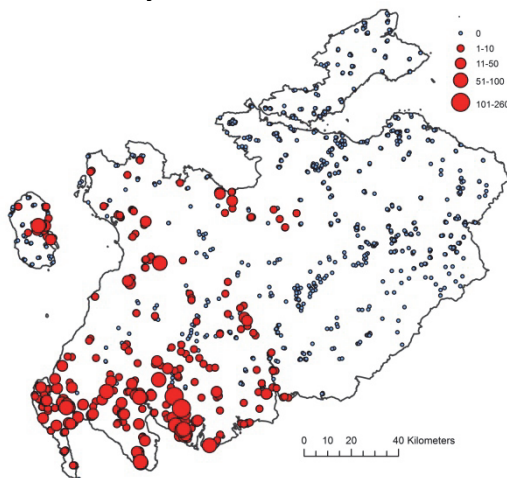
Natterer's bat, *Myotis nattereri*



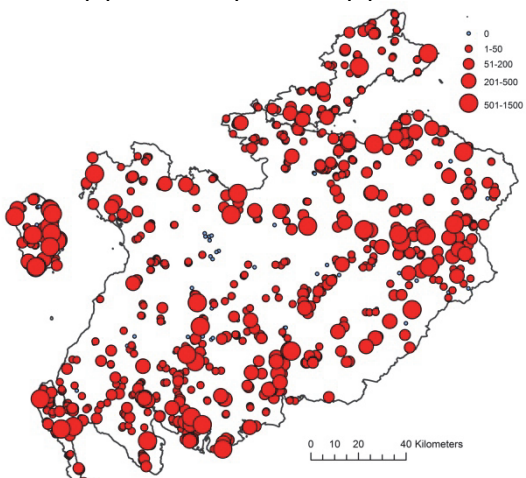
noctule, *Nyctalus noctula*



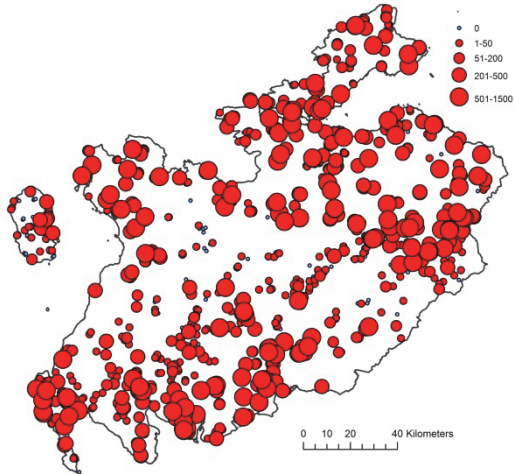
Leisler's bat, *Nyctalus leisleri*



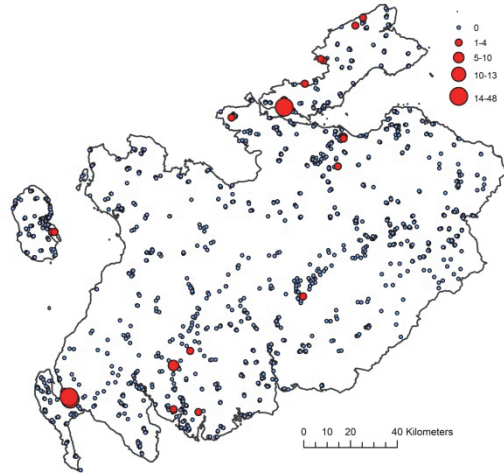
common pipistrelle, *Pipistrellus pipistrellus*



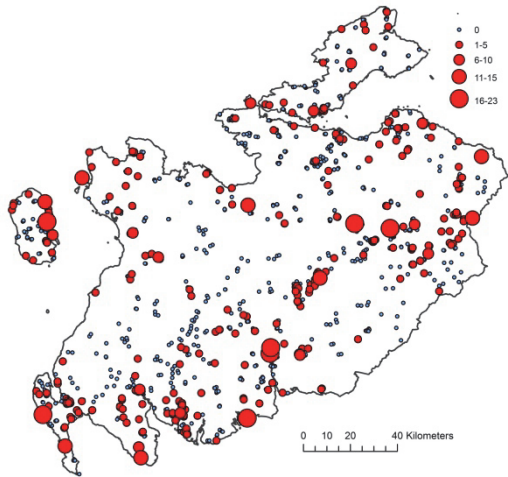
soprano pipistrelle, *Pipistrellus pygmaeus*



Nathusius' pipistrelle, *Pipistrellus nathusii*



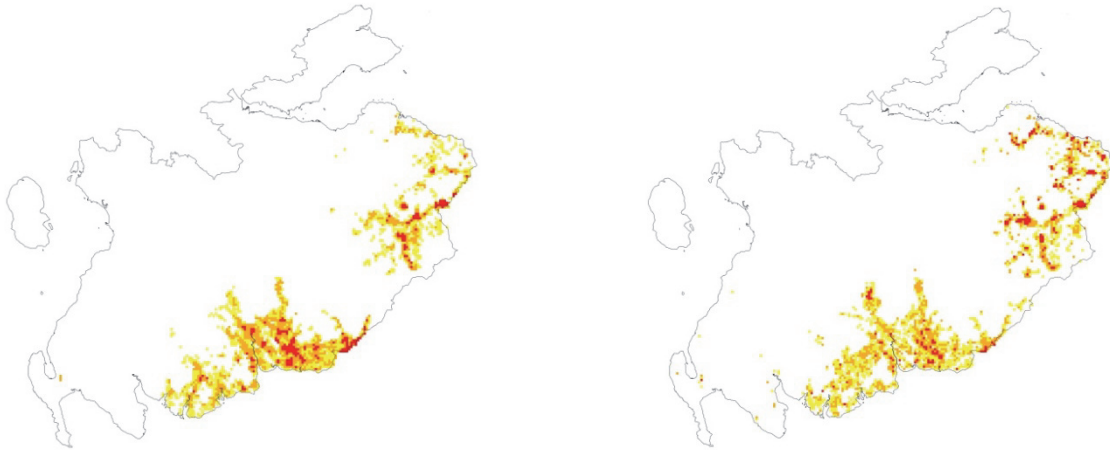
brown long-eared bat, *Plecotus auritus*



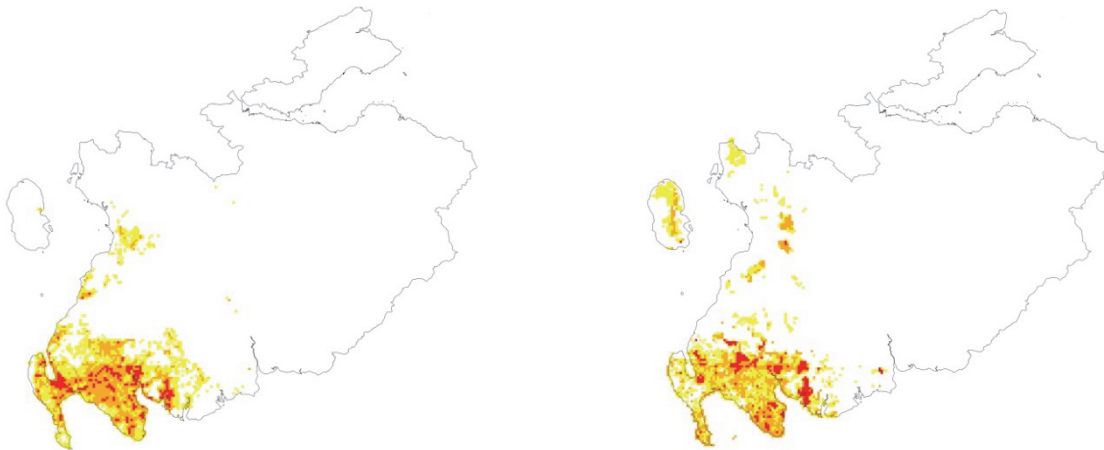
ANNEX 6. HOTSPOTS FOR NOCTULE, LEISLER'S BAT AND NATHUSIUS' PIPISTRELLE

Maps identifying the top 1%, 5% and 10% (red, orange and yellow) 1km squares in the survey area for noctule, Leisler's bat and Nathusius' pipistrelle based on ordered predictions of occurrence probability (left) and activity as a proxy for abundance (right).

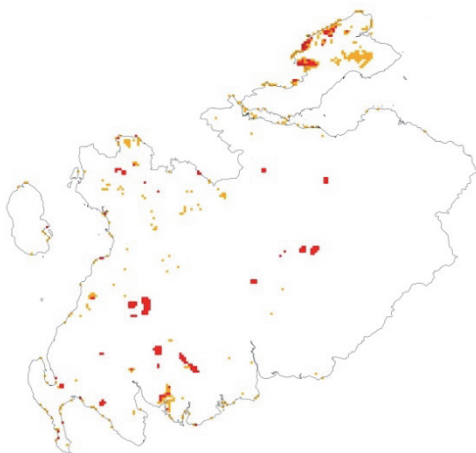
noctule, *Nyctalus noctula*



Leisler's bat, *Nyctalus leisleri*



Nathusius' pipistrelle, *Pipistrellus nathusii*



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