Habitat associations of nightjar
*Caprimulgus europaeus*
breeding on heathland
in England

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Executive Summary

The British nightjar population declined throughout much of the 20th century, due mainly to loss of
heathland, the nightjar’s traditional breeding habitat. The population has increased in numbers in
recent decades. However, this increase has not been uniform across the range, and the breeding range
itself has shown only marginal recovery during the period of population increase. Here, we present
the results of a study using data from the 2004/05 national survey, plus various habitat datasets, to
investigate habitat associations of nightjars breeding on heathland in England at two spatial scales:
firstly at the heathland patch level, and secondly at the territory level. These analyses are intended to
help inform heathland restoration for nightjar.

Nightjars were present on 327 heathland patches in England during the 2004/05 survey. These ranged
in size from 0.2 ha to 2 874 ha, or 28.7 km² (mean = 1.1 km², S.D. = 2.9 km²), although 100 patches (31
%) were smaller than 0.1 km² and 261 (81 %) smaller than 1 km² in size. The number of nightjar
breeding territories on these patches ranged from 1 to 105 (mean = 4.8, S.D. = 9.9), but 159 patches (49
%) contained just one nightjar territory, and 288 (88 %) contained ten or fewer. The minimum size
containing more than one nightjar territory was 1.5 ha. The median density of nightjars on the
heathland patches was 9.8 males per km². The range of densities was 0.08 males per km² to 540 males
per km², although this maximum value is an artefact of one nightjar on an unusually small patch of
heathland and is not biologically meaningful.

The effects of habitat fragmentation were investigated, in terms of patch size and isolation, and were
found to affect both occupancy of patches and densities on occupied patches. Occupied patches were
significantly larger than unoccupied patches. The likelihood of a patch being occupied increased with
increasing area of heathland in the vicinity (area within 10 km, excluding the area of the patch itself).
There was also an effect of number of heathland patches within 10 km, but this was dependent upon
the area effect. For patches with a smaller amount of heathland in the vicinity, it was better for this to
be in a larger number of patches. It is suggested this could be due either to correlation with area of
heathland within 10 km, or increased dispersal ability through a ‘stepping stone’ effect. For patches
with a larger area of heathland in the vicinity, likelihood of occupancy was increased where the
heathland was in fewer, i.e. larger, patches. Nightjar density increased with increasing connectivity to
other patches, particularly occupied patches. Overall, 40 % of the occupied heathland patches were
less than 100 m, and 86 % less than 500 m, from the nearest other occupied patch. There was a weak
effect of decreasing density with increasing patch size. However, the average size of heathland patch
in England is 0.17 km², and the average size of a patch occupied by nightjars is 1.06 km², thus
heathland restoration for nightjars should be aimed at increasing mean patch size. It was not possible
to investigate the effect of shape of heathland patch on occupancy or nightjar density separately, as
shape and size of patch were very highly correlated.

The effect of patch size and habitat types within the foraging range of territory locations was
compared with that of random points in suitable habitat. The area surrounding territory locations
contained more coniferous woodland on average than random points, and there was also a quadratic
relationship with broad-leaved woodland. These can both be explained in terms of nightjar nesting in
clearings in planted forests, usually coniferous forests, which may contain a small amount of broad-
leaved woodland, or, more unusually nesting in broad-leaved woodlands themselves. Territory
locations also had more agricultural land within the surrounding area than random points. Reasons
for this are unclear, and warrant further investigation, preferably by radio-telemetry. Given the
negative effects of urban development and disturbance on breeding nightjars found by other studies,
it is rather surprising that no effect was found of the area of urban land within 2 km on likelihood of
occupation. This could be as urban and suburban land were lumped, due to the relatively small
amount of urban land on average within 2 km of territories. Distance to edge of heathland patch did...
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...not differ for territory locations and random points, but in smaller patches (< 1 km²), territory locations were further from the edge than were random points, and approximately half of all occupied patches were this size.

The results support the current approach of recreating heathland close to other heathland and populations of nightjar, increasing mean patch size, and reducing the isolation of existing patches where they are fragmented. In areas with less heathland, the creation of ‘stepping stones’ of suitable habitat to facilitate dispersal between patches may be beneficial, where it is not possible to join patches.
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Introduction

The British nightjar population declined in both numbers and range throughout much of the 20th century, mainly as a result of loss of heathland, its traditional nesting habitat (Morris et al., 1994). There has been a massive loss of lowland heathland over the last two centuries (e.g. declines from approximately 40 000 ha to 5 000 between 1750 and 1987 in Dorset: Webb and Haskins, 1980; Webb, 1990; declines of 88 % since the 1880s in the Brecklands of East Anglia: Tate, 1989). Much of this loss was to forestry, but large areas have also been lost to arable cultivation, building development, and more recently scrub invasion due to lack of management (Webb and Haskins, 1980).

The nightjar population has increased in recent decades (Morris et al., 1994; Conway et al., 2007), largely due to increased availability of open areas within planted forests (Morris et al., 1994). However, this increase has not been uniform across the nightjar’s range, and the breeding range itself has shown only marginal recovery during the period of population increase (Conway et al., 2007; Langston et al., 2007a). The nightjar is a species of high conservation concern in the UK (Gregory et al., 2002), a priority species under the UK Biodiversity Action Plan (Anon., 1998), and is listed on Annex 1 of the EU Birds Directive (79/409/EEC), thus requiring the implementation of appropriate measures for population recovery and conservation.

In recent years, there has been extensive management on many heathland sites aimed at reducing the cover of dense scrub and pine and restoring areas of open, heathy communities (e.g. the RSPB Dorset Heathland Project, which has been running since 1992). Lake (2004) found that sites where more management was taking place in Dorset showed greater increases in nightjar numbers between 1992 and 2004. The population is now concentrated in areas of lowland heath and recently felled or restocked ground within conifer forests in the south and east of England (Morris et al. 1994; Conway et al., 2007; Langston et al., 2007a).

Despite recent population increases, the long-term outlook for the nightjar remains uncertain, with heathland sites still under threat from development, notably housing and road schemes on their margins, and degradation due to lack of management and recreational pressure. A continuing effort is needed to conserve and restore these sites. Whilst it is important that forests and woodlands are managed sympathetically for nightjar, heathland is particularly important in their stronghold of southern England.

Here, we investigate the habitat associations of nightjars breeding on heathland in England, to derive management recommendations, and to help target heathland re-creation. We do this by examining data from the 2004/05 national survey at two spatial scales: the heathland patch and the territory. Specifically, we investigate the effects of fragmentation (patch size and isolation) on the occupancy of heathland patches by nightjars and nightjar density at occupied patches, and the effect on location of territories of surrounding habitat types, patch size and shape, and distance to edge of the patch.

Methods

Nightjar data consisted of territory locations from the 2004 national survey, based on locations of churring males (see Conway et al., 2007 for full survey methodology), plus a small number of additional locations from Sites of Special Scientific Interest (SSSIs) surveyed in 2005 (Conway and Henderson, 2005; Goodyer and Kirby, 2005). These are hereafter referred to as the ‘2004/05 national survey’. The GIS programmes MapInfo Professional version 7.8 (MapInfo, 2000), ArcView 3.2 and ArcGIS 9.1 were used. The RSPB’s Heathland Extent and Potential (HEaP) database (RSPB, 2007) has mapped all heathland patches in England, and this was plotted, along with other habitat data, in
order to extract information at the heathland patch and territory level. Statistical models were run in SAS (SAS, 2003).

The effect of fragmentation on nightjar distribution was investigated in two ways, firstly its effect on the probability of a heathland patch being occupied, and secondly on the density of nightjars on occupied patches. This two-stage approach is often recommended as a way of resolving problems associated with datasets containing multiple zeros, as would be the case, for example, if count was used (Welsh et al., 1996; Martin et al., 2005).

Fragmentation of habitat has two effects on the remaining patches; by decreasing patch size, and increasing isolation of existing patches. Some studies combine these two facets of fragmentation (Bullock and Webb, 1995; Van den Berg et al., 2001; Liley and Clarke, 2003), partly due to the correlation between the two in some areas (Bullock and Webb, 1995). Here, the two were not highly correlated, and effects of patch size and isolation were investigated separately.

The second analyses were at the territory level, and involved comparing locations of territories with those of random points in order to investigate the effects on locations of territories of patch size and shape, distance to edge of patch, and surrounding (i.e. potential foraging) habitat.

Analysis at the heathland patch level

Effect of patch size and isolation on likelihood of a heathland patch being occupied

The effect of patch size on likelihood of occupation was investigated by comparing sizes of occupied and unoccupied patches using Wilcoxon tests (Snedecor and Cochran, 1980), overall and separately by region. Forestry Commission ‘Forest Districts’ were used to categorise regions, in these and other analyses, due to the suitability of spatial scale, and in order to correspond to other analyses being conducted on nightjar in planted forests (Figure 1). Nightjars were present in six of these regions, but populations in Sherwood and Lincolnshire and the West Midlands were of less than 50 territories, so these were not included when analyses were conducted separately by region.

Models were run to investigate the effects of fragmentation, with presence or absence of nightjars on heathland patches specified as the dependent variable. This was modelled as a function of area of surrounding heathland (excluding the area of the patch in question), and number of surrounding heathland patches, denoted by variable $N_i$, within 10 km of the focal patch. Number of patches was defined as a continuous variable, whereas area was included as a three-level fixed factor, $\text{Area}_{k}$: <10 km$^2$, 10 km$^2$ to 20 km$^2$ and >20 km$^2$. This was for ease of interpreting any interaction between the two effects. The interaction between the two terms was also included. In order to account for possible effects of spatial autocorrelation (i.e. pseudoreplication due to the overlap of 10 km buffers from nearby heathland patches) generalised linear mixed models (GLMMs) with binomial distribution and logit link, incorporating a spatial covariance structure were run. Analysis was conducted using the PROC GLIMMIX procedure in SAS, with the eastings and northings (from the Ordnance Survey National Grid) of the central point of each patch specified within the repeated measures command, using an exponential spatial model structure (Littel et al., 1996; see Sim et al., 2007 for example). Due to difficulties with model convergence of these spatial models, which would not run on the full dataset ($n = 2,500$), models were run on datasets from the New Forest and South East England only, to reduce dataset size. The model can be described as follows:

$$\log \left( \frac{P(Y_i = 0)}{1 - P(Y_i = 0)} \right) = a + \text{Area}_{k} + bN_i + c_i N_i + \varepsilon_i \quad \text{(model 1)}$$

where $Y_i$ is the presence ($Y_i = 1$) or absence ($Y_i = 0$) of nightjars in heathland patch $i$, $\text{Area}_{k}$ parameters for the intercept of the $k^{th}$ Area-class of patch $i$, $b$ a parameter for the slope for $N_i$, and $c_i$ parameters
for the interaction of the slopes for $N_i$ with the $k$ Area-classes. $\epsilon_i$ is used to model a spatial covariance structure, where the covariance between two observations depends on the euclidean distance $d_{ij}$ between patches $i$ and $j$. Here, we assumed that the covariance between two observations declined exponentially with distance, with rate $\alpha$: $\text{cov} (i, j) = \sigma^2 \exp \left( -\frac{d_{ij}}{\alpha} \right)$. Both $\sigma^2$ and $\alpha$ are parameters that were estimated interactively with the other parameters. We used stepwise deletion from a maximal model and a hypothesis testing framework to assess the significance of the variables, rather than comparing models using an information criterion (such as Akaike Information Criterion (AIC)), because to our knowledge there is as yet no satisfactory method to compute model complexity penalties for models with complicated covariance structures such as the spatial error structure that we used in model 1.

**Effect of patch size and isolation on nightjar density**

The effects of size and isolation of heathland patch on nightjar density were investigated. Isolation was quantified using two different methods. The first of these, Score1, was based on distances to other occupied patches, and was for each patch $i$ the sum of the number of nightjars in all other patches $j$ ($R_j$) weighted exponentially by the inter-patch distance for occupied patches. The exponential decline meant that generally only nightjar populations within about 4 km of a patch contributed to its score. Thus, occupied heathland patches surrounded by large patches supporting many nightjars had higher scores. This score can be described as follows:

$$\text{Score1}_i = \sum_{j \neq i} \exp \left( -d_{ij} \right) R_j$$

where $R_j$ denotes the number of nightjar territories in patch $j$.

The second score, Score2, was the exponential sum of distances to all other patches, occupied or unoccupied:

$$\text{Score2}_i = \sum_{j \neq i} \exp \left( -d_{ij} \right) I_j$$

where $I_j = 1$ for occupied patches and $I_j = 0$ for unoccupied patches.

The two scores were used in attempt to separate whether any observed effects of isolation were due to dispersal (as Score1 is based on distance to occupied patches) or effects on the habitat itself (Score2 represents a combination of the two as it includes occupied and unoccupied patches). The use of exponentially weighted distances reduced the influence of heathland patches further away from the patch of interest, meaning that the ecologically important influence of closer patches was better estimated.

There was a strong effect of zero-truncation on the relationship between density of nightjars and area of occupied heathland patch. This means that, as no zero counts were included in this part of the analysis, densities are inflated for smaller patches, as they always represent at least one bird, whereas for larger patches a more complete range of densities is being considered. In order to correct for this, zero truncated models (Welsh et al., 1996; Martin et al., 2005) were used, with negative binomial distribution and log link, using PROC NLMIXED in SAS (zero-truncated poisson models yielded similar results but had higher AIC values). Nightjar count, $R_i$, was the dependent variable, and log area was included as an offset, so that density was being modelled. Patch area was also included as a variable, to investigate its effect on density. This resulted in the following modelling framework:

$$R_i \sim \text{ZNTB} (\lambda_i, \alpha),$$

and

$$\log (\lambda_i) = a_m + b \text{Score}_1 + c \text{Score}_2 + \log (\text{area}_i) + d \text{Area}_i,$$

(model 2)
where $\alpha$ is the extra-variation parameter of the negative binomial distribution, $a_m$ a parameter for the intercept for each region ($m = 1, \ldots, 4$), and $b$, $c$ and $d$ are coefficients for the respective terms.

We assessed the support for the inclusion of each of the covariates of interest (Score1, Score2, their quadratic terms, and Area) into the model by fitting all possible permutations of models (18 different models in total, Table 1), and comparing model weights using the AIC, as suggested by Burnham and Anderson (2002):

$$w_j = \frac{\exp\left(-\frac{1}{2}\Delta_j\right)}{\sum_i \exp\left(-\frac{1}{2}\Delta_i\right)},$$

where $\Delta_j$ is the difference between the AIC from model $j$ and the AIC possessed by the most parsimonious model (the model possessing the minimum AIC). Where coefficients for terms are presented, these are from the model containing that term which had the lowest AIC value. Quadratic terms of Score1 and Score2 were included as exploratory analysis gave some indication of a quadratic relationship between Score1 and nightjar density (Figure 2).

It was originally intended to investigate the effect of heathland patch shape on density. The ratio of the circumference of a circle with the same area as that of the patch, and the patch’s actual circumference was used as an index of complexity of shape:

$$\text{Shape index} = \frac{2\pi\sqrt{\text{Patch area}}}{\text{Patch circumference}}.$$  

However, log(patch area) and log(patch shape) were highly correlated ($r = -0.93$), and so patch shape was excluded from analyses, as it would not be possible to distinguish its effect from that of patch area.

**Analysis at the territory level**

Habitat attributes of territory locations were compared with those of random points. These random points were generated (using Hawth’s Analysis Tools for ArcGIS: Spatial Ecology, 2007) in broadly suitable, but unoccupied habitat, defined as heathland patches within 1 km squares surveyed but not occupied during the national survey. The minimum distance between random points was set as the minimum nearest-neighbour distance between nightjars on heathland, from the 2004/05 national survey. The number of random points plotted was stratified by region, such that each region contained equal numbers of territory locations and random points. Area and shape of the heathland patch, altitude (from OS Land-Form PANORAMA® data (Ordnance Survey, 2004)) and region were determined for each point.

The effect of area of different habitat types within 2 km of each point was investigated to examine the influence of foraging habitat availability on territory location. This distance of 2 km was based on a literature review of foraging behaviour. Nightjars in Thetford Forest foraged up to 2 km from their nesting area, with most flights being less than 1 km (Bowden and Green, 1994). A range of other studies have found that nightjars forage mainly within their nesting territories (Lack, 1930; Koenig, 1952; Schelgel, 1967; Wichmann, 2004). Birds in Dorset foraged a mean distance of 3.1 km (+/- 1.2 km) from their nest site (Alexander and Cresswell, 1990). However, birds at this site had to travel 1.5 km to reach the forest edge, which could account for the relatively high foraging distances.

Data from the Land Cover Map 2000 (LCM 2000, Fuller et al., 2002) were used to determine habitat types. Habitat classes were grouped into thirteen broad habitat categories. Categories for which over 80% of the values were zeros (bracken; salt marsh; bog) or with mean values accounting for less than
5% of the total area (fen, marsh and swamp; inland bare ground; inland water; avoided (= lumping of sea/estuary; littoral rock; littoral sediment; supra-littoral rock, supra-littoral sediment; montane habitats)) were excluded from analyses. Thus, area of the following habitat categories within 2 km of each point were included in the full model:

- Broad-leaved woodland (BLW);
- Coniferous woodland (CW);
- Agricultural (AG) (cereals; horticultural/non cereal/unknown; non annual crop and improved grassland);
- Unimproved grassland (UG) (set aside grass, rough grass, managed neutral grass, calcareous grass and acid grassland);
- Heathland (H) (dwarf shrub heath, open shrub heath);
- Urban plus suburban (URB).

However, there was a large degree of overlap between these 2 km circles, due to the highly clumped nature of both territory locations and random points. This meant that spatial autocorrelation was a problem, i.e. pseudoreplication due to the same area being included in the analysis several times, and this could lead to Type 1 errors (spurious significant results).

The degree of spatial autocorrelation also varied between territory locations and random points, and between Forest Districts. Attempts to overcome this problem were made by including heathland patch as a random effect, by running mixed models with spatial terms in the error structure, and by forcing autologistic terms into the models. The first two methods would not run, presumably because the degree of spatial autocorrelation was too high, and also as both occupied locations and random points tended to be clumped. The third method, including an autologistic score, did work, but produced models which were not robust, with results changing dramatically following slight changes made to the models, leading to concerns that the spatial autocorrelation was not being adequately corrected for.

Thus, it was decided the best approach was to take a random sub-sample from the full dataset (using a free ‘add-on’ to ArcView 3.2, Jenness Enterprises’ Random Point Generator, v. 1.3, Jenness Enterprises, 2007), where points were constrained to be a minimum distance (1 km) apart, thus reducing overlap between surrounding habitat. Five sub-samples were drawn from the full dataset, to check for consistency of results.

The distance from each point to the edge of the supporting heathland patch was calculated (using the ETGeoWizards add-on in ArcGIS, ETGeoWizards, 2007). Distances from all points to the nearest nightjar territory location on heathland were also calculated (using ETGeoWizards).

Unimproved grassland; urban/suburban; area of patch; shape of patch; distance to edge of patch and distance to nearest heathland territory were logged, and the square root of heathland area was taken, in order to correct for right-skewedness (i.e. a long tail due to a few unusually large values).

As before, heathland area and shape were highly correlated ($r = 0.77$) and so shape was excluded from the analysis. Heathland patch area and the amount of heathland within 2 km were highly correlated ($r = 0.58$). In an attempt to reduce this correlation, the area of the heathland patch was subtracted from the amount of heathland within 2 km. The correlation was still high ($r = 0.57$), but it was decided to include both variables (bearing in mind the correlation when interpreting results) as they were both of interest.
Logistic models were run to examine the relationship of the response variable (presence or absence) with each explanatory variable with and without its quadratic term, in turn, and AIC values compared, in order to decide which quadratic terms to include in the maximal model.

Framework for formula:

$$\log \left( \frac{P(Y = 0)}{1 - P(Y = 0)} \right) = a + \sum_{k=1}^{n} b_k X_{kj},$$

where $b_k$ (k = 1..number of covariates) are the slopes for the covariates $X_k$.

The following maximal model was selected:

Presence or absence = BLW + CW + AG + logUG + OtherHeath + logURB + logArea + Altitude + log (Distance to edge) + log (Distance to nearest heathland territory) + BLW² + logUG² + logURB² + (log (Distance to edge))²

This maximal model was run as a logistic model and step-up, step-down selection automated to find terms that were significant at the 5% level. These were then entered into a mixed model with binomial distribution and logit link. As before, a spatial covariance structure was incorporated, using the PROC GLIMMIX procedure in SAS, and including eastings and northings of each point within the repeated measures command, with an exponential spatial model structure. For reasons outlined previously, we used stepwise deletion from a maximal model, rather than comparing models using an information criterion (such as AIC).

**Distance to edge of patch**

In the previous models, random points were not necessarily distributed at random with respect to edge of the patch, as their density depended upon the area of suitable habitat to plot them in. Therefore, the effect of distance to edge of the heathland patch was also investigated separately.

Points were plotted at random within occupied patches (using Hawth’s Analysis Tools), such that equal numbers of territory locations and random points were present in each patch. Distance to the edge of the patch was measured for occupied and random points (using ET Geowizards, 2007), and compared using Wilcoxon signed rank tests (Snedecor and Cochran, 1980). Given that the size of a patch will affect the variation in distance to edge, and that distance to edge could be affected by other factors such as level of disturbance, which may vary by region, tests were run on the full dataset, and separately for different size classes of heathland patch and different regions.

**Results**

**Analysis at the heathland patch level**

**Effect of patch size and isolation on likelihood of a heathland patch being occupied**

Nightjars were present on 327 heathland patches in England during the 2004/05 surveys. These ranged in size from 0.2 ha to 2 874 ha, or 28.7 km² (mean = 1.1 km², S.D. = 2.9 km², Figure 3), although 100 patches (31 %) were smaller than 0.1 km² and 261 (81 %) smaller than 1 km² in size. The number of nightjar breeding territories on these patches ranged from 1 to 105 (mean = 4.8, S.D. = 9.9), but 159 patches (49 %) contained just one nightjar territory, and 288 (88 %) contained ten or fewer. The minimum size containing more than one territory was 1.5 ha.

Occupied patches were significantly larger than unoccupied patches; this was true both overall and for each region separately (Table 2).
Area of heathland in the vicinity, and the degree of fragmentation of this heathland, also had a significant effect on the likelihood of a patch being occupied (results from model 1: Table 3, Figure 4). This likelihood increased with increasing area of heathland within 10 km of the patch (excluding the area of the patch itself). The effect of number of patches within 10 km depended upon the area of heathland within this radius. For patches with a small area of heathland within 10 km (<10 km²), there was a positive relationship between number of patches and likelihood of occupation, whereas for larger patches (10 km² to 20 km², >20 km²), likelihood of occupation decreased with increasing number of patches within 10 km. The estimate of the slope (and standard error) for $N_i$ was: $-0.005$ (0.003), and estimates of the slopes of $N_i$ for the different area classes were: area class 1 (<10 km²): $0.028$ (0.008); area class 2 (10 km² to 20 km²): $-0.002$ (0.005); area class 3 (>20 km²): coefficient = 0.

**Effect of patch size and isolation on nightjar density**

The median density of nightjars on occupied heathland patches was 9.8 males per km². The range of densities was 0.08 males per km² to 540 males per km², although this maximum value is an artefact of one nightjar on an unusually small patch of heathland and is not biologically meaningful.

As would be expected, the number of nightjars increased with increasing patch size (Figure 5). The plot of nightjar count against patch size indicates that there may be an asymptote at larger patch sizes, i.e. density of nightjar appears to be decreasing with increasing patch size. However, there is a strong effect of ‘zero truncation’ (see methods) as only patches with at least one nightjar territory have been included, meaning that densities are inflated for smaller patches. Models were run accounting for this effect. The AIC scores and model weights for all possible variations of model 2 investigating effects of area and isolation of heathland patches on nightjar density are given in Table 1. Models showed some evidence of an effect of patch size on density, with larger patches supporting lower densities of nightjars (coefficient = -17.25 (14.17); Table 1). This was a relatively weak trend, however, with models containing this term having a combined normalised weight of 0.47, and any existing effect appeared to occur only at relatively large patch sizes (Figure 5).

Table 1 shows that the six best-fitting models all have relatively large weights (indicating good support for these models), and all of these contain Score1 and its quadratic, thus there is strong evidence for an effect of these terms (estimates for the slope (and standard error) for Score1: 2.18 (0.65), and Score1²: -1.81 (0.64)). Score2 appeared in four of the best six models, providing some evidence for an effect of Score2 (estimate of slope: 0.50 (0.28)), but with the effect of Score 1 being more significant. Thus, there is strong evidence that isolation of heathland patches in the landscape had an effect on density, with more connected patches supporting higher densities of nightjar (Figure 2). This was true for both the score of connectivity to any patches, and connectivity to occupied patches, but the effect of the latter was stronger. There was also an effect of the quadratic of the connectivity to occupied patches score, indicating that increased connectivity led to increased density, reaching an asymptote.

This effect of connectivity to other patches can be illustrated by comparing occupied and unoccupied patches, the latter being a random sub-sample of unoccupied patches drawn so that the same number of occupied and unoccupied patches were compared in each Forest District. A Wilcoxon test showed that distance to the nearest occupied patch was significantly lower for occupied patches than for unoccupied patches (occupied: mean = 1.39 km, S.D. = 5.54 km; unoccupied: mean = 4.53 km, S.D. = 7.63 km, $Z = 8.93$, $p < 0.0001$, n = 654). One hundred and thirty of the occupied heathland patches (40%) were less than 100 m, and 226 (86%) less than 500 m from the nearest occupied patch (minimum = 6 m, maximum = 78 761 m). Distance to any heathland patch (i.e. occupied or unoccupied) was also significantly lower for occupied patches than unoccupied patches (occupied: mean = 0.18 km, S.D. = 0.43 km; unoccupied: mean = 0.38 km, S.D. = 1.50 km, $Z = 3.53$, $p = 0.0004$, n = 654). Two hundred and
twelve (65%) of the occupied heathland patches were less than 100 m from other patches, and 303 (93%) were less than 500 m from other patches.

**Analysis at the territory level**

Territory locations had more agricultural land and coniferous woodland within 2 km than did unoccupied random point locations on heathland (Table 4, Figure 6). There was a significant positive quadratic relationship with broad-leaved woodland (Table 4, Figure 6), that is, territory locations were more likely to have a very small area or a large area of broad-leaved woodland within 2 km.

Of the four categories that comprised agricultural land, ‘non annual crop’ and ‘improved grassland’ made up less than 5% on average of the area surrounding nightjar territory locations/ random points. Thus, the ‘horticultural/non cereal/unknown’ and ‘cereal’ categories were likely to be the ones driving the association. In order to investigate this relationship further, the two categories were analysed separately, and significant positive effects were found for both.

Effects on distance to nearest nightjar on heathland and distance to edge were both influenced by how random points were plotted (e.g. by the area of suitable habitat within which to plot them), and so were accounted for in these models, but were also investigated separately.

**Distance to edge of patch**

Wilcoxon signed rank tests showed that overall there was no effect of distance to edge of the heathland patch on its likelihood of occupation (Table 5). That is, territory locations were distributed at random within patches, with respect to distance to edge.

Analyses were also run for patches of different sizes (Table 5). The premise of these separate analyses was that there might be a difference for larger patch sizes, as there would be more possibility for variation in distance to the edge of the patch. However, when analyses were run for patches of six size categories (< 1 km², < 5 km², < 10 km², > 1 km², > 5 km², > 10 km²), a highly significant difference (p < 0.0001) was found for distance to edge only within smaller patches (less than 1 km²). This difference was not significant for larger patches. For patches under 1 km² in size (it should be noted this refers to approximately half of occupied patches), territory locations were significantly further from the edge than random points.

Analyses were also run separately for each region, but an overall difference was only found for East Anglia, again with territory locations being significantly further from the edge than random points. East Anglia did have the smallest mean patch size (0.4 km²) of all regions (New Forest: 1.37 km²; South East England: 0.60 km²; Peninsula: 1.80 km², Table 5), and this effect is magnified when analysing data at the territory level, as in regions with a higher mean patch size, the larger patches are likely to contain more territories.

**Discussion**

One of the main results to arise from these analyses is the importance of fragmentation of heathland patches, in terms of isolation from other patches, both on the likelihood of a patch being occupied, and on the density of nightjars present. The area of heathland within 10 km of a patch (excluding that of the patch itself) had a positive effect on the likelihood of the patch being occupied. This appears to contradict Alexander and Cresswell (1990) who found that dry heath was avoided as a foraging habitat. However, their study was of nightjar breeding in a planted forest in Dorset, and preferences may differ in other habitat mosaics at other locations. The two studies are also looking at different
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spatial scales, in that Alexander and Cresswell (1990) were examining foraging ranges of individual birds, whereas here we investigated effects of heathland within a 10 km radius of a heathland patch. The observed contrasting effect of number of heathland patches within 10 km, dependent on the areas of heathland within 10 km, could be due to the relatively strong correlation between the area of heathland and number of heathland patches within 10 km (r = 0.61). For patches with a small amount of heathland in the vicinity, the effects of fragmentation may be masked by the positive effect of area of heathland. For larger patches, fragmentation has a negative effect on the likelihood of occupancy. This could be a genuinely negative effect of fragmentation, or could be due to greater availability of suitable habitat in these areas than the current population can occupy, so that where it is divided into more patches each one is less likely to be occupied.

An alternative explanation is that the interaction is due to dispersal. If birds are assumed to disperse to suitable habitat patches within a threshold distance from their natal area, then for nightjars with a relatively large area of heathland in the vicinity, dispersal is more likely. Where there is a smaller amount of heathland, the long distance to the nearest suitable habitat patch may limit dispersal. If this heathland is fragmented, then it could provide ‘stepping stones’ of suitable habitat facilitating dispersal. Where more suitable habitat is available in the vicinity, there is already sufficient heathland to enable dispersal, and fragmentation has a negative effect. The observed effect of isolation on nightjar density also could be explained in terms of dispersal.

The effects of fragmentation have been shown previously for a range of heathland species (Bullock and Webb, 1995; Van den Berg et al., 2001). For example, Bullock and Webb (1995) showed that local extinction was more likely and species richness lower on smaller, more isolated heathland patches. Rates of colonisation by dispersal and migration were also lower on such patches. The distributions of a suite of species, including the nightjar, were affected by area and isolation of heathland patch. Van den Berg et al. (2001) found that the presence of Dartford warbler Sylvia undata was associated with a fragmentation index, with larger and/or more connected heathland patches being more likely to be occupied. Liley and Clarke (2003), however, found no effect of the same index on nightjar occupancy. Here, we found deleterious effects of habitat fragmentation on nightjar breeding on heathland in England. The results show that both occupancy and density of nightjar on heathland patches are influenced by connectivity to other patches. The difference between this and Liley and Clarke’s (2003) findings could be due to the different approaches taken. Here, we investigated the effects of patch size and isolation separately, whereas Liley and Clarke (2003) used a ‘fragmentation index’ (as used by Van den Berg et al., 2001), which incorporated both size of patch and connectivity to other patches. Liley and Clarke’s (2003) study also focused on nightjar breeding in Dorset, where patch size and isolation are closely correlated (r = 0.76: Bullock and Webb, 1995), whereas here we investigate the effects of patch size and isolation throughout England, where only a weak correlation between the two was found (e.g. r = 0.11 for correlation of patch size and the three-level factor ‘area of heathland within 10 km’).

In this study, heathland patches do not represent populations of nightjar (given that approximately half of them supported only one pair of nightjars), and so, as Van den Berg et al. (2001) considered for Dartford warbler, a metapopulation explanation of the response to fragmentation (e.g. Bright et al., 1994; Villard et al., 1995) is not appropriate at this scale. If a local population is described as a population within which individuals move during routine daily activities and interact with other individuals, and within which most individuals are born and die, a metapopulation is a system of such local populations connected by dispersing individuals (Hanski and Gilpin, 1991). Although there will be metapopulations of nightjar at the landscape scale, at the heathland patch scale there is more likely to be a patchy distribution of individual nightjars, rather than a metapopulation (Hanski and Gilpin, 1991).
Van den Berg et al. (2001) considered that it was likely there was only one population (or very few populations) of Dartford warbler in Dorset, with some degree of movement between fragments. Bullock and Webb (1995) considered that species investigated in their study (which included species of invertebrates, birds and reptiles), were likely to use the landscape at different spatial scales, but still showed similar responses to spatial configuration of the landscape. They considered that for the three bird species (which included nightjar), a single population was likely to cover several, if not all, of the Dorset heath fragments, and so their dynamics conformed more to the ‘patchy population model’ (Harrison, 1994), with the heathland fragments representing a resource for the population. More studies of movements of nightjars, including dispersal distances, would be valuable in shedding light on these questions.

Patch size had an effect on occupancy, with occupied patches being larger on average than unoccupied patches. There was some indication of a weak effect of patch size on nightjar density, with a trend for nightjar density to decrease with increasing patch size. This trend for density to decrease with increasing patch size is similar to that found by Liley and Clarke (2003), who suggested that this was due to avoidance of heathland as a foraging habitat (Alexander and Cresswell, 1990). However, their observation was based on the results from radio-tracking work of one population of nightjar in a planted forest in Dorset, and foraging habitat preferences may differ for nightjar breeding in other habitats and locations. Observations of foraging birds, especially during chick rearing, indicate that nightjars foraged on their nesting heaths in Dorset (R. Langston pers. comm.), and other authors have reported that nightjar forage predominantly within their nesting territory (e.g. Lack, 1930; Koenig, 1952; Schelgel, 1967; Wichmann, 2004). The suitability of the heathland habitat and proximity to other foraging habitat are likely to determine foraging behaviour by breeding nightjars. In any case, effects of patch size and isolation on occupancy, and of isolation on density, were far more significant. The effect of decreasing density with increasing patch size also only occurred at relatively large patch sizes (Figure 5). Given that the average patch size overall is 0.17 km², and average size of an occupied patch was 1.06 km², this result is of more importance, and heathland restoration for nightjar should be aimed at increasing mean patch size.

As patch size was so strongly correlated with patch shape, it was not possible to include both in the analyses, and their effects cannot be distinguished. Previous studies have found an effect of patch shape on nightjar occupancy. Ravenscroft (1989) found a preference for a lower circumference/area ratio (i.e. less complex shapes, approaching circular) for clearings in forestry, but for more complex shapes in heathland. This was explained in terms of preference for tree edge habitat on heathland, where such habitat was relatively limited compared with forests, where clearings with a greater extent of tree edge habitat could become overgrown and unsuitable. Wichmann (2004), made similar comparisons for occupied locations and random points in an Austrian pine forest, also found a preference for simpler clearing shapes. However, this difference was no longer significant when the comparison was restricted to clearings larger than 0.7 ha (the minimum size of clearing occupied), highlighting the importance of considering the correlation between shape and area of clearing (or heathland patch).

There was no overall difference in distance to edge for territory locations compared with random points within the same heathland patches. However, reanalysis by size class revealed a highly significant difference for patches smaller than 1 km², with territory locations being significantly further from the edge of patches than expected by chance. This result is important, as approximately half of all occupied patches were less than 1 km² in size. Analysis by region, for patches of all sizes, found a significant difference only for East Anglia, where patches were smaller than in other regions. Liley et al. (2006) found that territories were located further from the edge of sites in the Thames Basin Heaths, as well as away from access points and in areas of lower visitor pressure. This influence of
heathland patch size on whether or not there is an edge effect is not surprising. If nightjars avoid certain habitats (for example, urban habitats due to disturbance, Liley and Clarke, 2003), then distance to edge would be expected to be greater in smaller patches where the effects of disturbance were more prevalent (as a higher proportion of the habitat will be close to the source of disturbance, or the disturbance will be less dissipated through the patch).

The positive quadratic relationship for nightjar territory locations with broad-leaved woodland is perhaps explained by nightjars either breeding on heathland within coniferous forests containing a small amount of broad-leaved woodland, or, more unusually (as can be seen from the few data points at the high end of the scale on Figure 6), nightjars nesting in heathy clearings in broad-leaved woodland. Whether or not the association with coniferous forests indicates a preference for heathland within coniferous forests compared with heathland surrounded by other habitats is less clear. Liley and Clarke (2003) found that the amount of woodland within 500 m of a heathland patch in Dorset was a significant predictor of nightjar numbers. Alexander and Cresswell (1990), in their study of nightjar on heathland clearings in planted forests found a preference for deciduous or mixed woodland, but avoidance of coniferous forests.

This study has investigated habitat associations, which may or may not reflect habitat preference. When comparing territory locations with random points, differences in habitat surrounding the two clearly depend on the constraints applied to random points. In this study, random points were restricted to heathland that had been surveyed but was unoccupied during the national survey. There could be reasons other than surrounding habitat to explain why these areas were unoccupied, which might correlate with the surrounding habitat, or there could be other factors leading to lack of occupation and habitat differences. The association with agricultural land at first seems surprising, but is difficult to tease apart using LCM 2000, because of the broad categories of land use. Alexander and Cresswell (1990) found avoidance of improved grassland/arable land. In this study, improved grassland was limited in extent around territories or random points, but association with arable land was found. The unexpected association with agricultural land found in our study merits further investigation, either remotely using more detailed agricultural data, or preferably as a field based project.

Alexander and Cresswell (1990) also found a preference for gardens/orchards for foraging, and a preference for wetlands, although these were rare in the study landscape. It would be valuable for more radio-telemetry studies to take place at a number of different sites, in different regions, to compare habitat use with habitat availability in the surrounding area. There are likely to be site-specific differences.

It is perhaps surprising that no effect of the area of urban land within 2 km on likelihood of occupation was found in this study, given the negative effects of urban development and human disturbance on breeding nightjars found by other studies (Murison, 2002; Liley and Clarke, 2003; Woodfield and Langston, 2004; Langston et al., 2007b). There are a few possible explanations for this. Firstly, urban land constituted such a small proportion (on average less than 5%) of the area within 2 km of points, that it was combined with suburban land. Even then, the two categories together accounted for a relatively small area in comparison to other habitat types, making it less likely that an effect would be found at the large geographical scale of this analysis. Most of the disturbance studies have looked at urban habitat within a smaller radius from territories, and were carried out at a sample of sites within a region.

The Government UK Biodiversity Action Plan for Lowland Heathland (Anon., 1998) includes targets for establishing more of this habitat. The RSPB’s Heathland Extent and Potential (RSPB, 2007) data are useful in showing where this heathland could be located, taking account of suitable soil types and
land uses for conversion, and aiming to expand existing patches and reduce their isolation. This project found that if all the identified suitable heathland within 250 m of current patches was converted, the overall area of heathland would be doubled and the number of patches reduced from 3278 to 479. Arnold (2006) refined this work to identify the best areas for heathland recreation with respect to four key species of heathland bird; stone curlew *Burhinus oedicnemus*, nightjar, woodlark *Lullula arborea* and Dartford warbler. Results from the current study would be useful for work such as that by Arnold (2006).

Fragmentation, as well as habitat loss, may have been an important factor in nightjar range contraction. The results also provide an explanation for the slow range recovery of nightjar, despite the population expansion in recent years, and should be borne in mind when setting Biodiversity Action Plan (BAP, Anon., 1998) targets for range expansion. The negative effects of fragmentation are of particular concern, given how fragmented the current nightjar population is, with 80% of occupied heathland patches being smaller than 1 km$^2$ in size, and 31% smaller than 0.1 km$^2$. Approximately half (49%) of all patches contained just one nightjar territory.

Radio-tracking studies to investigate the foraging preferences of nightjars on heathland would be valuable, particularly as previous radio-tracking studies have focused on nightjars within clearings in planted forests (Alexander and Cresswell, 1990; Bowden and Green, 1994). Studies of dispersal distances would also be very valuable in terms of gaining a better understanding of the effects of fragmentation.

It has not been clear, from previous studies, to what extent defragmentation might benefit nightjars (Bullock and Webb, 1995; Liley and Clarke, 2003). Here, we find evidence to support the current approach of recreating heathland in the vicinity of other heathland and nightjar populations, increasing mean patch size, and reducing the isolation of existing patches where they are fragmented. In areas with less heathland, the creation of ‘stepping stones’ of suitable habitat to enable dispersal between patches may be beneficial, where it is not possible to join patches.

**Acknowledgements**

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References

Alexander, I. and Cresswell, B. (1990) Foraging by Nightjars Caprimulgus europaeus away from their nesting areas. Ibis 132: 568-574


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Table 1. Effect of patch size and isolation on nightjar density within occupied patches. AIC values for all possible models. Score1 is based on connectivity to occupied patches, Score2 is based on connectivity to any patches.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>Normalised weight</th>
<th>Cumulative weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Score1 + Score2 + (Score1)^2</td>
<td>1057.2</td>
<td>0.256</td>
<td>0.256</td>
</tr>
<tr>
<td>Score1 + Score2 + Area + (Score1)^2</td>
<td>1057.9</td>
<td>0.181</td>
<td>0.437</td>
</tr>
<tr>
<td>Score1 + Area + (Score1)^2</td>
<td>1058.1</td>
<td>0.163</td>
<td>0.601</td>
</tr>
<tr>
<td>Score1 + (Score1)^2</td>
<td>1058.4</td>
<td>0.141</td>
<td>0.741</td>
</tr>
<tr>
<td>Score1 + Score2 + (Score1)^2 + (Score2)^2</td>
<td>1058.7</td>
<td>0.121</td>
<td>0.862</td>
</tr>
<tr>
<td>Score1 + Score2 + (Score2)^2 + Area + (Score1)^2</td>
<td>1059.6</td>
<td>0.077</td>
<td>0.940</td>
</tr>
<tr>
<td>Score2 + Area</td>
<td>1063.7</td>
<td>0.010</td>
<td>0.950</td>
</tr>
<tr>
<td>Score1 + Score2 + Area</td>
<td>1064.3</td>
<td>0.007</td>
<td>0.957</td>
</tr>
<tr>
<td>Score1 + Area</td>
<td>1064.6</td>
<td>0.006</td>
<td>0.963</td>
</tr>
<tr>
<td>Score1 + Score2</td>
<td>1064.8</td>
<td>0.006</td>
<td>0.969</td>
</tr>
<tr>
<td>Score 2</td>
<td>1064.9</td>
<td>0.005</td>
<td>0.974</td>
</tr>
<tr>
<td>Score2 + Area + (Score2)^2</td>
<td>1064.9</td>
<td>0.005</td>
<td>0.980</td>
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<tr>
<td>Score1 + Score2 + (Score2)^2</td>
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<td>0.005</td>
<td>0.985</td>
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<td>Score1 + Score2 + Area + (Score2)^2</td>
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<td>0.005</td>
<td>0.990</td>
</tr>
<tr>
<td>Score2 + (Score2)^2</td>
<td>1065.9</td>
<td>0.003</td>
<td>0.994</td>
</tr>
<tr>
<td>Area</td>
<td>1065.9</td>
<td>0.003</td>
<td>0.997</td>
</tr>
<tr>
<td>Score 1</td>
<td>1066.4</td>
<td>0.003</td>
<td>0.999</td>
</tr>
<tr>
<td>Null model</td>
<td>1069.5</td>
<td>0.001</td>
<td>1.000</td>
</tr>
</tbody>
</table>

Table 2. Comparison of heathland patch size for occupied and unoccupied patches.

<table>
<thead>
<tr>
<th>Region</th>
<th>Mean patch size (km^2, +/- S.D.)</th>
<th>Z statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All combined</td>
<td>1.06 (2.94)</td>
<td>22.11</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>New Forest</td>
<td>1.37 (3.99)</td>
<td>13.91</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>South East England</td>
<td>0.60 (1.35)</td>
<td>13.53</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Peninsula</td>
<td>1.80 (2.80)</td>
<td>8.53</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>East Anglia</td>
<td>0.40 (0.42)</td>
<td>6.86</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
Table 3. Effect of area of heathland and number of heathland patches in the surrounding area (radius 10 km from the focal patch) on occupancy of a heathland patch by nightjar.

<table>
<thead>
<tr>
<th>Term</th>
<th>d.f.</th>
<th>F value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area of heathland within 10 km</td>
<td>2</td>
<td>18.62</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Number of patches within 10 km</td>
<td>1</td>
<td>1.14</td>
<td>0.2851</td>
</tr>
<tr>
<td>Area * Number</td>
<td>2</td>
<td>6.81</td>
<td>0.0012</td>
</tr>
</tbody>
</table>

Models were run only for the regions New Forest and South East England, as spatial mixed models would not run for larger datasets.

Table 4. Comparison of habitat surrounding nightjar territory locations and random points.

<table>
<thead>
<tr>
<th>Term</th>
<th>d.f.</th>
<th>F value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agricultural (AG)</td>
<td>1</td>
<td>24.37</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Coniferous woodland (CW)</td>
<td>1</td>
<td>5.6</td>
<td>0.0188</td>
</tr>
<tr>
<td>Broad-leaved woodland (BLW)</td>
<td>1</td>
<td>50.69</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>BLW^2</td>
<td>1</td>
<td>32.36</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Log (distance to NJ on heathland)</td>
<td>1</td>
<td>46.85</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Log (distance to edge of patch)</td>
<td>1</td>
<td>7.27</td>
<td>0.0073</td>
</tr>
</tbody>
</table>

Models were run on five randomly drawn samples of random points from the full dataset, at least 1 km apart, but are presented from only one of these as results were very similar.

Table 5. Comparison of distance to edge of heathland patch for nightjar territory locations and random points.

a) By size of heathland patch

<table>
<thead>
<tr>
<th>Data included</th>
<th>S statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>All data</td>
<td>-25623</td>
<td>0.1559</td>
</tr>
<tr>
<td>Patches under 1 km^2</td>
<td>-19007.5</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Patches under 5 km^2</td>
<td>-16947.5</td>
<td>0.0896</td>
</tr>
<tr>
<td>Patches under 10 km^2</td>
<td>-7489.5</td>
<td>0.5441</td>
</tr>
<tr>
<td>Patches over 1 km^2</td>
<td>4881.5</td>
<td>0.6251</td>
</tr>
<tr>
<td>Patches over 5 km^2</td>
<td>-2751.5</td>
<td>0.4146</td>
</tr>
<tr>
<td>Patches over 10 km^2</td>
<td>-3455.5</td>
<td>0.0716</td>
</tr>
</tbody>
</table>

b) By region

<table>
<thead>
<tr>
<th>Region</th>
<th>S statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>East Anglia</td>
<td>-865.5</td>
<td>0.0137</td>
</tr>
<tr>
<td>New Forest</td>
<td>-10737</td>
<td>0.1824</td>
</tr>
<tr>
<td>Peninsula</td>
<td>-82.5</td>
<td>0.8341</td>
</tr>
<tr>
<td>South East England</td>
<td>-21</td>
<td>0.9928</td>
</tr>
</tbody>
</table>
Habitat associations of nightjar

Figure 1. Forestry Commission ‘Forest Districts’, labelled where nightjar are present on heathland. These were used as a measure of region in analyses.

Figure 2. Relationship between density of nightjar on a heathland patch and a score based on the patch’s connectivity to other occupied heathland patches. The relationship is plotted only for larger patches (1.5 km²) to minimise the effects of zero-truncation.
Figure 3. Frequency distribution of areas of occupied heathland patches.

Figure 4. Likelihood of a heathland patch being occupied in relation to the area of heathland within 10 km (excluding that of the patch in question), and the number of heathland patches within 10 km.

- : heathland patches with 0-10 km$^2$ of other heathland within 10 km.
- : heathland patches with 10-20 km$^2$ of other heathland within 10 km.
- : heathland patches with over 20 km$^2$ of other heathland within 10 km.
Figure 5. Number of nightjar (churring males) against heathland patch size.
Figure 6. Predicted likelihood of occupation of a location in relation to amount of three habitat types within 2 km, controlling for other terms in the model (maximum area within 2 km = 1257 ha).