Journal of Biogeography (J. Biogeogr.) (2005) 32, 697–707

ORIGINAL ARTICLE

Characterization of moorland vegetation and the prediction of bird abundance using remote sensing

Graeme Buchanan[1]*, James Pearce-Higgins[1], Murray Grant[1], Duncan Robertson[2] and Tony Waterhouse[2]

[1]RSPB, Dunedin House, Edinburgh, UK and [2]SAC, Hill and Mountain Research Centre, Edinburgh, UK

ABSTRACT

Aims To characterize and identify upland vegetation composition and height from a satellite image, and assess whether the resulting vegetation maps are accurate enough for predictions of bird abundance.

Location South-east Scotland, UK.

Methods Fine-taxa vegetation data collected using point samples were used for a supervised classification of a Landsat 7 image, while linear regression was used to model vegetation height over the same image. Generalized linear models describing bird abundance were developed using field-collected bird and vegetation data. The satellite-derived vegetation data were substituted into these models and efficacy was examined.

Results The accuracy of the classification was tested over both the training and a set of test plots, and showed that more common vegetation types could be predicted accurately. Attempts to estimate the heights of both dwarf shrub and graminoid vegetation from satellite data produced significant, but weak, correlations between observed and predicted height. When these outputs were used in bird abundance–habitat models, bird abundance predicted using satellite-derived vegetation data was very similar to that obtained when the field-collected data were used for one bird species, but poor estimates of vegetation height produced from the satellite data resulted in a poor abundance prediction for another.

Conclusions This pilot study suggests that it is possible to identify moorland vegetation to a fine-taxa level using point samples, and that it may be possible to derive information on vegetation height, although more appropriate field-collected data are needed to examine this further. While remote sensing may have limitations compared with relatively fine-scale fieldwork, when used at relatively large scales and in conjunction with robust bird abundance–habitat association models, it may facilitate the mapping of moorland bird abundance across large areas.

*Correspondence: Graeme Buchanan, RSPB, Dunedin House, 25 Ravelston Terrace, Edinburgh, EH4 3TP, UK.
E-mail: graeme.buchanan@rspb.org.uk

Keywords
Bird–habitat associations, heather, land cover, landsat, mapping bird habitats, satellite image, Scotland uplands.

INTRODUCTION

The UK uplands are of international conservation importance, particularly for their range of moorland and blanket bog plant communities and the associated breeding bird assemblage (Thompson *et al.*, 1995). The scale of the uplands, and the logistical problems of surveying remote areas, makes it difficult to estimate the abundance and distribution of upland birds. However, habitat can be an important determinant of bird densities on moorland (e.g. Haworth & Thompson, 1990; Brown & Stillman, 1993; Stillman & Brown, 1994), so that appropriate habitat data, used in conjunction with reliable bird

 doi:10.1111/j.1365-2699.2004.01187.x

abundance–habitat association models, could allow accurate prediction of bird abundance across upland areas. However, to achieve this requires habitat data to be collected from these extensive, often remote, areas, which again may be impractical or prohibitively expensive by field methods alone (Sutherland, 1996).

Remote sensing can provide objective assessments of vegetation composition, offering the potential to measure habitat characteristics across extensive areas, as demonstrated for a range of different habitats (e.g. Trisurat *et al.*, 2000; Bobbe *et al.*, 2001; Clark *et al.*, 2001; Wang & Moskovits, 2001). Previously in the UK uplands, satellite images have been used primarily to map the distribution of relatively broad habitat categories (e.g. Harding & Brown, 1990; Johnston & Morris, 2000). A recent study suggested that heather *Calluna vulgaris* (L. Hull) biomass can be predicted from satellite imagery (Egan *et al.*, 2000), indicating that measurements of potentially important habitat characteristics, at a sufficiently fine-scale to be useful in predicting bird densities on moorland, may be feasible.

In this paper, we use data on the composition and structure of moorland vegetation in south Scotland in conjunction with a Landsat 7 satellite image to produce a supervised classification of vegetation composition, and assess the performance of the satellite data in calculating the height of moorland vegetation. The resulting predictions are used in conjunction with bird abundance–habitat association models, derived from a wider data set from south Scotland, to predict the abundance of red grouse, *Lagopus lagopus scoticus* (Latham), and golden plover, *Pluvialis apricaria* (L.), two birds characteristic of UK moorlands that were sufficiently abundant and prevalent to enable the investigation of bird–habitat associations and the testing of the resultant predictions. The performance of the satellite-derived bird abundance predictions, based on the estimates of vegetation composition and height, were compared with the observed abundance and that obtained using the field-collected vegetation data.

METHODS

Study plots

Habitat and bird data were collected from a total of 85, 2 km^2 plots located on unenclosed hill ground in southern Scotland and northern England in either 1999 or 2000. Plots were located largely by using National Countryside Monitoring Scheme (NCMS) (Mackey *et al.*, 1998) plots together with a selection derived from a 1990 Landsat Thematic Mapper heather cover map of Scotland (RSPB, unpubl. data). NCMS plots are a stratified random sample from across Scotland, providing information on vegetation cover, so that from both sources study plots could be randomly selected from three strata of heather cover (i.e. < 30%, 30–60% and > 60%), ensuring coverage of a range of moorland types. Most were at least 1 km apart, although four were within 500 m of another plot. Thirty-six of these plots, within an area of *c.* 6000 km^2, were covered by a Landsat 7 image of south-east Scotland (path 204, row 21) from 7 May 2000. The data from a random selection of 26 of these 36 plots were used as training plots, while the data from the remaining 10 plots were used as an independent test of the vegetation maps and bird abundance predictions produced from the training plot data analysis.

Data collection

The vegetation data used for training the satellite image were originally collected to produce statistical models relating bird abundance to habitat, and were collected by a point sampling method, using a grid of 100–120 samples per plot (Pearce-Higgins & Grant, 2002). Sampling was conducted between 21 June and 24 July in each year, with the sampling points located using 1 : 25,000 maps, and by pacing along compass bearings. Thus, data collection was not specifically designed for the training of satellite image data, and differed from conventional methods which generally use multiple large stands of homogeneous vegetation as training areas (e.g. Campbell, 2002).

At each sampling point, vegetation composition beneath a 1 m stick placed horizontally on the ground was recorded to the nearest 5%. All dwarf shrubs were identified to species, whilst the following grasses, sedges and rushes were distinguished: *Nardus stricta* (L.), *Molinia caerulea* (L.), smooth grasses [mainly *Agrostis* (L.) spp., *Deschampsia flexuosa* (L.), *Festuca* (L.) spp.], *Eriophorum vaginatum* (L.), *E. angustifolium* (Honck), *Scirpus cespitosus* (L.), *Luzula* spp., tall rushes [*Juncus effusus* (L.), *J. conglomeratus* (L.) and *J. acutifloris*] and *J. squarrosus* (L.), along with bracken [*Pteridium aquilinum* (L.)]. Mosses were separated into *Sphagnum* spp. and others. Three measures of the maximum height (rounded down to the nearest 5 cm) of graminoids (i.e. grasses, sedges and rushes) and dwarf shrubs were made at each sampling point. These values were averaged to produce measures of both graminoid and dwarf shrub height at each sampling point at which they were present.

The abundance of the two bird species (red grouse and golden plover) was assessed using a three-visit census method with surveys from 17 April to 8 May, 9 May to 30 May and 31 May to 20 June. On each visit, routes were walked such that the observer walked within 100 m of every point within the plot, and the distribution and activities of birds mapped (Brown & Shepherd, 1993). The maximum count of presumed breeding pairs from the three visits to the plot was used as the measure of abundance.

Manipulation of the satellite image and development of models to characterize vegetation composition

Manipulation of the satellite image was conducted in IDRISI 32.2 (Clarke Laboratories 2001, Worcester, MA, USA), with bands 1–5 and band 7 geo-referenced to OSGB on Transverse Mercator projection to within 1 pixel (RMS < 30 m), and shade-corrected using a 50 m digital terrain model (Panorama, Ordnance Survey, Southampton, UK). The methods used to collect vegetation data meant there were potential problems in relating these to the satellite image, as the area covered by the vegetation sampling points (1 m) was considerably smaller than a Landsat 7 pixel (30 m × 30 m). Additionally there was potential error in the location of sampling points, which, although difficult to quantify, should have been controlled for by basing the analysis on reflectance values averaged over blocks of 3 × 3 pixels (equivalent to 90 m × 90 m) surrounding and including the pixel representing the estimated sampling point location. This process was repeated for every pixel in the image. Whilst this increased the discrepancy in scale between the field-collected and satellite-derived data, so increasing the risk that the vegetation at the sampling point was unrepresentative of that within the nine-pixel block on the image, we considered that this error would be offset by the large number of sampling points (> 2000).

Spectral signatures were then developed for the nine vegetation types that were present in at least 10% of the sampling points (Table 1), using the Makesig command in IDRISI with the digital reflectance values (between 0 and 255) of bands 1–5 and 7. Scarcer land cover or vegetation (e.g. bare ground, *Carex* patches, *Erica* spp.) was not considered further. Linear discriminant analysis (LDA) was used to produce a supervised classification of vegetation using the standard LDA procedure in IDRISI. Thus, vegetation was classified according to the dominant vegetation type present. As the LDA procedure in IDRISI does not provide the information required to enable variable selection based upon statistical significance levels, all bands were included in the classification.

Developing models to predict vegetation height

Predictive models of vegetation height were produced using linear regression. The heights of dwarf shrubs [*C. vulgaris* and *V. myrtillus* (L.)] and graminoids (*N. stricta*, *M. caerulea*, smooth grasses, *E. vaginatum* and *J. squarrosus*) were considered separately, while the tall rushes (*J. effusus*, *J. conglomeratus* and *J. acutiflorus*) were excluded from the predictions of graminoid height because of their markedly different structure and low number of sampling points at which they were dominant. To avoid modelling distribution, rather than height, only sampling points where either dwarf shrubs or graminoids were present at each of the three height points were included.

Vegetation height was the dependent variable with the digital reflectance values of bands 1–5 and 7, along with the normalized-derived vegetation index (NDVI), and greenness (e.g. Campbell, 2002) as covariates. The values of each covariate were averaged across all points with the same height value to reduce the influence of non-representative points, and the analysis was weighted by the number of points contributing to that average. Analyses were conducted using the GENMOD procedure in SAS v.8 (SAS Institute 2001, Cary, NC, USA), specifying a normal error structure and identity link function. Variable selection was conducted using a step-up procedure, in which the variable with the most significant change in deviance at each stage was incorporated into the model until no other variables were significant at the $P < 0.05$ level. After the inclusion of each new variable, the significance of terms already in the model was tested using type 3 contrasts (SAS Institute, 1997), removing any whose effect was no longer significant at the $P < 0.05$ level. To model curvilinear relationships, the quadratic term of each variable was included in conjunction with the linear term if the change in deviance associated with its inclusion was significant at the $P < 0.05$ level, or if the effect of the linear and quadratic terms were significant when considered together (e.g. Tharme *et al.*, 2001). The final relationships were then used to calculate dwarf shrub and graminoid heights across the whole satellite image at pixels where the appropriate vegetation type (dwarf shrubs or graminoid) was predicted to be present by the LDA. Finally, predicted vegetation heights were converted to three categories (short < 15 cm; medium 15–30 cm; tall > 30 cm) for consistency with the bird abundance–habitat modelling described below.

Developing models to predict bird abundance

Bird abundance–habitat models were constructed for the two moorland species (red grouse and golden plover). In order to maximize the data available to build these models, we used 75 of the original 85 plots (i.e. all available data bar the 10 test plots). Bird abundance was the dependent variable, whilst the covariates comprised the field-collected vegetation composition and structure data, together with a number of physical and management variables, all of which could be measured remotely, i.e. without having to visit the plot (Appendix 1). For the purposes of predicting bird abundance, vegetation height

Table 1 Output coefficients from the linear discriminant analysis performed in IDRISI for the supervised classification of vegetation composition. Significance values were not calculated

	Constant	Band 1	Band 2	Band 3	Band 4	Band 5	Band 7
C. vulgaris	−98.50	3.26	−0.98	−1.53	−0.09	1.60	−1.61
E. vaginatum	−101.65	3.37	−1.41	−1.28	−0.01	1.58	−1.61
Smooth grass	−98.99	3.11	−0.84	−1.54	−0.01	1.62	−1.63
J. squarrosus	−102.61	3.32	−1.15	−1.46	0.03	1.58	−1.61
M. caerulea	−91.55	2.94	−1.05	−1.08	−0.13	1.69	−1.77
Mosses	−97.70	3.23	−1.00	−1.43	−0.07	1.59	−1.65
N. stricta	−90.05	2.88	−0.61	−1.50	−0.04	1.60	−1.65
Rushes	−97.32	3.19	−1.07	−1.43	−0.01	1.57	−1.56
V. myrtillus	−94.45	3.10	−0.81	−1.49	−0.05	1.60	−1.67

data were summarized as the proportion of each plot comprising each of three categories (short, medium and tall). Considering the extent of different height categories in this way provides information that may be of more value in determining bird distribution across large areas than simply considering the overall mean height (Brown & Stillman, 1993; Stillman & Brown, 1994).

Analyses were performed using the procedure GENMOD in SAS, with a Poisson error distribution, log link function and a step-up method (see above), but with a Bonferroni corrected significance level ($P < 0.0019$) due to the large number of independent variables used. The resulting models of bird abundance were applied to the 26 training plots and 10 test plots, using both the field-collected vegetation data and the satellite-derived vegetation data, producing two predictions of abundance for each species.

RESULTS

Characterization of vegetation composition

The coefficients of the reflectance bands used to distinguish the different vegetation types by the LDA are displayed in Table 1. Across the training plots the estimates of predicted vegetation composition derived from the satellite data were significantly related to those derived from the field-collected data (observed) for six of the nine vegetation types considered (Table 2, Fig. 1). Here the relationship was close to 1 : 1 for *C. vulgaris* (indicating absolute prediction), but for other types there was considerable under- or overprediction, indicating that only relative composition was predicted well (Fig. 1). In the three cases where observed vs. predicted estimates were not significantly correlated (mosses, rushes and *V. myrtillus*), the vegetation types were relatively scarce (Table 2).

Table 2 Correlations between the observed values for the percentage composition of different vegetation types and those predicted from an analysis of satellite image data using linear discriminant analysis, across the 26 training plots. Observed values are as derived from field-collected data. Mean difference between observed and predicted percentage cover is the difference for each plot averaged over the total number of plots (26). *P = 0.05–0.01; *P = 0.01–0.001; n.s., not significant

Vegetation type	Pearsons *r*-value	Mean difference between observed and predicted % cover	No. of sample points
C. vulgaris	0.90**	12.1	958
E. vaginatum	0.78**	11.0	170
Smooth grass	0.78**	11.1	570
J. squarrosus	0.48*	5.9	122
M. caerulea	0.95**	7.2	194
Mosses	0.13 n.s.	5.4	132
N. stricta	0.68**	6.3	146
Rushes	−0.001 n.s.	4.6	115
V. myrtillus	0.32 n.s.	5.4	119

Across the 10 independent test plots, the predicted and observed percentage compositions were significantly correlated for four vegetation types (Table 3), with the relationships for heather, smooth grass and *M. caerulea* indicating that the cover of these vegetation types was predicted accurately, although the relationship for *V. myrtillus* should be viewed with caution, given the lack of a significant correlation across the training plots (Table 2). Although the correlations between the predicted and observed percentage composition on the test plots were non-significant for the other vegetation types, the relatively small mean differences between observed and predicted cover for several of these suggest that predictions were of approximately the correct magnitude (Table 3). These non-significant relationships were associated with a low degree of variation in cover between plots, with the maximum observed cover for any of these vegetation types on a test plot being 12.5% (Table 3). Such limited variation in cover, combined with the small sample size (10) would have reduced the chance of detecting a significant correlation between observed and predicted cover.

Across the nine vegetation types examined, there was a strong correlation between the number of training points used (i.e. the number of points at which the vegetation type was dominant on the training sites) and the level of correlation of the observed against the predicted cover on the test plots ($r_s = 0.72$, $P < 0.001$). This suggests that the reliability of the spectral signatures increased with sample size, although the absence of a correlation between observed and predicted covers for scarcer vegetation types could also be due to low variation in their cover values. This latter possibility may be more plausible, given that the mean error between the observed and predicted cover of vegetation types (Tables 1 and 2) was not significantly correlated with the number of training points used ($r_s = 0.42$, $P = 0.22$).

Characterization of vegetation height

Regression models produced to predict the height of dwarf shrubs and graminoids included different spectral reflectance bands, while the NDVI was also incorporated into the graminoid height model (Table 4). Both models explained a relatively small proportion of the deviance in the data (Table 4), potentially due to the difference in scale between the sampling point and the pixels summarizing the reflectance for that point. Despite this, there was a significant, but weak, positive relationship between the observed height and that predicted from the satellite image over the 26 training plots for both dwarf shrubs and graminoids, with overprediction of short vegetation height for both vegetation types (Fig. 2). These relationships remained positive, and significant, when considering the data from across the 10 independent test plots ($r_{610} = 0.24$, $P < 0.001$ for dwarf shrubs, and $r_{423} = 0.13$, $P = 0.01$ for graminoids).

Bird abundance

The bird abundance–habitat models describing red grouse and golden plover abundance explained 69% and 51% of the

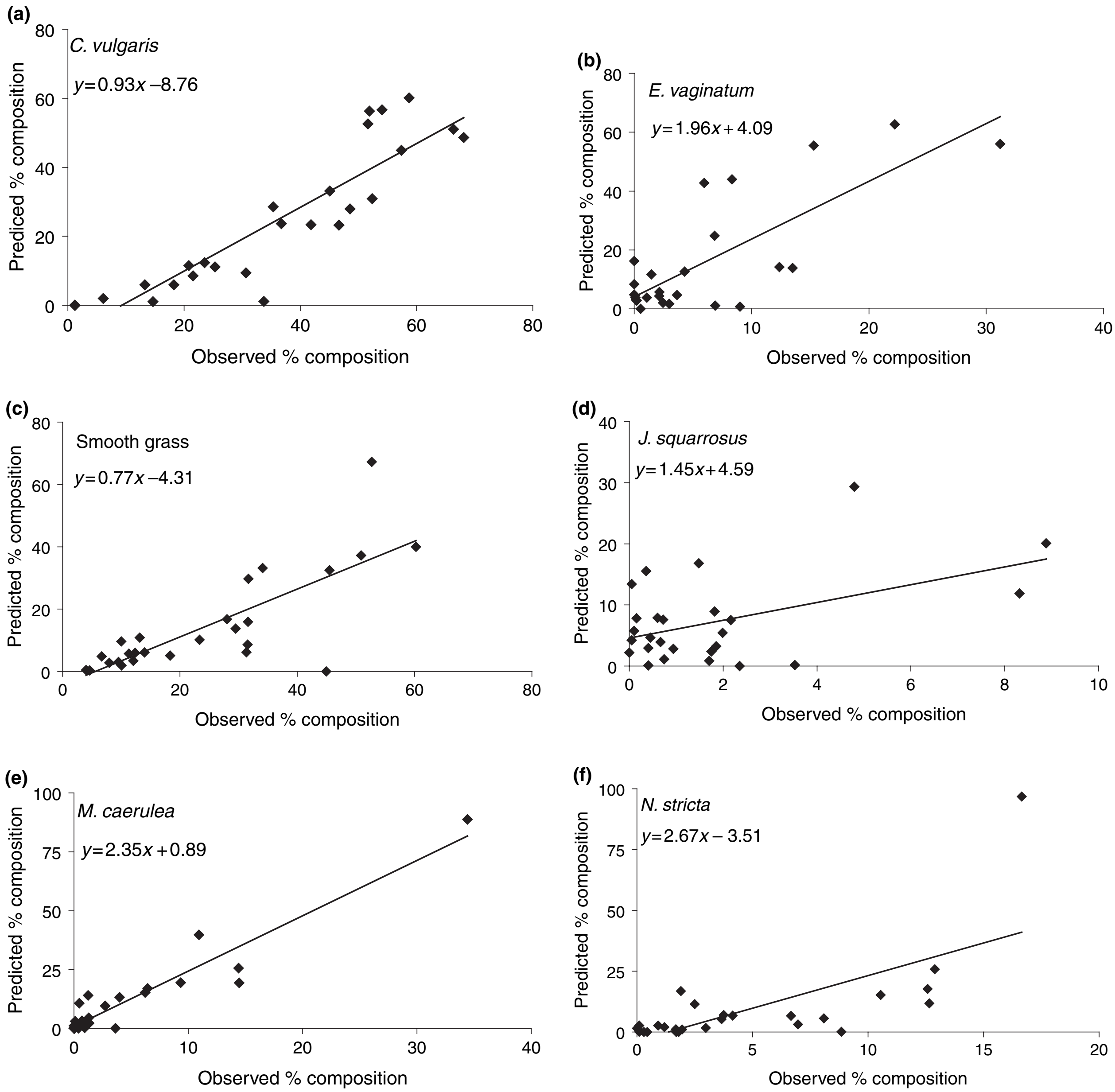

Figure 1 Observed (x-axis) and predicted (y-axis) percentage composition of upland vegetation types across 26, 2 km^2 training plots. Predicted values are derived from a supervised classification of a Landsat 7 image, whilst observed values are from field-collected data. Regression lines are shown (see Table 3 for correlation coefficients).

deviance in the abundance of these two species, respectively. Heather cover was the only measure of vegetation composition or structure included in the red grouse model, whilst the cover of both short dwarf shrubs and *E. vaginatum* were included in the golden plover model (Table 5). As described above (see Methods), the cover of short dwarf shrubs was derived from the satellite image by combining the maps of height and vegetation composition. The predicted cover of short dwarf shrubs was significantly correlated with the observed cover over the 26 training plots ($r_{26} = 0.49$, $P = 0.011$), but not over the test plots ($r_s = 0.16$, $P = 0.66$), although this may again be partially due to the reduced sample size.

Predicted red grouse abundance was strongly correlated with observed abundance across the 26 training plots (all of which were included in the data set used in model building), irrespective of whether the field-collected or satellite-predicted vegetation data were used in this model ($r_{26} = 0.74$, $P < 0.001$ and $r_{26} = 0.73$, $P < 0.001$, respectively; Fig. 3). The correlations were weaker for golden plovers, with the correlation between observed abundance and that predicted from field-collected data being slightly stronger than that predicted from satellite-derived data ($r_{26} = 0.63$, $P = 0.001$ and $r_{26} = 0.55$, $P = 0.004$, respectively; see Fig. 4).

Vegetation type	Spearman's rank correlation coefficient	Mean (range) of values		Mean difference between observed and predicted % cover
		Observed %	Predicted %	
C. vulgaris	0.92**	46.6 (1.0–72.4)	37.8 (0.0–83.7)	12.26
E. vaginatum	0.53 n.s.	2.7 (0.0–8.9)	8.8 (0.2–46.4)	6.78
Smooth grass	0.85**	23.3 (3.9–53.0)	12.0 (0.3–43.7)	11.32
J. squarrosus	−0.20 n.s.	1.2 (0.0–2.9)	3.2 (0.2–12.9)	3.15
M. caerulea	0.87**	3.4 (0.0–26.5)	3.8 (0.0–18.4)	2.54
Mosses	−0.49 n.s.	4.8 (0.8–12.5)	8.6 (0.1–60.8)	8.86
N. stricta	0.21 n.s.	3.5 (0.1–7.8)	8.6 (0.0–35.9)	7.26
Rushes	−0.05 n.s.	2.1 (0.0–7.1)	5.2 (0.3–11.5)	3.75
V. myrtillus	0.63*	4.0 (0.0–11.1)	11.9 (0.5–20.4)	8.05

Table 3 Correlations between the observed values for the percentage composition of different vegetation types and those predicted from an analysis of satellite image data, across the 10 independent test plots. Observed values are as derived from field-collected data. Mean difference between observed and predicted percentage cover is the difference for each plot averaged over the total number of plots (10). $*P = 0.05–0.01$ $**P = 0.01–0.001$; n.s., not significant

Table 4 Summary of generalized linear models describing the height of dwarf shrubs and graminoids across the 26 training plots. Models were produced by generalized linear modelling using a Poisson error distribution and step-up procedure. *F*-values are those associated with removal of the parameter from the final model

Vegetation	Model	% Deviance explained
Dwarf shrubs	−152.849 + (−3.7864 Band 4) + (5.2504 Band 1)	7
Graminoids	118.7387 + (−507.773 NDVI) + (1391.108 NDVI^2) + (−0.6713 Band 5)	24

As these 26 training plots had been used in the construction of the bird–habitat models, observed and predicted estimates were compared across the 10 independent test plots. For red grouse, the correlation between observed abundance and the model predictions across these 10 plots approached significance when using the field-collected vegetation data ($r_s = 0.58$, $P = 0.08$; Fig. 3), but not when using the satellite-predicted heather cover ($r_s = 0.37$, $P = 0.30$). However, the model predictions of abundance when using the two different estimates of heather cover were highly correlated ($r_s = 0.95$, $P < 0.001$), supporting the contention that the non-significance of the correlation was at least partially due to the reduced sample size.

For golden plover, observed abundance was highly correlated with the model predictions across the test plots when field-collected vegetation data were used ($r_s = 0.86$, $P < 0.001$). However, the model performed poorly when using the satellite-predicted vegetation data compared with the observed count ($r_s = -0.03$, $P = 0.98$; Fig. 4) and that calculated using the field-collected data ($r_s = -0.06$, $P = 0.98$). This was due to the poor prediction of short dwarf shrub cover, as the substitution of the satellite-derived estimates of short dwarf shrub cover with the field-collected estimates produced a better fit between observed and predicted abundance ($r_s = 0.82$, $P < 0.001$) than was achieved from the same substitution for *E. vaginatum* cover ($r_s = -0.01$, $P = 0.98$). Correcting for the overprediction of dwarf shrub height by using the relationship in Fig. 2 did not improve this relationship ($r_s = -0.28$, $P = 0.43$).

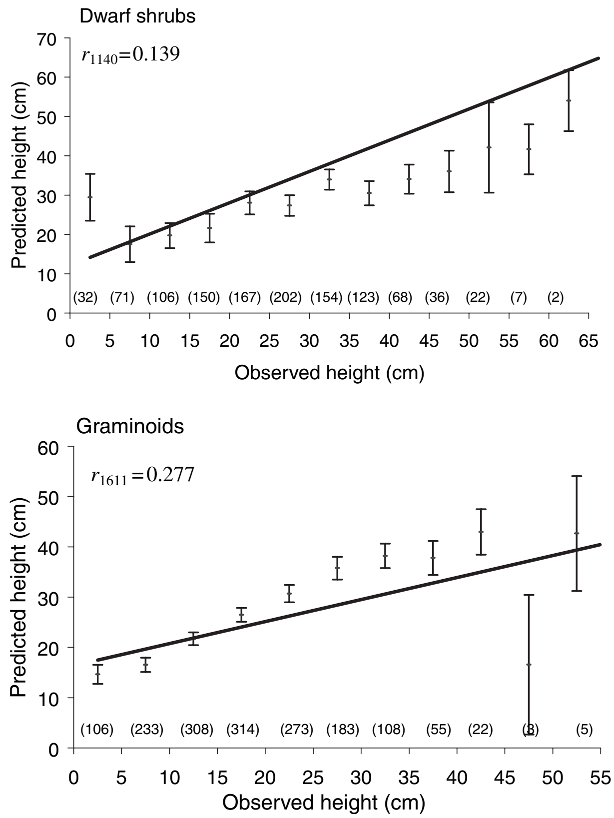

Figure 2 Observed and predicted heights (cm) of dwarf shrubs and graminoids across 26, 2 km^2 training plots. Predicted values are derived from a classification of a Landsat 7 image, using regression modelling, whilst observed values are from field-collected data. For the purposes of presentation, data are binned by 5 cm categories of observed height, with the mean (± SE) predicted value shown. Figures in brackets are sample size of each category. Least squares trend line is based on all data.

Table 5 Coefficients and *F*-values for parameters included in the regression models produced to describe the abundance of two moorland bird species. Models were produced by generalized linear modelling using a Poisson error distribution and step-up procedure. *F*-values are those associated with removal of the parameter from the final model

Parameter	Coefficient (± 1 SE)	*F*-value	d.f.	*P*
Red grouse				
Constant	−0.07 (± 0.90)	–	–	–
C. vulgaris cover	0.03 (± 0.01)	34.1	1,69	0.0001
Keeper index	2.93 (± 0.55)	26.2	1,69	0.0001
Altitude	0.003 (± 0.001)	14.7	1,69	0.0001
Longitude	−0.39 (± 0.15)	10.4	1,69	0.0019
Golden plover				
Constant	−112.38 (± 21.64)	–	–	–
Longitude	−1.62 (± 0.26)	49.3	1,69	0.0001
Latitude	2.12 (± 0.39)	35.3	1,69	0.0001
Short dwarf shrub cover	4.09 (± 0.91)	17.8	1,69	0.0001
E. vaginatum cover	0.05 (± 0.02)	10.9	1,69	0.0015

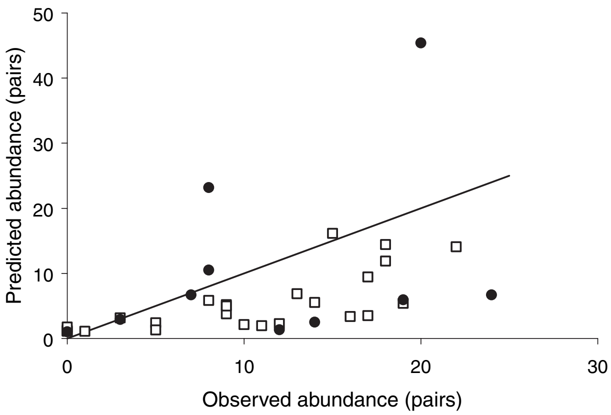

Figure 3 Predicted red grouse abundance (number of pairs) in relation to the observed abundance across 26, 2 km^2 training plots (open squares; $r_{26} = 0.73$, $P < 0.001$) and 10, 2 km^2 test plots (filled circles; $r_s = 0.37$, $P = 0.29$). Predicted abundance is calculated from a regression model incorporating environmental and management variables, and including vegetation variables that are mapped from a Landsat 7 image (see text). The training plots were used for the supervised classification of the Landsat 7 image, and were included in the building of the regression model for predicting abundance, whilst the test plots were excluded from both processes (see text). The line shows a 1 : 1 relationship.

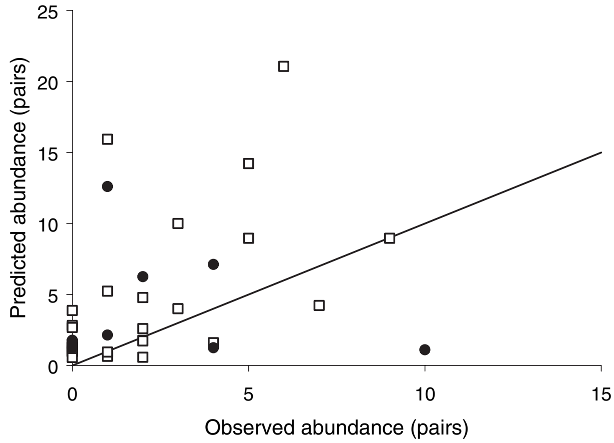

Figure 4 Predicted golden plover abundance (number of pairs) in relation to the observed abundance across 26, 2 km^2 training plots (open squares; $r_{26} = 0.55$, $P = 0.008$) and 10, 2 km^2 test plots (filled circles; $r_s = -0.03$, $P = 0.91$). Predicted abundance is calculated from a regression model incorporating environmental and management variables, and including vegetation variables that are mapped from a Landsat 7 image (see text). The training plots were used for the supervised classification of the Landsat 7 image, and were included in the building of the regression model for predicting abundance, whilst the test plots were excluded from both processes (see text). The line shows a 1 : 1 relationship.

DISCUSSION

Characterization of moorland vegetation using the satellite image

We were able to map moorland vegetation composition by supervised classification of a satellite image using a large number of small sampling points, although these vegetation data were collected without considering their potential application for this purpose. While the strong relationships between observed and predicted cover across the 26 training plots may have been due, in part, to these plots containing the data used to develop the spectral signature, the 10 test plots provide an independent test of the classification, and demonstrated that we were able to produce accurate maps of commoner moorland vegetation types. Variation in cover values, together with the number of sampling points contributing to the characterization of spectral signatures, were important in determining the accuracy of the vegetation maps. Therefore, using more plots on which there is a greater compositional range for the scarcer vegetation types (e.g. rushes, *N. stricta*) should increase the accuracy of mapping scarcer vegetation.

The results of this study indicate that the composition of individual plant taxa can be mapped accurately, at least within the 2 km^2 scale examined here, despite moorland vegetation frequently being heterogeneous, in terms of both composition and structure, often comprising mosaics at varying scales of dwarf shrub and graminoid dominant vegetation (e.g. Clarke *et al.*, 1995). Such relatively fine-taxa measures of vegetation composition, especially considered together with larger, landscape-scale vegetation data (e.g. Buchanan *et al.*, 2003, J. Pearce-Higgins and M. Grant, unpubl. data), may be of more value in understanding and predicting upland bird distribution than the broader categories than have been used previously (e.g. Stillman & Brown, 1994).

The present study was less successful in producing accurate predictions of the height of moorland vegetation from the satellite image. Whilst there were significant correlations (across both the training and the independent test plots) between the recorded heights and those predicted from satellite data, for both dwarf shrub and graminoid vegetation, these predictions were based upon relatively weak relationships, especially for the latter. Despite the apparent relationships between observed and predicted height, the accuracy of the predicted height values was apparently inadequate for the purposes of predicting bird abundance, as the incorporation of predicted short dwarf shrub cover into the golden plover model resulted in inaccurate predictions of abundance. However, given the limitations of the field-collected data used for training the satellite image (in terms of both the small area covered by sampling points, and the potential locational errors), the significant relationships between the observed and predicted heights suggest that satellite image reflectance data could potentially be used to produce accurate information on the structure of moorland vegetation. In support of this contention, previous studies have demonstrated that heather biomass can be predicted accurately from satellite data, when using training data that have been collected from stands of relatively continuous heather cover (Egan *et al.*, 2000), whilst structure or biomass have been mapped successfully by remote sensing methods in a range of other habitats (e.g. Pitt *et al.*, 1996; Mumby *et al.*, 1997; Jobbagy *et al.*, 2002).

Given that moorlands often comprise a heterogeneous mosaic of different vegetation types in different condition, the main difficulty in achieving accurate predictions of structure from satellite data is likely to be that of disentangling the effects of compositional variation from those associated with structural variation on the reflectance values. This may be more important when estimating graminoid height than dwarf shrub height, as dwarf shrubs may tend to have more homogenous stands and consist of one species, compared with the more heterogeneous stands of graminoids that may vary in height and species composition.

Mapping of bird abundance using the satellite image

Vegetation characteristics were important in both bird models, with heather cover being the most important variable in the red grouse model (in terms of percentage deviance explained), and two vegetation variables contributing to the golden plover model. The use of vegetation information derived from the satellite image, in conjunction with models describing the associations between bird abundance and habitat, indicated that it may be possible to estimate bird abundance across large areas using satellite images to produce vegetation maps, given the accuracy of the predicted abundance of two moorland birds on the training plots. The accuracy of the predictions will be influenced by the ability of these models to describe bird abundance as well as our ability to map vegetation accurately. The poorer performance of the red grouse model over the test plots was probably due, at least partly, to the small sample (10 plots), but perhaps also to a failure of the model to accurately describe abundance on the test plots, as indicated by the variability around the relationship between observed and predicted abundance. Although heather cover was predicted well from the satellite image, the small inaccuracies resulted in a poorer prediction of red grouse abundance when these data were incorporated in the bird abundance models compared with those produced when the field-collected data were used. However, the strong correlation between both of the predictions of red grouse abundance on the test plots indicated that more of the error was due to the limitations of the model than to inaccuracies in the prediction of heather cover from the satellite data. For golden plover, the strong correlation across the test plots between the observed abundance and that predicted from the model when field-collected vegetation data were used, suggested this model was more robust than the red grouse model. The failure to estimate abundance accurately when the satellite-derived vegetation data were used appeared to be due to the poor prediction of short dwarf shrub cover, as described above.

Previous studies attempting to predict bird abundance or distribution using satellite images to measure vegetation characteristics have had mixed success. On UK moorlands, an earlier study provided little suggestion that these methods were potentially valuable in this respect, producing weak associations between satellite-derived habitat data and bird abundance for golden plover, and no significant associations for two of the three bird species examined (Harding & Brown, 1990). However, in that study, broad vegetation categories were related to satellite data, whilst bird abundance–habitat models were produced from relatively coarse vegetation data. This contrasts with the present study, which demonstrates the potential of satellite data to predict the distribution of fine-scale vegetation taxa and relates bird abundance to detailed, taxonomically discrete information on both vegetation composition and structure. More generally, the approach adopted in the present study of using habitat information extracted from passive reflectance satellite images may be more applicable on structurally simple habitats, such as moorlands (as in the present case) or tundra habitats (e.g. Morrison, 1997), than on structurally complex habitats, such as woodlands (e.g. Saveraid *et al.*, 2001). Predicting bird abundance and distribution in structurally complex habitats may require the use of a combination of passive reflectance images and remote sensing methods that produce height or structural information (e.g. LiDAR used by Gutelius, 1998).

Bird abundance has also been related directly to the values of the different reflectance bands and derived indices (e.g. NDVI) of the satellite image, sometimes in combination with other land use and topographic data (Avery & Haines-Young, 1990; Lavers *et al.*, 1996; Osborne *et al.*, 2001; Buchanan & Pearce-Higgins, 2002) although there are potential problems in using satellite data directly. In particular, there may be difficulties in applying relationships to areas (or time periods) covered by different satellite images, due to differences in soil types or in the time of year at which images have been taken altering reflectance values. Additionally, predictive models produced by this approach would provide no understanding of the habitat requirements underlying the observed relationships. Despite such limitations, a more thorough comparison of the performance of predictive models based upon the two different approaches would be valuable.

This approach was tested in the current study, using values of the different reflectance bands (instead of vegetation data) averaged across each of the 26 training plots, together with the environmental and management variables in Appendix 1. The reflectance of band 4 was included in a model of red grouse abundance, but no satellite-derived variables were included in a model of golden plover abundance (unpubl. data). Predicted red grouse abundance from this model was correlated with the observed abundance across the training plots ($r_{26} = 0.61$, $P < 0.001$), but not across the 10 test plots ($r_s = 0.29$, $P = 0.41$). The performance of this approach is likely to be improved by using the reflectance values at a finer-scale resolution, such as around specific bird locations (e.g. Buchanan & Pearce-Higgins, 2002), as opposed to averaging values across large plots but it would be more appropriate to compare the performance of such an approach to those produced from observed habitat data treated in the same way, rather than the approach outlined here, where vegetation data was averaged across plots.

In addition to the type of approach used in the present study, satellite image data offer the potential to measure other habitat variables that may be difficult to measure by field methods alone, but which may improve the performance of bird abundance–habitat models. Thus, through further development of the techniques used in the present study, analysis of satellite images could be used to quantify the spatial distributions of different moorland vegetation types and to enable measurement of habitat fragmentation and the occurrence of surrounding habitat types at a range of scales. This could be important for species that require mosaics of moorland vegetation types (e.g. ring ouzels *Turdus torquatus* (L.); Buchanan *et al.*, 2003), breed on moorland but forage elsewhere (e.g. golden plover; Whittingham *et al.*, 2000), or require measurement of habitat characteristics at a range of scales to enable successful prediction of their abundance (e.g. at nest sites, home range and landscape scales).

In summary, this study suggests that it is possible to produce detailed vegetation maps using satellite images, despite the limitations of the vegetation data upon which this study is based. Further work is required however, particularly to establish whether scarcer vegetation types can be mapped accurately, and to test sub-pixel classification of heterogeneous moorland habitat, as has been attempted elsewhere (e.g. Vikhamar & Solberg, 2002). Vegetation structure can also be an important predictor of bird abundance, and whilst we detected an underlying relationship between height and satellite reflectance values in this study, we were unable to resolve whether this relationship was weak because of the limitations of our field-collected vegetation data, or because of confounding effects of habitat heterogeneity. Further work, using more appropriate ground-truthed data, is required to resolve such issues. If such work demonstrates that the important determinants of moorland bird abundance, including scarcer vegetation types and elements of vegetation structure can be mapped accurately by satellite imagery, it should be possible to produce accurate predictions of bird abundance across extensive areas. Such methods would be of considerable value, providing a cost-effective means of mapping bird distribution across UK upland areas (e.g. we estimate the cost of conducting breeding bird surveys across the entire moorland area of southern Scotland to be seven times greater than that required to produce maps of predicted abundance from satellite image data by the methods outlined in the present study). While this approach will not replace the need for actual bird surveys in all instances (e.g. site designation purposes or environmental impact assessments), it would be a valuable technique, allowing objective assessments of bird distributions and a means of targeting surveys to areas likely to hold highest densities or be of highest conservation value. Clearly, the potential value of such an approach is not limited to the UK uplands, but could be extended to bird populations on other remote and extensive open habitats, where comprehensive survey coverage is even less practical (e.g. arctic tundras).

ACKNOWLEDGEMENTS

We are grateful to the field workers who collected the vegetation and bird data used in this study, and to the landowners, tenants, graziers and keepers who allowed access to the land. Ellen Wilson and Chris Hill provided help or advice during this work and Jeremy Wilson gave comments on a draft manuscript. We are also grateful to the two anonymous referees whose comments improved an earlier draft of this manuscript. This work was funded by RSPB. SAC receives financial assistance from Scottish Executive Environment and Rural Affairs Department.

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BIOSKETCHES

Graeme Buchanan is a research biologist, interested in factors influencing upland bird populations, remote sensing of upland habitats, landscape ecology and avian mating systems.

James Pearce-Higgins is a research biologist interested in the conservation and ecology of upland birds, especially modelling the impacts of land-use and management change on upland bird populations and combining autecological studies with extensive, regression-based approaches.

Murray Grant is a senior research biologist, with extensive experience of applied ornithological research, interested in how land-use changes affect upland breeding birds, predicting responses of bird populations to future environmental changes and assessing bird–habitat relationships using modelling.

Duncan Robertson is a research biologist interested in upland grassland system ecology, scaled habitat remote sensing, GPS-based vegetation surveying and GIS applications.

Tony Waterhouse is a land-use systems scientist interested in the interaction between anthropenic issues (e.g. grazing, burning) and upland environments and in tools to characterize and understand the habitat.

Editor: Philip Stott

Appendix 1 Summary of landscape and management variables considered in bird abundance–habitat models

Variable	Description
Latitude	Latitude of plot centre
Longitude	Longitude of plot centre
Proportion of plot with slope $< 5°$	Averaged from max slope over 200 m to north or east of 50 points, 200 m apart across plot
Proportion of plot with slope 5–10°	Averaged from max slope over 200 m to north or east of 50 points, 200 m apart across plot
Average altitude	Averaged from 50 points, 200 m apart across plot
Keeper index	Supplied by estates
Area of plot within 400 m of forestry	Derived from maps
Annual precipitation (mm)	Extracted from White & Smith (1982)
Mean spring temperature	Extracted from White & Smith (1982)
Proportion of plot with brown earth soil	Extracted from Walker *et al.* (1982)
Proportion of plot with podzol soil	Extracted from Walker *et al.* (1982)
Proportion of plot with peat soil	Extracted from Walker *et al.* (1982)
Proportion of plot with surface water gley soil	Extracted from Walker *et al.* (1982)