

The role of habitat composition in determining breeding site occupancy in a declining Ring Ouzel *Turdus torquatus* population

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Ring Ouzel *Turdus torquatus* breeding site occupancy in the Moorfoot Hills, southeast Scotland, was determined during the periods 1952–85 and 1998–2000, and sites were classed as either occupied or deserted during the latter period. Site occupancy during 1998–2000 was related to habitat data derived from a supervised classification of a Landsat 7 satellite image. Breeding sites were more likely to have remained occupied if they were at higher altitudes and had more heather cover within radii of both 200 and 450 m, although these effects became non-significant when spatial autocorrelation was accounted for. Using only topographical variables, potential breeding sites were predicted and the habitat surrounding them was compared with actual breeding sites. Actual breeding sites were more likely to have heather or grass–heather mosaic within 100 m than potential breeding sites, but there were no further habitat differences between actual and potential breeding sites within radii of 200 or 450 m. These results indicate that breeding sites at higher altitudes and with a higher cover of heather were less likely to have been deserted, and that lack of heather may prevent otherwise suitable breeding sites from becoming occupied by Ring Ouzels. More detailed field studies are needed to understand the mechanisms underlying these associations.

The breeding Ring Ouzel *Turdus torquatus* population of the UK is thought to have been in decline since the early 20th century, although the species is still found throughout much of the uplands (Baxter & Rintoul 1953, Thom 1986, Gibbons *et al.* 1996). This decline has continued in recent decades, with a substantial range contraction between 1968–72 and 1988–91, and an estimated 58% decrease in breeding numbers between 1988–91 and 1999, giving a UK population of 6157–7549 breeding pairs in 1999 (Gibbons *et al.* 1993, Gregory *et al.* 2002, Wotton *et al.* 2002). As a result of this decline, the Ring Ouzel is now listed as a species of high conservation concern in the UK (Gregory *et al.* 2002). By contrast, breeding populations in most countries in continental Europe

appear to be stable (BirdLife International 2004), and although monitoring in some countries may be less comprehensive than in the UK, and may sometimes depend on qualitative assessments, it seems unlikely that declines of the magnitude witnessed in the UK would have gone undetected. This apparent stability in European populations, together with evidence of at least some overlap in the wintering areas of continental and UK breeders (Burfield 2002), suggests that the decline may be due to factors operating on the UK breeding grounds. However, there is also the possibility that adverse factors impinge particularly severely on UK breeding birds on migration (Burfield & Brooke 2005).

Ring Ouzels in the UK favour steep-sided valleys and gullies as breeding areas, particularly where crags and scree are found (Gibbons *et al.* 1993). Breeding densities can vary considerably between areas, with the average distances between adjacent nesting pairs tending to range from 350 to 680 m, although in some particularly suitable areas they may be just 90–200 m

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apart (Poxton 1986, Appleyard 1994, Arthur & White 2001, Burfield 2002). Broad-scale studies have shown that variation in breeding densities may be associated with a range of habitat characteristics, including positive correlations with the extent of heather *Calluna vulgaris* moorland, grass–heather mosaics, rough grassland, rock and bracken *Pteridium aquilinum* (Buckland *et al.* 1990, Haworth & Thompson 1990, Stillman & Brown 1994, Buchanan *et al.* 2003). Additionally, contrasting associations with the extent of improved pasture have been found in different studies (Haworth & Thompson 1990, Buchanan *et al.* 2003). Finer-scale habitat selection studies have shown that, whilst Ring Ouzels select heather nesting sites, they select short grass for foraging during the nestling period, with most foraging occurring within 450 m of the nest during this period (Burfield 2002, Prigmore 2003). Taken together, these findings suggest that changes in the fine-scale mosaic of grass and heather cover in their moorland breeding areas may have effects on habitat quality for Ring Ouzels.

UK moorlands have been subject to several major land-use and management changes during the past few decades, including large-scale afforestation, declines in grouse moor management and increasing numbers of Sheep *Ovis aries* and, in the Scottish Highlands, Red Deer *Cervus elaphus* (Avery & Leslie 1990, Fuller & Gough 1999, Robertson *et al.* 2001). Changing grazing levels are likely to have been particularly important in affecting the composition and structure of moorland vegetation, specifically causing reduction in heather cover and condition and consequent increases in grass cover (Mackey *et al.* 1998, Fuller & Gough 1999). Thus, increases in the numbers of large herbivores on moorlands, together with changes in their management (e.g. less active shepherding), are likely to have altered the extent and distribution of both nesting and foraging habitat for Ring Ouzels. Additionally, areas of potentially important grass–heather mosaics are particularly vulnerable to such changes, given the tendency for grazing pressures on heather to be relatively high along interfaces with grass (Clarke *et al.* 1995, Palmer & Hester 2000). Correlative analyses, indicating that declines in Ring Ouzel abundance have been greatest where the extent of smooth grass–heather mosaic was initially greatest, provide some support for the hypothesis that such changes to moorland habitats are a cause of decline, although stronger effects of topography and of the extent of conifer afforestation were also detected (Buchanan *et al.* 2003). This

study investigated the hypothesis that declines in Ring Ouzel abundance may be due to changes in moorland habitat composition, by relating long-term data on breeding site occupancy in a declining population to current habitat composition (as derived from satellite imagery). Additionally, it tested the hypothesis that habitat composition differed between currently occupied breeding sites and sites that appeared to be topographically suitable but at which breeding had not been recorded.

METHODS

Study area

The study took place in the Moorfoot Hills in south-east Scotland (55°42'N, 3°01'W), which has been identified as an Important Bird Area (IBA) on the basis of its breeding Ring Ouzel population (Heath & Evans 2000). This range of hills extends over an area of approximately 200 km², and comprises largely flat-topped hills ranging from 250 to 660 m in altitude, dissected by many steep-sided valleys. The study concentrated on an area of approximately 65 km² in the central part of these hills. At higher altitudes wet heath, characterized by heather and blanket mire, predominates. On lower ground, drier heather moorland, species-poor heath and herb-rich grasslands occur, whilst bracken is also widespread (SNH 1989). The principal land use is livestock grazing, mainly by Sheep, but some areas are also managed for Red Grouse *Lagopus lagopus scoticus*, by rotational heather burning and predator control. Some afforestation with exotic conifers has also occurred.

Determining breeding site occupancy and changes in occupancy

Historical data on Ring Ouzel breeding site occupancy were obtained from several sources, principally the diaries of the late William Brotherston. During 1952–79, he conducted 2–4 surveys per month between April and July, of 20–55 known breeding sites in any one year. This information was supplemented by another survey, carried out in 1985 (Murray 1986, Poxton 1987), and data from other sources that provided information on the location of breeding pairs (e.g. Morrison 1978, Badenoch 1981, L. Vick unpubl. data). From these sources, 128 distinct six-figure grid references (i.e. accurate to 100 m) were identified which were considered by these earlier surveys to have been occupied by breeding Ring

Ouzels in at least one year between 1952 and 1985. All historical breeding sites identified in this way were at least 200 m apart, as determined from the associated grid references.

Of these 128 sites, 73 were re-surveyed in two years and 59 in three years, during 1998–2000 as part of an intensive study of Ring Ouzel breeding ecology (Burfield 2002). Each breeding site was surveyed approximately once per week from late March to late June, except in 2000 when fieldwork ceased in early May. No surveys were carried out in strong winds, persistent precipitation or when visibility was poor. Observations were conducted from one or more vantage points within 100 m of the six-figure grid reference that was used to define the historical breeding site. If no birds were detected after 30 min, and if none had been seen during previous surveys that year, a tape of male Ring Ouzel song was played at full volume using a portable stereo for 1 min. Previous surveys had established that tape playback increases the chances of detecting breeding birds, especially males, particularly during April and May (Wotton *et al.* 2002, I. Sim unpubl. data). Following tape playback the observation continued for a further 10 min, after which it ended if no Ring Ouzels had been detected.

For each year of study, the surveyed breeding sites were classified as occupied if at least one bird was seen within 100 m of the six-figure grid reference defining that breeding site, between late March and late June. This definition of occupancy was used because it was consistent with that used in the previous surveys, and because the elusive nature of breeding Ring Ouzels means that breeding can be difficult to prove, particularly if pairs fail early in the season (I. Sim pers. obs.). Using these criteria, breeding sites were considered to have been 'historically' occupied but to have become deserted if they had been surveyed in at least three (mean = 23.0, range 3–31) years during 1952–85, had been occupied in at least 50% (mean = 80.7, range 50–100) of years during this period, and were unoccupied during 1998–2000. They were considered to have been 'historically' occupied and to have remained occupied if they had been surveyed in at least one (mean = 10.0, range 1–31) year during 1952–85, had been occupied in at least 33% (mean = 76.8, range 33–100) of the surveyed years during this period, and were occupied in at least one year during 1998–2000. This resulted in a sample of 17 sites that were classed as having been 'historically' occupied but had become deserted, and 35 that had remained occupied since the earlier

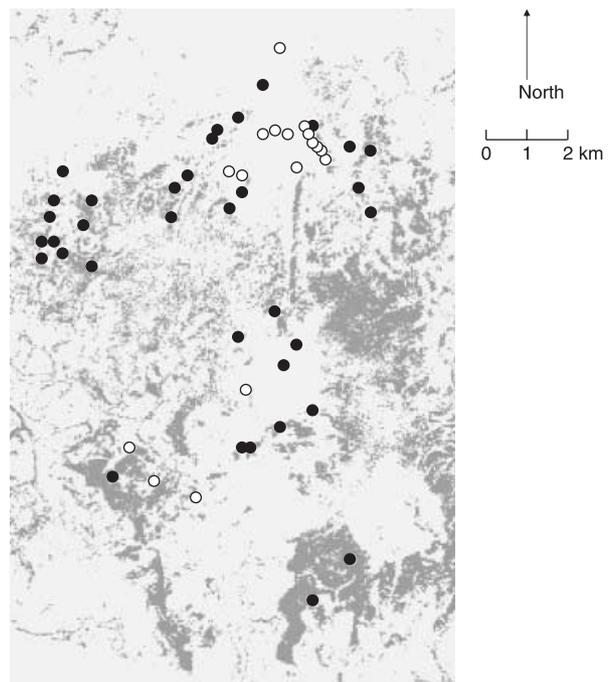


Figure 1. Location of the 35 historical breeding sites that had remained occupied in 1998–2000 (filled circles), and the 17 sites that were deserted in 1998–2000 (open circles). Heather pixels are shaded grey.

survey period (Fig. 1). These criteria were chosen to minimize the risk of misclassifications, while maximizing the sample size. For deserted breeding sites, it was important to be confident that they had been regularly occupied during 1952–85, so those surveyed in fewer than three years or occupied in fewer than half of survey years were excluded. However, for historical breeding sites that had remained occupied, it was less important that they had been regularly occupied during 1952–85, so the criteria for historical occupancy were relaxed. For these sites, the key criterion was that they had been occupied in at least one year during 1998–2000.

Determining habitat composition and topography

Habitat composition across the study area was derived using a Landsat 7 satellite image of southeast Scotland (path 204, row 21) from 7 May 2000, which has an image resolution of 30 m (i.e. each pixel on the image represents a 30 × 30 m area). Image manipulation was carried out using IDRISI Kilimanjaro 14.02 (Clarke Laboratories 2003). Reflectance bands

Table 1. Definition of the variables used in the analyses to determine factors associated with the continued occupancy of 'historical' breeding sites and the occupancy of topographically suitable breeding sites. Variables 1–7 are the percentage composition (i.e. the percentage of all pixels within radii of 200 and 450 m of breeding sites attributed to each habitat) of that habitat type.

Variable	Definition
1. Bracken	Stands of continuous bracken
2. Grass	Unenclosed semi-natural grassland, dominated by grasses
3. Heather	Dwarf shrub heath, dominated mainly by heather
4. Grass–heather mosaic	Areas with grass and heather habitats interspersed, such that each of the habitats covers 30–70% of each 30 × 30-m pixel within the area
5. Cotton-grass–heather mosaic	Areas with Cotton-grass and heather interspersed, such that each of the heather habitats covers 30–70% of each of the 30 × 30-m pixels within the area
6. Improved pasture	Enclosed grassland
7. Forest	Coniferous plantation
8. Distance to forest	Distance in m to nearest forest
9. Altitude	Altitude of the site (metres above sea level)
10. Mean slope	Average slope (°) of all 30 × 30-m pixels within either 200 m or 450 m of the breeding site (or potential breeding site)
11. Distance to stream	Distance in m to nearest stream

1–5, and 7, were geo-referenced to Ordnance Survey Great Britain (OSGB) on Transverse Mercator projection to within one pixel (root mean square < 30 m), and illumination-corrected using a 50-m digital terrain model (Panorama, Ordnance Survey, UK).

The major habitats within the study area were mapped from the image data (Table 1). This was achieved for the two non-moorland habitats (i.e. conifer plantation and improved grassland) by combining information from a supervised classification based upon the colour-composite image produced using bands 2, 3 and 4 (Clarke Laboratories 2003), with that from Ordnance Survey 1 : 25 000 maps. For the moorland habitats, a supervised classification was undertaken using a series of training sites from each habitat category. Between 12 June and 3 July 2003, representative plots of each habitat were located across the study area. To match the resolution of the satellite image, plots were at least 30 × 30 m (900 m²) in area (mean = 5504 m² ± 232 se). At each plot, a ten-figure grid reference (i.e. accurate to 1 m) was taken from each corner of the polygon, using a Garmin Global Positioning System (GPS) 12 Personal Navigator. In total, 19 such training plots were used to define Cotton-grass *Eriophorum vaginatum*–heather mosaics, 20 for bracken, 37 for grass–heather mosaics and 40 for each of the heather- and grass-dominated habitats, with more samples being located in those habitats known to be important to breeding Ring Ouzels (Burfield 2002). The two mosaic habitat categories were defined as areas comprising between 30 and 70% of each vegetation type, and where the two main vegetation components were distributed

such that no 30 × 30-m block comprised less than 30% or more than 70% of either component.

Using these training sites, spectral signatures were developed with the digital reflectance values (between 0 and 255) of bands 1–5 and 7, using the Makesig command in IDRISI. These spectral signatures were then used, in combination with altitude, slope and two other measures derived from the satellite image (i.e. MOIST – an index of soil moisture content; and the Normalized Difference Vegetation Index – NDVI), to classify the five moorland habitats using the Maxlike procedure. This uses a maximum-likelihood classification based upon the probability density function associated with a particular training site signature. In this way, each pixel is assigned to the most likely habitat category based on a comparison of the posterior probability that they belong to each of the signatures being considered.

To test the accuracy of the classification, a predicted habitat map was produced based upon a stratified random sample of 75% of the training plots of each habitat. The predicted and actual habitat types of the pixels in the remaining 25% of plots were compared. The final predicted habitat map was produced using all the training plots. Measures of altitude and slope were derived directly from a 50-m digital terrain model (Panorama, Ordnance Survey, UK).

Determining differences between occupied and deserted breeding sites

The relationships between the likelihood of 'historical' breeding sites becoming deserted and habitat and

topographical variables (Table 1) were examined at radii of 200 and 450 m around the occupied and deserted breeding sites, using data from all 30×30 m pixels lying wholly or partly within these radii. The 200 m radius represented approximately half the mean nearest-neighbour distance of currently occupied nests (i.e. 450 m), whilst the 450 m radius was used because two independent studies found that 93–96% of adult foraging sites during chick-rearing were within 450 m of the nest (Burfield 2002, Prigmore 2003).

Probability that a breeding site remained occupied was modelled using binary logistic regression using the GENMOD procedure in SAS v8 (SAS Institute 2001). Habitat proportions were arcsine square root transformed prior to analysis to normalize the data. Analyses were conducted using a step-up procedure, where the variable causing the most significant change in deviance at each stage was incorporated into the regression model until no other variables were significant at the $P < 0.05$ level. After inclusion of each new variable, the significance of existing terms in the model was tested using type 3 contrasts, removing any that were no longer significant at $P < 0.05$. To allow for possible curvilinear relationships, the square of each variable was included in the model in conjunction with that variable if the change in deviance associated with its inclusion was significant at the $P < 0.05$ level, or if the effect of the variable and its square were significant when included together. The statistical significance of each variable was tested by treating the difference between the deviance of the models that did and did not include the variable as χ^2 with the appropriate degrees of freedom (i.e. equivalent to the number of parameters being added to the model).

To account for possible effects of spatial autocorrelation, the significance of terms in the minimum adequate model (MAM) was tested using a generalized linear mixed model (GLMM) incorporating a spatial covariance structure. Analysis was conducted using the GLIMMIX macro in SAS v8, with the eastings and northings (from the Ordnance Survey National Grid) of each point specified within the repeated measures command, using a spherical spatial model structure (Littell *et al.* 1996). Due to the relatively small sample size, there were difficulties with the simultaneous estimation of both spatial covariance and fixed effects, and the GLMMs failed to converge. Therefore, values for the spatial covariance term were first estimated using a null model (i.e. one without fixed effects), and the spatial covariance

term constrained to this value when estimating the significance and parameter estimates for the fixed effects. This is likely to over-estimate the degree of spatial covariance and produce results that are conservative with regards to the significance of the fixed effects. Where the inclusion of the spatial covariance structure resulted in a decrease in AIC (Akaike Information Criterion) values relative to the non-spatial model, the adjusted parameter estimates and P -values for the fixed effects within the MAM are presented, applying the Kenward–Roger correction to the degrees of freedom (Kenward & Roger 1997).

Determining habitat differences between actual and potential breeding sites

In addition to determining whether the likelihood of breeding site desertion was associated with variation in habitat composition, a further aim was to determine whether the occupancy of topographically suitable sites could be predicted by surrounding habitat. Thus, it was necessary to first define potential breeding sites on the basis of topography.

Using 41 breeding sites recorded as occupied in at least one year during 1998–2000, the extent to which breeding sites could be predicted by a number of topographical variables was determined. Altitude, slope (both determined as above) and distance to nearest stream (measured from Ordnance Survey 1 : 25 000 maps to the nearest 25 m) were determined for these breeding sites and for 41 randomly located points in the study area. The extent to which these topographical variables distinguished breeding sites from the random points was determined by performing logistic regression analysis and producing a MAM as described above. The receiver operating characteristics (ROCs) were then used to assess the performance of the regression model, and the most appropriate cut-off probability for distinguishing breeding sites from random points was determined from the area under the ROC curve (AUC) (Metz 1978). A further 2000 random points were then located within the study area, of which 109 were classified as potential breeding sites based upon the probability value from the MAM. Those within 200 m of an actual breeding site were excluded, as this was the minimum distance between breeding sites occupied in the same year during the intensive studies of 1998–2000 (Burfield 2002), as were any where none of the 30×30 -m pixels immediately surrounding the site grid reference was classified as

heather or grass–heather mosaic. This latter restriction was included because 90% of Ring Ouzel nests in the study area occur in, under or behind heather bushes (Burfield 2002), and it was decided to exclude from consideration sites that had no suitable nesting habitat. This left 74 potential breeding sites, from which 41 were randomly selected. These analyses compared the habitat composition of actual and potential breeding sites using the same logistic regression and spatial autocorrelation methods as described above (for analyses of breeding site desertion), again examining composition within 200 and 450 m radii.

RESULTS

Accuracy of habitat mapping/measuring habitat composition

The most accurate habitat classification was produced using bands 1–5 and 7 from the satellite image in combination with altitude, with an overall kappa value of 0.729. This resulted in highly accurate predictions of the distribution and cover of bracken and grass, with over 90% of pixels from the relevant test plots (i.e. those not included in producing the classification) being classified correctly (Table 2). Predictions for heather and the two heather mosaic categories were poorer, with approximately 70% of pixels from test plots being classified correctly. Much of the error in classifying these three latter habitats arose from misclassifications among these categories, and there was a 97% (141/145) success rate in classifying pixels from the test plots in these habitats when they were combined into a single category. Therefore, although some caution is required in using the resulting information on the distribution and cover of each of these three habitats individually, the habitat map did provide reliable information on the distribution of all habitats comprising a substantial heather component.

Factors affecting the probability of continued occupancy of 'historical' breeding sites

'Historical' breeding sites were more likely to have remained occupied if they were at higher altitudes and had more heather habitat, within both the 200 and the 450 m radii (Table 3). In addition, continued occupancy was associated with increasing distance from the nearest stream within the 450 m radius (Table 3). On average, occupied breeding sites were 78 m higher in altitude, and contained 18 and 14% more heather habitat within the 200 and 450 m radii, respectively, than those sites that had apparently become deserted (Table 4). Bracken (at both radii) and grass (within 450 m) were the two habitats that compensated for the lower heather cover around deserted sites. The predicted probability of historical sites remaining occupied increased rapidly as heather cover increased up to *c.* 20–40% at both the 200 and the 450 m radii, although there was a more marked levelling off beyond this cover at the 450 m radius (Fig. 2). Occupied breeding sites were, on average, 20 m further from the nearest stream than apparently deserted sites.

The inclusion of the geographical coordinates of each site to model spatial covariance patterns produced a significant improvement in model performance, relative to a non-spatial model, at both 200 m ($\Delta\text{AIC} = -9.1$) and 450 m ($\Delta\text{AIC} = -36.1$) radii. Although the parameter estimates were largely unchanged, the significance values of the fixed effects were reduced, largely through the apparent reduction in sample size, as reflected in the revised degrees of freedom calculated using the Kenward–Rogers correction (Table 3). Thus, none of the fixed effects remained significant, although the effects of altitude within 200 m, and of distance to stream within 450 m, approached $P < 0.05$. The likely cause of the spatial autocorrelation of the heather effect is that

Table 2. The percentage of test pixels of each moorland habitat-type classified correctly in a supervised classification of satellite image data. The test pixels were taken from a sample of plots that were not used in producing the supervised classification.

Habitat	No. of test pixels	Correctly predicted (%)	Misclassifications
Bracken	20	95	Heather (5%)
Grass	73	93	Bracken (6%), grass–heather (1%)
Heather	49	71	Cotton-grass–heather (23%), grass–heather (4%), bracken (2%)
Grass–heather	56	68	grass (12%), Cotton-grass–heather (11%), heather (5%), bracken (4%)
Cotton-grass–heather	40	70	Grass–heather (22%), heather (5%), grass (3%)

Table 3. Summary of the logistic regression models determining variables associated with the likelihood of continued occupancy of 'historical' breeding sites within radii of 200 and 450 m. Variables are listed in order of entry to model. Significance was tested using χ^2 , except for the spatial autocorrelation model when an F -test was used.

Variable	Coefficient	se	χ^2/F	df	P
200 m					
Intercept	-10.525	3.404			
Altitude	0.027	0.009	17.16	1	< 0.0001
Heather	0.050	0.026	4.82	1	0.028
200 m (accounting for spatial autocorrelation effects)					
Intercept	-9.613	4.232			
Altitude	0.025	0.011	5.03	1, 5.9	0.067
Heather	0.041	0.031	1.72	1, 10.9	0.216
450 m					
Intercept	-13.342	4.059			
Altitude	0.030	0.010	17.51	1	< 0.0001
Heather	0.085	0.040	6.78	1	0.009
Distance to stream	0.027	0.016	4.50	1	0.034
450 m (accounting for spatial autocorrelation effects)					
Intercept	-9.670	4.266			
Altitude	0.020	0.011	3.27	1, 15.4	0.090
Heather	0.076	0.044	3.02	1, 13.9	0.104
Distance to stream	0.023	0.011	4.06	1, 28.5	0.054

Table 4. The percentage composition of different habitats in the study area, and within 200 and 450 m of occupied and deserted 'historical' breeding sites, and of potential breeding sites. An additional 3.2% of the study area was comprised of fresh water and bare ground. Potential breeding sites are defined by their topography, proximity to occupied sites and the immediately adjacent habitat (see text). Values of the other habitat and topographical variables used in the logistic regression analyses are also given for the different categories of breeding site, and all values are means (± 1 se). Variables that are statistically significant in one or more of the logistic regression analyses are shown in bold type.

	Study area	200-m radius			450-m radius		
		Occupied	Deserted	Potential	Occupied	Deserted	Potential
Bracken	20.9	24.5 \pm 3.6	50.7 \pm 3.8	26.4 \pm 2.9	24.1 \pm 2.9	45.8 \pm 4.1	22.4 \pm 1.8
Grass	14.6	10.6 \pm 3.2	14.3 \pm 4.6	16.5 \pm 3.0	13.6 \pm 2.6	24.2 \pm 5.0	19.3 \pm 3.0
Heather	19.3	30.5 \pm 4.6	12.3 \pm 3.3	25.0 \pm 4.6	24.2 \pm 3.5	9.9 \pm 3.2	23.4 \pm 3.7
Grass-heather	14.3	22.9 \pm 2.5	16.4 \pm 3.3	25.0 \pm 2.5	24.1 \pm 2.2	13.0 \pm 2.1	23.8 \pm 1.7
Cotton-grass-heather	15.2	9.4 \pm 1.7	2.2 \pm 0.8	6.2 \pm 1.2	12.4 \pm 1.8	3.7 \pm 1.6	9.3 \pm 1.3
Improved pasture	0.5	0.1 \pm 0.0	0.4 \pm 0.3	0.0 \pm 0.0	0.2 \pm 0.1	1.1 \pm 0.4	0.0 \pm 0.0
Forest	12.0	0.4 \pm 0.2	0.7 \pm 0.4	0.2 \pm 0.2	0.6 \pm 0.3	0.8 \pm 0.4	1.3 \pm 0.8
Altitude		414 \pm 10	336 \pm 11	421 \pm 7	414 \pm 10	336 \pm 11	421 \pm 7
Mean slope		6.7 \pm 0.2	6.1 \pm 0.4	6.8 \pm 0.3	5.9 \pm 0.2	5.5 \pm 0.3	6.1 \pm 0.2
Distance to stream		58.6 \pm 8.8	38.2 \pm 5.3	89.3 \pm 10.6	58.6 \pm 8.8	38.2 \pm 5.3	89.3 \pm 10.6

35% (6/17) of the deserted territories were located in one valley with little heather cover (Fig. 1). To assess whether the relatively strict (but arbitrary) criteria used for selecting the historically occupied breeding sites (see Methods) influenced the main findings of this analysis, the models in Table 3 were recalculated with the additional 12 sites occupied in less than 50% of survey years during 1952–85 included (four of which were also occupied during 1998–2000).

Final models, including the spatial covariance term, failed to retain both altitude ($F_{1,17} = 2.54$, $P = 0.130$) and heather ($F_{1,32.2} = 2.96$, $P = 0.095$) at the 200-m radius. However, both heather ($F_{1,15.9} = 4.68$, $P = 0.046$) and distance to stream ($F_{1,60} = 4.29$, $P = 0.043$) were retained at the 450-m radius, although altitude was not ($F_{1,13.2} = 2.65$, $P = 0.127$).

Several of the independent variables considered in the above analyses were highly intercorrelated, as

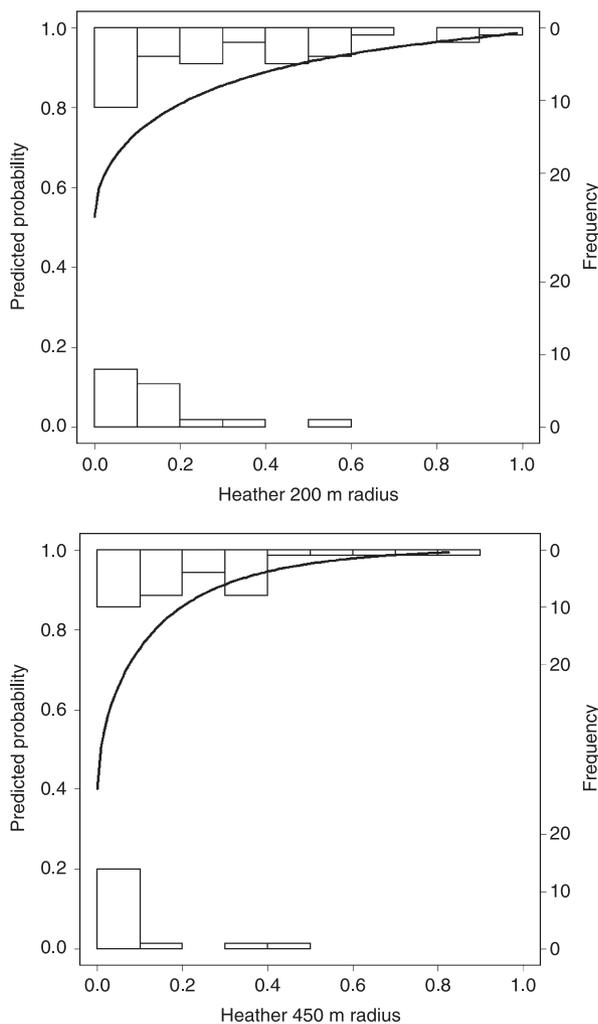


Figure 2. Modelled probability of continued occupancy of breeding sites in relation to heather cover within radii of 200 and 450 m. The bars indicate the number of sites in each heather cover category that had become deserted (lower axis) and that had remained occupied (upper axis).

might be expected from the nature of compositional data and the likely strong influence of topography on habitat (Appendix). In particular, altitude was strongly and negatively correlated with bracken cover and, in both models, there was a significant effect of bracken on the likelihood of continued occupancy when altitude was replaced by bracken ($\chi^2 > 15.09$, $df = 1$, $P < 0.001$ in both cases). There was a strong positive correlation between Cotton-grass–heather mosaic and altitude, and, unsurprisingly, grass and heather cover showed strong negative correlations at both radii.

Table 5. Summary of the logistic regression model distinguishing occupied breeding sites from random points on the basis of topographical variables. Curvilinear terms are indicated by superscript (²). Variables listed in order of entry to model.

Variable	Coefficient	se	χ^2	df	P
Intercept	−32.890	11.888			
Distance to stream	−0.023	0.007	22.43	1	< 0.0001
Mean slope	0.719	0.261	10.32	1	0.0013
Altitude	0.150	0.055	11.32	1	0.0008
Altitude ²	−0.0002	0.0001	11.44	1	0.0007

The influence of habitat in determining occupancy of topographically suitable breeding sites

Occupied breeding sites were closer to streams, had a higher mean slope within the 200 m radius and were located at more intermediate altitudes than were randomly selected sites in the study area (Table 5). The model explained 56% of the deviance in the data, and the ROC plot indicated a high model performance ($AUC = 0.94 \pm 0.05$ se, $P < 0.001$). Based upon the AUC, random sites were considered to be topographically suitable for breeding Ring Ouzels if the predicted probability of being a breeding site from the topographical model was greater than 0.41.

After accounting for topography and the minimum recorded distance between occupied breeding sites, actual breeding sites were more likely to have at least one heather or grass–heather mosaic pixel among the nine immediately surrounding pixels than were the potential breeding sites (i.e. 93% compared with 68%, $\chi^2 = 8.26$, $df = 1$, $P = 0.004$). In addition, the mean number of heather and grass–heather mosaic pixels among these nine was significantly higher for actual breeding sites (4.8) than for potential sites (3.4) ($\chi^2 = 4.01$, $df = 1$, $P = 0.045$). Following the incorporation of a spatial covariance term to account for spatial autocorrelation in these analyses (see above), the effect of the presence of at least one heather or grass–heather mosaic pixel remained significant ($F_{1,80} = 6.48$, $P = 0.013$), but the effect of the mean number of pixels did not ($F_{1,76.3} = 3.41$, $P = 0.069$).

Having accounted for the differences in the immediately adjacent habitat (by selecting a sample of potential breeding sites where at least one of the nine surrounding pixels comprised heather or grass–heather mosaic), no variables were found to have a significant (at $P < 0.05$) effect in distinguishing actual and potential breeding sites. This applied to

the logistic regression analyses performed using habitat data from within both 200 m and 450 m.

DISCUSSION

Potential limitations of the study

Most of the surveys during 1952–85 were carried out 2–4 times per month, whereas those during 1998–2000 were conducted on a weekly basis and included tape playback, which increases detectability (Wotton *et al.* 2002). The more rigorous survey methods used in 1998–2000 reduced the risk of misclassifying breeding sites as deserted when they were in fact still occupied. Therefore, the differences in survey methods between the two time periods were unlikely to have affected the results.

Analyses of the continued occupancy of breeding sites were affected by spatial autocorrelation, which when taken into account generally caused the heather and altitude effects to become non-significant (although heather cover remained significant, irrespective of spatial autocorrelation, in the 450-m radius analysis when all 64 breeding sites were included). This was probably caused by the aggregation of 35% of all deserted sites within one valley in the study area. Land management regimes (notably livestock grazing and burning) are likely to be critical in determining the distribution of heather cover on moorlands in southern Scotland (Thompson *et al.* 1995, Mackey *et al.* 1998), and given that these will vary between farming units or estates, substantial spatial variation in heather cover between adjacent valleys within a hill range is likely. Thus, if heather cover is important in causing desertion of breeding sites, deserted sites are likely to be aggregated in this way. In addition, if the altitudinal effects detected in this study are surrogates for habitat effects (see below), they could be similarly affected.

Although there is a growing awareness of the importance of accounting for spatial patterns in ecological data, relatively few studies have attempted to deal with the potential problems, particularly by modelling spatial covariance within a mixed model. In contrast to the more widely used autocovariate term (Augustin *et al.* 1996), this allows the spatial structure of the explanatory variables to be accounted for as well as the spatial component of the bird data, and in conjunction with the Kenward–Rogers correction, the degrees of freedom recalculated to account for the non-independence of adjacent samples. However, by doing so in this analysis, the effects of

heather and altitude in determining the continued occupancy of breeding sites became of marginal significance, or non-significant. Thus, although we discuss the biological relevance of the putative effects of heather and altitude below, the potential for the aggregation of the deserted nest-sites (Fig. 1) to have resulted in non-independent data and Type I errors cannot be discounted. Therefore, our conclusions about the causes of breeding site desertion must be interpreted with caution.

Effects of habitat composition on breeding site occupancy

Deserted breeding sites were found at lower altitudes, and contained less than half the heather cover of sites that continued to be occupied by Ring Ouzels, within both 200 m and 450 m of the site. In addition, the only difference detected between currently occupied sites and those that were topographically suitable for breeding, but at which no breeding had been recorded, was the higher likelihood of heather or grass–heather mosaic in the immediate vicinity of the occupied sites. Ring Ouzels are known to select heather nest-sites, both in the Moorfoot Hills and elsewhere (Arthur & White 2001, Burfield 2002). However, during the nestling period they often select short grass for foraging, and occupy home ranges that comprise more short grass habitat and less heather moor than expected from their availability (Burfield 2002, Prigmore 2003). The findings of the present study suggest that topographically suitable, but unoccupied, sites lacked only sufficient heather cover for nesting purposes, and that desertion of sites may be associated with heather loss.

The lack of comparable historical habitat data precluded a formal analysis of breeding site desertion in relation to habitat change. However, a comparison of broad habitat categories discernible from aerial photographs from 1946 and 1988 found that increases in the extent of conifer plantation and decreases in the extent of heather-dominated moorland were the main changes in the study area (Burfield 2002). Additionally, the 42% reduction in the extent of heather moorland recorded in the Scottish Borders region between the 1940s and 1980s, due largely to conversion to grass- (and possibly bracken-) dominated vegetation, provides further evidence to suggest that heather loss is likely to have occurred in the Moorfoot Hills (Mackey *et al.* 1998).

Given the known habitat preferences of Ring Ouzels, the loss of heather for nesting cover may be

the critical factor leading to breeding site desertion. Annual variation in Ring Ouzel nesting success within different UK breeding areas appears to be strongly density dependent, with fewer fledglings produced per nesting attempt in years of high population densities (Beale *et al.* 2006). Predation of clutches and broods is often the main proximate cause of nest failure (Burfield 2002, Beale *et al.* 2006), and the occupancy of more vulnerable breeding sites at higher breeding densities is one possible mechanism underlying the observed density dependence. Variation in heather cover around nest-sites in the Moorfoot Hills may affect predation risk, such that sites with little heather cover are more vulnerable to predation, with heather loss leading to lower breeding success and the eventual desertion of sites. The occurrence of heather close to preferred short grass foraging areas could also be important, as it may provide ready access to cover from predators for foraging birds; alternatively it may provide access to a wider range of invertebrate prey. However, if the interspersed heather with grass at the scale of foraging patches is important in determining continued site occupancy, effects of grass–heather mosaic on occupancy would have been expected. Unfortunately, the power to detect such effects was limited by the difficulty of distinguishing grass–heather mosaic from more continuous heather cover.

Desertion of breeding sites was also more likely at lower altitudes. If this desertion is due to habitat change, then the relationship with altitude could represent a surrogate for heather loss (as opposed to the current cover measured in this study), which tends to be greatest at lower altitudes on moorland (e.g. Redpath & Thirgood 1997). Alternatively, it could result from detrimental effects of bracken, as bracken cover was strongly and negatively inter-correlated with altitude, and is likely to have increased in cover during the study period (Marrs & Pakeman 1995, Mackey *et al.* 1998). However, other studies provide some circumstantial evidence of benefits to Ring Ouzels from bracken (Haworth & Thompson 1990, Stillman & Brown 1994, Chamberlain *et al.* 2000, Burfield 2002). Other habitat changes resulting from agricultural intensification (e.g. drainage and grassland improvement), which may reduce the availability of prey or nesting cover, may also have been most marked in moorland edge areas, possibly contributing to the relationship with altitude. Broader-scale analyses from across Scotland have detected similar effects of altitude, with declines more likely at altitudes below 350 m (Buchanan *et al.* 2003). These analyses also suggested a higher likelihood of declines at the upper

altitudinal range, beyond 750 m (which is more difficult to attribute to habitat change), but this was higher than any breeding sites in the Moorfoot Hills.

Explaining the causes of Ring Ouzel population declines

Reductions in heather cover and consequent increases in grass cover, resulting largely from increased grazing, have been a major habitat change in many parts of the UK uplands since the 1940s (Huntings Surveys 1986, Mackey *et al.* 1998). This change could help explain the decline in the UK's breeding Ring Ouzel population (Gibbons *et al.* 1993, Gregory *et al.* 2002), if the association between heather cover and the continued occupancy of breeding sites identified in the present study is causal. Some support for the possibility that heather loss has had a widespread impact on the Ring Ouzel population comes from broad-scale analyses from across Scotland, in which Ring Ouzel declines were found to be more likely in areas where smooth grass–heather mosaics were initially extensive (Buchanan *et al.* 2003). Given the greater susceptibility to heather loss where it is present as a fine-scale mosaic with grass (Clarke *et al.* 1995), Buchanan *et al.* (2003) proposed this as an explanation for the relationship.

However, it is possible that the association between the continued occupancy of breeding sites and heather cover simply reflects a contraction of birds into favoured breeding sites, as the population declines for other reasons. This could occur as a consequence of the buffer effect (Kluyver & Tinbergen 1953), causing more marginal breeding sites with less heather cover to have been occupied when breeding densities in the study area were previously higher. The topographic associations with population declines and/or the desertion of breeding sites, identified in this and in other studies (Buchanan *et al.* 2003), may support this possibility, although as described above such associations could be surrogates for habitat change. Other studies have pointed to alternative causes of decline, including both other land-use and climatic effects. Thus, afforestation with conifer plantations has caused direct habitat loss (Avery & Leslie 1990), whilst declines also appear to be more likely on moorland with extensive afforestation in the surrounding area (Buchanan *et al.* 2003). As with the findings from the present study, this longer-term association with the extent of conifer plantations (i.e. beyond the initial direct habitat loss) could reflect a contraction into more

favoured breeding areas, as opposed to being a cause of decline. Although conifer plantations are present in the Moorfoot Hills, they comprised just 12% of the study area (and much less of the land within 200 or 450 m of known or potential breeding sites), so that effects of their proximity on site occupancy were not expected. Evidence for a link between population decline and large-scale climatic processes has also been found in analyses using the same long-term dataset on Ring Ouzel occupancy as the present study (Beale *et al.* 2006). These analyses suggest that increasing temperatures during late summer (June–August) in the UK may be sufficient to account for the decline in the Moorfoot Hills, with reduced food availability during the post-breeding period being one possible explanation for such an effect.

Clearly, there is circumstantial evidence for a number of different causes of decline in the UK breeding Ring Ouzel population. These different lines of evidence need not be contradictory and several factors may be acting together to drive the decline. However, conservation action aimed at halting and reversing the decline will require clear diagnosis of which of the potential factors are most important, and this will require further detailed investigation. In relation to the findings from the present study, testing for potential mechanisms that cause lower altitude breeding sites with less heather cover to become deserted would appear to be of highest priority, whilst studies to test the wider applicability of the finding would also be valuable. Large-scale management trials may eventually be required to test whether heather restoration produces population recovery in areas where Ring Ouzels have declined, and where heather loss has occurred. Further studies should also consider potential interactions that may exist between breeding site habitat composition, productivity and weather variables.

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APPENDIX

Matrix of significant ($P < 0.05$) Spearman's rank correlation coefficients ($n = 52$) for the ten explanatory variables used in analyses to determine factors associated with the continued occupancy of 'historical' breeding sites at the 200- and 450-m radii. Figures have been multiplied by 100 and rounded to the nearest whole number for presentation.

	Bracken	Grass	Heather	Grass– heather mosaic	Cotton-grass– heather mosaic	Improved pasture	Forest	Altitude	Mean slope	Distance to stream
200-m radius										
Grass										
Heather	–42	–78								
Grass–heather mosaic	–29									
Cotton-grass–heather mosaic	–57			+60						
Improved pasture	+39				–28					
Forest	+39			–38	–47	+58				
Altitude	–85			+40	+74	–41	–47			
Mean slope			+29		–40					
Distance to stream					–34					
450-m radius										
Grass										
Heather	–33	–89								
Grass–heather mosaic	–47									
Cotton-grass–heather mosaic	–78			+66						
Improved pasture	+75			–41	–62					
Forest	+40	–29		–48	–61	+56				
Altitude	–86			+50	+87	–74	–46			
Mean slope		–36	+41	–28				+33		
Distance to stream										