

APPENDIX 3B.1

BIRD MODELLING: BIRD-HABITAT ASSOCIATIONS

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Testing the generality of moorland bird habitat associations to inform conservation management

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ABSTRACT

Within Britain, heather and grass moorlands are extensive, semi natural habitats of economic and environmental importance, supporting nationally and internationally important bird populations. However, the effects of recent anthropogenic habitat changes on these bird populations they support are of concern. Using bird and habitat data collected from four British upland regions, we identify correlations between vegetation characteristics and bird abundance and test the generality of these across regions. Five of the nine species considered benefited from some dwarf shrub cover, but their abundances peaked when there was a mix of dwarf shrubs and grasses, whilst skylark was the only species negatively correlated with heather cover. The abundance of five species increased and two decreased with vegetation typical of damp conditions. Abundances of all nine species were correlated with vegetation structure; three increased with the extent of short or open vegetation, and two increased with the extent of long vegetation. Variation in vegetation height was also important – four species increased and one decreased in abundance when height was more variable. Critically, the direction and form of these relationships between bird abundance and vegetation were consistent across the four study regions in the majority (c. 90 %) of cases, indicating that birds responded to variation in habitat composition and structure in the same way across the four regions, and potentially the British uplands. Therefore, the relationships identified in this study can justifiably be used to inform the conservation management of these bird species across much of their British breeding range. However, these often contrasting habitat associations means that it is not possible to suggest one habitat type that management should be aimed at producing. Instead, a heterogeneous mix of vegetation heights and composition (dwarf shrubs and

graminoids) may benefit the majority of species, while more extensive areas of short open vegetation should be produced for the rest.

INTRODUCTION

UK moorlands are semi-natural habitats of high international conservation importance. They include blanket bogs and dwarf shrub heaths, both of which are UK Biodiversity Action Plan priority habitats (Anon 1995, Thompson *et al* 1995). Their breeding bird communities comprise a unique assemblage of species, including several with internationally important populations (Thompson *et al* 1995), making a major contribution to the conservation value of these habitats and potentially their economic and social value through sport shooting (mainly of red grouse *Lagopus lagopus scoticus*) and tourism (Defra 2004). Moorlands have been subject to long-term agricultural (largely sheep grazing) and game (deer stalking and grouse shooting) management, with moorland biodiversity depending on future management decisions, which in turn be affected by economic decisions. Sheep numbers increased between the 1950s and 1990s and combined with increases in red deer (*Cervus elaphus*) numbers in the Scottish Highlands, have caused the conversion of heather (*Calluna vulgaris*) to graminoid dominated vegetation on a substantial scale (Anderson & Yalden 1981, Staines *et al* 1995 Mackey *et al* 1998, Fuller and Gough 1999). Change in moorland grazing management may have been exacerbated by the decline in management for the sport shooting of red grouse (Robertson *et al.* 2001), whilst extensive afforestation of moorlands with exotic conifers has also occurred during the post war period (Mackey *et al.* 1998). Further major changes to moorland management are probable given ongoing reforms of the EU Common Agricultural Policy (CAP) linked to reductions in stocking densities, and the potential impact of climate change on moorland habitats.

There is already evidence of recent declines in some moorland bird populations (e.g. Hancock *et al* 1999, Wotton *et al* 2002, Sim *et al* 2005) and of some potential causal links between livestock management and meadow pipit (*Anthus pratensis*) demography (Evans *et al* 2005, Evans *et al* 2006).

Consequently, an understanding of the inter-relationships between management, vegetation condition and bird abundance is essential to determining the role of land-use changes in affecting bird abundance, and to predicting the impacts of future change.

Several previous studies have attempted to describe birds: habitat associations on moorland (e.g. Haworth & Thompson 1990, Brown & Stillman 1993, Stillman & Brown 1994) but few have attempted to separate the effects of variation in vegetation composition and structure from those of other site and management factors that may also influence bird abundance. However, Pearce-Higgins and Grant (2006) examined variation in moorland bird abundance as a specific function of vegetation characteristics, and found heterogeneity in composition and structure and habitats associated with wetness were associated with bird abundance (Pearce-Higgins & Grant 2006). Two of the nine bird species studied were also closely associated with extensive heather cover, whilst several others were associated with at least some short or open vegetation on the study plots. Such findings can be used to guide management for moorland birds, but because they are based largely upon data from one part of the British uplands only, it is important to assess their generality across a wider range of the areas to which the guidance may be applied. Indeed, comparisons amongst previous studies of moorland bird-habitat associations suggest that they may vary regionally, with, for example, Eurasian curlew (*Numenius arquata*) found to be associated with grass cover in the eastern Highlands but with wet flushes and tall heather in the South Pennines (Brown & Stillman 1993, Stillman & Brown 1994). Such regional variation may however be an artefact of differences in the methods and analytical approaches used, or result from the use of broad habitat measures.

The few studies that have examined this issue for other bird communities have often found predictions derived from particular locations to have varying applicability in other geographical areas (e.g. Fielding & Haworth 1995, Morris *et al.* 2001, Whittingham *et al.* 2003, Binzenhofer *et al.* 2005). Therefore, if recommendations are to be made on management for moorland birds across Britain, there is a need to test whether study habitat associations are consistent across multiple regions, and test whether they are consistent

across these regions. To achieve this, we develop the approach of Pearce-Higgins & Grant (2006) by examining the abundance of nine relatively common and characteristic moorland bird species in relation to detailed measures of vegetation characteristics, extending their work by using comparable data from four upland regions of Britain and testing the generality of the resultant relationships across these regions.

METHODS

Site selection

Data were collected from 154, 2 km² plots of variable shape, in four upland regions of Britain that have each undergone substantial increases in sheep stocking densities over the last 60 years (Fuller and Gough 1999). Twenty-five plots were in the North Pennines (nine surveyed in 1999 and 16 in 2003), 37 in the South Pennines (surveyed in 2002), 71 in southern Scotland (surveyed in 1999 and 2000) and 21 in three of the main hill ranges in northern Wales (surveyed in 2002) (Figure 1). In each region, plots were located largely from a random sample stratified by dwarf shrub cover such that they included a similar number of plots with a low, medium and high percentage cover of dwarf shrub. This sample was derived from a combination of National Countryside Monitoring Scheme plots (Mackey *et al.* 1998) and a 1990 Landsat Thematic Mapper imagery map of heather distribution (RSPB, unpubl. data) in south Scotland (Pearce-Higgins & Grant 2006), and from the Land Cover Map 2000 (LCM2000 - Haines-Young *et al.* 2000) in the other three regions. However, due to access refusals, this selection was supplemented by 13 plots in the North Pennines and 22 plots in southern Scotland where access was assured. All plots were at least 1 km apart, were at least 200 m from the nearest forest edge, and did not include enclosed land.

Bird surveys

Breeding grouse, waders and passerines (excluding meadow pipits and skylarks *Alauda arvensis*) were surveyed using a three-visit census method following Pearce-Higgins & Grant (2006). Each plot was visited once in each three week period from 17 April to 20 June, with successive visits to a plot made at least 7 days apart. Surveys were not undertaken in rain or strong winds. At least one visit was made within three hours of dawn or dusk to estimate common snipe (*Gallinago gallinago*) abundance. On each visit, the entire plot was walked to within 100 m, with bird locations mapped and the numbers of breeding pairs derived by counting apparently paired individuals, singing, displaying or alarm-calling birds, nests or broods, or other single birds (excluding those overflying). The maximum count of breeding pairs over the three visits was used as a measure of abundance for all species, except Eurasian curlew, for which the mean count was used (Pearce-Higgins & Grant 2006). At least two of the visits to each plot were undertaken by different observers to minimise potential bias resulting from observer variability.

Skylarks and meadow pipits were surveyed on only 145 plots, using two parallel, 1 km transects located at least 600 m apart. Transects were walked between 06:00 and 09:00 on the latter two survey visits, with the two visits usually completed by different observers. The count of meadow pipits estimated to be within 25 m of transects (distances estimations were calibrated before each survey) and the total count of skylarks were used as indices of abundance as these are least prone to observer effects (Buchanan *et al.* 2006a). Counts for each species were then averaged across the two transects on a plot for each visit and averaged across the two visits to produce the estimated abundance on each plot.

Vegetation assessments

Vegetation data were collected from point samples distributed evenly across each plot (Pearce-Higgins & Grant 2006, Table 1). Structure was measured at 50 points (located every 200 m along transects spaced at 200 m intervals

across plots) during the first bird survey, whilst both composition and structure were measured at 100 points (located every 100 m along the transects) between 21 June and late July. At each point vegetation cover was assessed to the nearest 5 % along a 1m length of cane, marked at 5 cm intervals, placed horizontally on the ground. Dwarf shrubs were identified to species (except *Erica* spp. which were combined), as were several of the common graminoid (grass, sedge and rush) species. Most fine-leaved grasses or *Carex* spp. were not identified to species, while mosses were separated into *Sphagnum* spp. and others. Both *Juncus effusus* and *J. conglomeratus* were grouped as tall rushes. Bracken *Pteridium aquilinum* cover was measured separately at ground (including litter) and canopy level. The mean percentage cover of these different taxa was calculated across the 100 sample points for each plot, whilst an index of variation in dwarf shrub cover (VDSC) was derived from the change in the log-ratio of dwarf shrub to graminoid cover between adjacent sampling points (Pearce-Higgins & Grant 2006).

Three measures of vegetation height were made at each point using a marked cane held at arms length, to the front and either side of the observer, recording the heights of dwarf shrubs, graminoids and other vegetation separately. The number of white marks at heights of 0, 10, 20, 30 and 40 cm, on a cane held vertically by the standing surveyor were used as an index of density (fewer marks visible indicated more structurally complex and dense vegetation), whilst the proportion of points at which all three 10 cm marks were visible was used as an index of vegetation openness. Height measurements were averaged for each sampling point and were grouped into three classes (0 - 15 cm, 15 - 30 cm, > 30 cm) for all vegetation, and separately for graminoids and dwarf shrubs, and the percentage cover of each height class within each plot calculated. Variation in vegetation height (termed height variation) was calculated as the absolute mean change in maximum vegetation height between successive sampling points from the late visit.

Physical, landscape and management data

A range of potentially confounding topographic, climate and management effects were measured for each plot (Pearce-Higgins & Grant 2006; Table 1). On each plot peat depth and the presence of hagged (broken and eroded) peat were recorded at every second point during the late vegetation sample period, whilst broad soil associations were assessed from 1:250000 soil maps (Soil Survey of England and Wales 1983; Walker *et al* 1982). Topographical data for each plot were obtained from 50 m digital elevation models (Panorama, Ordnance Survey, UK) and mean monthly summaries of climate data between 1961 and 1990, at a 10 km square resolution, from the Climate Research Unit, University of East Anglia. To assess the effects of adjacent land-use, measures of forest cover and enclosed farmland surrounding each plot were obtained from Land Cover Map 2000. Indices of game management intensity and generalist predator abundance were derived from a measure of gamekeeper density (based upon information provided by the relevant estates and landowners), while the late vegetation survey recorded the extent and frequency of muirburn by recording the number of muirburn patches passed during the survey and the number vegetation sample points falling within patches of muirburn. Also the abundance of and number of groups of carrion crows *Corvus corone* were recorded during bird surveys (Tharme *et al.* 2001; Table 1). Additionally, the identity of each surveyor and the date of each survey visit were recorded as potential nuisance variables.

Statistical analysis

Variables were divided into those derived from measures of vegetation composition and structure, and hence of primary interest in this study (subsequently termed 'vegetation variables'), and those concerned with other aspects of the plot and its management, or of the survey itself ('non-vegetation variables'). Variables describing vegetation composition were limited to the 20 plant taxa recorded on at least 40 % of plots, which when combined with the structural measures gave 45 vegetation variables, whilst there were 44 non-vegetation variables (Table 1). This large number of

potential predictor variables was required to maximise the chances of describing key vegetation features (given the complexities of moorland habitats and the range of bird species considered), and to account for other factors affecting bird abundance. However, the use of large numbers of variables in correlative studies may cause problems of collinearity, inappropriate model selection and overfitting of variables to produce unreliable models (Rushton *et al.* 2004). To minimise these risks, we carried out an initial variable reduction phase (similar to Beale & Monaghan 2004) by conducting a series of correlations (including quadratic terms) between bird abundance and variables that described several closely related attributes (Table 1). For each bird species, the most significantly correlated variable from each of these groups was selected for inclusion in subsequent multivariate analyses (Pearce-Higgins & Grant 2006). Thus, candidate variables for subsequent analyses were reduced to 27 vegetation and 14 non-vegetation variables.

Subsequent analyses were conducted in two stages, and in such a way as to try to minimise the risks of Type I errors in identifying relationships with vegetation variables, which could result from inter-correlations between variables (Annex 1a and b; Pearce-Higgins & Grant 2006). First, minimum adequate models (MAMs) were constructed using only the 14 non-vegetation variables, including region as a fixed effect (termed non-vegetation MAMs). Because regions were surveyed by different observers, and in different years, some of the variation in intercept between regions may be attributable to annual differences in abundance (particularly likely for red grouse - Hudson 1992) or variation between observers (Buchanan *et al.* 2006a). Second, vegetation variables were individually added to these non-vegetation MAMs to identify additional significant vegetation correlates of bird abundance. This describes the full range of correlations between bird abundance and the vegetation variables, having first accounted for non-vegetation effects. We do not attempt to select between these significant vegetation variables because several are highly inter-correlated (Annex 1b). There were no correlations between non-vegetation and vegetation variables stronger than 0.6. Simple codes are used to describe the nature of quadratic relationships between

vegetation variables and bird abundance. The following five classes were identified according to the shape of the fitted relationship within the range of the central 90% of values of the independent variable: convex increasing (\cap), convex decreasing (\cup), concave increasing (\cup), concave decreasing (\cap), and maximum within the 90% range (\cap) following Tharme *et al.*(2001). At this stage, interactions between region and both the linear and quadratic terms of each significant vegetation variable were tested, forcing region into the model if previously non-significant. This provides the test of whether relationships between bird abundance and vegetation differed between regions. Where significant regional interactions were detected, the form of the relationship was described separately for each region using the parameter estimates and the upper and lower 95 % confidence intervals for the interaction term obtained from model output.

Analyses were conducted using the GENMOD procedure in SAS 8.02 (SAS Institute, 2001), specifying a Poisson error distribution and log-link function. MAMs were constructed using a forward selection procedure, incorporating the variable that caused the most significant change in deviance at each stage (provided $P < 0.05$). Quadratic terms for each variable were included in conjunction with the linear term, if their addition produced a significant change in deviance, or if the effect of the variable and its quadratic were significant when considered together. Existing terms in the model that became non-significant following the inclusion of a new variable were deleted. The statistical significance of each variable was tested by treating the change in residual deviance associated with removal of the term from the model as χ^2 with the appropriate degrees of freedom, unless data were over-dispersed, in which case the residual deviance was rescaled to equal the residual degrees of freedom, and statistical significance assessed using the F-test (Crawley, 1993).

RESULTS

Study species and their occurrence

Analyses considered the nine bird species studied by Pearce-Higgins and Grant (2006). All of these species are typical of moorlands, were recorded on more than 20 % of the plots and were present in all regions (Table 2). The densities of these nine species varied between regions. Bird assemblages in the North and South Pennines were characterised by high densities of red grouse and some wader species, while plots in Wales were characterised by high passerine densities. The South Scotland plots tended to be intermediate on this spectrum, but held relatively high densities of Eurasian curlew and common snipe. These densities may not be representative of overall densities of moorland birds in each region, because plot selection was stratified by habitat. Further, densities may not be directly comparable, as regions were surveyed in different years, and by different observers.

The stage 1 models explained 29 – 72 % of the deviance in the abundance of each of the nine species, with 50 % or more being explained for seven (Annex 2). Thus, for some species (particularly red grouse and Eurasian golden plover – *Pluvialis apricaria*), the initial incorporation of the non-vegetation variables left relatively little variation in the abundance data to be explained by the vegetation effects, whilst for common snipe and northern wheatear (*Oenanthe oenanthe*) non-vegetation variables accounted for relatively little of this variation. At this stage, region had an additional significant effect on the abundance of all species except northern wheatear. Variables relating to the intensity of grouse moor management were included for five species, while the effects of surrounding land use (extent of adjacent enclosed farmland or conifer plantations) were included for six (Annex 2).

Relationships between bird abundance and vegetation characteristics, and consistency across regions

Most of the vegetation composition and structure variables differed significantly between regions (Table 3). For example, heather cover was

lowest in the South Pennines, but greatest in the North Pennines and south Scotland, whilst vegetation density was greatest in south Scotland and Wales. Despite this, the majority of bird : habitat associations were consistent across all regions (Tables 4 and 5). Five species showed significant correlations with heather cover (Table 4, Figure 2). Meadow pipit and whinchat (*Saxicola rubetra*) abundance peaked at about 30 % cover whilst stonechat (*Saxicola torquata*) and red grouse abundance peaked at approximately 40 - 50 % cover. Red grouse abundance was also positively related to the cover of other dwarf shrubs, namely, *E. nigrum* and *Erica* spp. Taken together with the positive correlations of red grouse, stonechat, whinchat and northern wheatear with VDSC (Table 4), six species were therefore most abundant on moors with a mix of dwarf shrub and graminoid cover. Conversely, skylark abundance was negatively correlated with heather cover, but positively with the frequency of *Deschampsia flexuosa* occurrence (Table 4).

All three wader species were associated with vegetation characteristic of wet heath and bog (*Scirpus cespitosus*, *Eriophorum vaginatum* or *Sphagnum* spp.) or wet flushes (*Juncus acutiflorus*, tall rushes or *Carex* spp. - Table 4). Both meadow pipit and skylark abundances were also positively correlated with *Carex* spp. cover. None of the three chats were associated with vegetation typical of wet conditions; whinchat and stonechat abundances were negatively correlated with *Sphagnum* cover and *Carex* spp cover respectively. The abundance of all three chat species was positively correlated with bracken cover, the relationship being strongest for whinchat.

There were significant relationships with at least one measure of vegetation height or structure for all species (Table 5). Red grouse, whinchat and stonechat were each associated with dense vegetation, as indicated by positive correlations (quadratic in the case of stonechat) between abundance and density or negative correlations between abundance and openness (Table 5). However, positive correlations with height variation for both whinchat and stonechat, as well as Eurasian curlew and northern wheatear, and a quadratic correlation between meadow pipit abundance and vegetation density (Figure 3) indicate that five species may benefit from a heterogenous

sward structure, such as the presence of short vegetation within a tall sward. Conversely, Eurasian golden plover, common snipe, and skylark were all associated with open or short vegetation cover (Figure 3), the strong negative relationship between Eurasian golden plover abundance and height variation indicates that this species is most common on uniformly short swards.

Clearly there was considerable variation in the extent to which the different bird species responded to differences in vegetation composition and structure after accounting for non-vegetation variables, but importantly relationships between bird abundance and vegetation appeared generally consistent across the four regions. Thus, interactions with region were significant in just 10 % of the relationships between bird abundance and vegetation variables (Tables 4 and 5), affecting correlations for Eurasian curlew, Eurasian golden plover, meadow pipit and skylark (Figure 4). Neither of the interactions for Eurasian curlew, (tall grass and short dwarf shrub cover) were particularly strong (Figure 4a and b), and could be attributed to weak relationships in Wales, where Eurasian curlew sample sizes were small (Table 2), contrasting with stronger relationships across the other regions. For Eurasian golden plover, regional interactions were significant for four vegetation variables. Although the magnitude of the correlations and differences for heather and fine leaved grass cover and *D. flexuosa* frequency were small (Figure 4 c - e), there were apparently strong regional differences in the relationship with *M. caerulea* cover. Eurasian golden plovers in Wales were associated with *M. caerulea*, while more strongly avoiding heather, in contrast to the other three regions (Fig 4 e,f). This appears to be because open vegetation cover, a key vegetation characteristic for Eurasian golden plover (Table 5), is positively correlated with *M. caerulea* cover in Wales ($r = 0.52$) but not in the other regions ($r = 0.09$ to -0.46), whilst heather cover was more strongly negatively correlated with vegetation openness in Wales ($r = -0.93$) than in the other regions ($r = -0.49$ to -0.10). Thus, different vegetation compositions were associated with the required habitat structure for Eurasian golden plover in different regions. The interactions for meadow pipit and skylark were with only one vegetation variable, and from relationships that were weakly

significant in one of the regions only (Figure 4 g and h), indicating that neither of these variables were major determinants of abundance.

DISCUSSION

Bird-habitat relationships and generality of bird-habitat relationships

This is the first time that spatial variation in moorland bird abundance has been related to vegetation characteristics across different upland regions. It extends Pearce-Higgins & Grant (2006) by augmenting their data with those from a wider range of upland regions and produced broadly similar relationships between bird abundance and vegetation. In terms of variation in heather to grass cover (the vegetation gradient most widely regarded as a main consequence of high grazing levels - Fuller & Gough 1999), there were associations of red grouse and stonechats with heather, meadow pipits with intermediate heather cover, and avoidance of heather by skylarks, all of which showed wide generality across all regions. Relationships with vegetation structure (also strongly influenced by grazing management) described associations between both Eurasian golden plover and skylark and open vegetation, and both stonechat and whinchat with tall or dense vegetation. These relationships replicate those of Pearce-Higgins & Grant (2006), and were again consistent across regions. Eurasian curlew, northern wheatear, whinchat and stonechat were each more abundant on sites with spatial heterogeneity in vegetation height, whilst meadow pipit abundance peaked at intermediate levels of vegetation density. The importance of such structural heterogeneity for several species (particularly, Eurasian curlew, common snipe and whinchat) was highlighted in the earlier study but the incorporation of data from other regions in the present study, suggests that it is important for a wider range of species. Additionally, there were significant associations for four species with vegetation characteristic of wet flushes (*Carex* spp. *J. acutifloris*, tall rushes), six species being similarly associated with such vegetation in the earlier study (Pearce-Higgins & Grant 2006), whilst Eurasian golden plover were associated with *E. vaginatum* cover, which is characteristic of blanket bogs.

Where observed bird: habitat associations differed between regions these were typically weak correlations and were based on just one or two habitat variables for a given species. The exception was Eurasian golden plover, for which four vegetation composition variables displayed variation in the gradient or direction of the relationship between regions. Even for this species, eight of 12 relationships were consistent across regions, of which the strongest were structural (i.e. short, open vegetation). Thus, vegetation structure appears to be the most important determinant of Eurasian golden plover abundance (Pearce-Higgins & Yalden 2003, Pearce-Higgins & Grant 2006), whilst the composition of vegetation providing the structural variation to which Eurasian golden plover were responding varied between regions.

There were some species-specific differences between the findings of the present study and those of Pearce-Higgins & Grant (2006), and these may have arisen from differences in the stage one models produced in each study. Most notable amongst these was the positive association between common snipe abundance and the extent of open vegetation reported in this study. Also, northern wheatear showed no strong associations with vegetation characteristics previously, but the current study found that abundance was positively correlated with both dwarf shrub mosaic and *P. aquilinum* cover.

Overall, moorland bird - habitat relationships appear to have a high degree of generality across the four regions. Similar studies of farmland birds have found that habitat selection tends to be consistent between different regions (Morris *et al.* 2001, Whittingham *et al.* 2003). The importance of using detailed measures of both vegetation composition and structure is demonstrated by the regional interactions detected between Eurasian golden plover abundance and vegetation composition; had we not measured vegetation structure then we would have concluded that consistent management prescriptions could not be identified. Previously observed regional differences in the habitat associations of moorland bird species are therefore likely to be due to methodological differences between regions, or because assessments of habitat were insufficiently detailed.

Management implications

Generality in the response of birds to habitat variation is a requirement if broad management prescriptions and agri-environment schemes are to be a generic (e.g. Kleijn *et al.* 2002). Where this generality does not exist, geographically targeted prescriptions may be required. The relative, if not absolute, consistency between bird habitat associations across regions demonstrated in this study means that these relationships can be used to inform the development of broad management prescriptions for the conservation of moorland birds in the uplands of Britain, rather than localised prescriptions. The habitat associations described in this paper suggest that management to produce heterogeneous moorland vegetation is likely to best promote the abundance of the widest range of moorland species studied. This should firstly be at the fine-scale; five species were positively associated with increased variation in heather and grass cover, vegetation height, or both, between vegetation sample points 100m apart. However, heterogeneity at a larger landscape scale is also important; such as to provide extensive areas of short / open vegetation associated with some species (eg golden plovers and skylarks), in addition to areas with taller vegetation to provide the required heterogeneity for other species. This is illustrated by figure 5 which indicates schematically where each species would fall along a gradient from grass dominated vegetation, through a mix, to heather dominated vegetation, and similarly where species would occur along a structural gradient from all short vegetation, through a mix of heights to domination by tall vegetation. This principle is likely to hold for other moorland species of conservation concern, such as black grouse, hen harrier and ring ouzel, that are each likely to benefit from spatial heterogeneity in heather and grass cover, albeit it at varying spatial scales (Redpath & Thirgood 1997, Burfield 2002, Pearce-Higgins *et al.* 2007), as already highlighted for many farmland bird species (Benton *et al.* 2003). In addition to there being a greater diversity of potential invertebrate prey being associated with mixed vegetation (Coulson & Butterfield 1985, Usher & Thompson 1995), heterogeneity at varying scales may affect visibility and accessibility of prey and detection and avoidance of predators (Lima and Dill 1990) and provide habitats for both nesting and

foraging, where these require different vegetation (e.g. ring ouzel – Burfield 2002).

Details of the precise livestock and burning management regimes required to produce these habitats is beyond the scope of this paper because the effects of grazing and burning upon vegetation will differ between geographical locations as a result of variation in climate, soil and initial vegetation (Hope *et al.* 1996, Hulme *et al.* 2002, Pakeman *et al.* 2003). Current conservation objectives are often aimed at restoring areas of heather moorland (Thompson *et al.* 1995) following its widespread replacement by grassland after intensive grazing or burning regimes (e.g. Hobbs & Gimingham 1984, Grant *et al.*, 1985; Thompson *et al.* 1995; Welch & Scott, 1995; Hulme *et al.*, 1999). This is often sought through reductions in management intensity, such as reduced grazing levels under agri-environment schemes. However, these changes do not necessarily restore heather moorland, and may instead result in the development of tall, rank graminoid vegetation (Marrs & Welch 1991, Hope *et al.* 1996, Hulme *et al.* 1999), which our results suggest is likely to be detrimental to moorland birds. Careful grazing management, perhaps with direct intervention, may be required for the recovery of dwarf shrubs (Pywell *et al.* 1995, Hulme *et al.* 2002, Pakeman *et al.* 2003) and to maximise the benefits of such management to birds and many invertebrates on which they feed (Buchanan *et al.* 2006b), a heterogeneous mix of heather and grass patches, and tall and short swards, should be produced. Setting appropriate levels of livestock grazing and burning will be an important tool to achieve such heterogeneity (Vandvik *et al.* 2005). For example, animals selectively graze areas of grass and short vegetation, whilst leaving heather and taller vegetation ungrazed (Palmer & Hester 2000), while cattle grazing can, under some circumstances, promote heather grass mosaics (Bokdam & Gleichman 2000). Clearly this may require the maintenance of livestock on hill farms in economically unfavourable areas. Thus, extensification in grazing may be as great a problem as intensification of grazing, with widespread losses of livestock from hill farms potentially resulting in declines in many moorland bird populations in Britain. Already large-scale land abandonment already shown to have been detrimental to upland bird communities in the Alps (Laiolo *et al.*

2004). Therefore it is important to get the correct management for the future of moorland biodiversity, and the generality of the results presented here means they can be used with confidence to develop appropriate management for birds.

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Table 1 Non vegetation (*in italics*) and vegetation variables considered in the analysis

Variables in bold indicate groups of similar variables, of which only the one with the strongest correlation to abundance was considered in the analysis (see methods)

Variable	Definition
<i>Region</i>	Fixed effect for the four regions. Includes potential observer and year effects
<i>Northing/Easting</i>	Position of centre of each plot using OS grid
<i>Altitude</i>	Mean altitude of plot (m)
Slope	Percentage of plot covered by 3 categories of slope (0° - 5°; 5°-10°, >10°)
Climate	30-year means of annual rainfall (mm) and spring (Apr-Jun) rainfall (mm) and spring temperature (°C)
Soil cover	Peat depth. Percentage of sample points located on mineral soil, shallow (0-50 cm) and deep (>50 cm) peat
	Soil cover. Percentage of plot covered by 6 soil categories (see text).
<i>Peat Hags</i>	Percentage of sample points with peat hags between them
Muirburn	Mean number of muirburns between sample points and percentage of sample points located in muirburn
<i>Keeper density</i>	Density of gamekeepers per 1000 acres
Predator index	Mean number of crows and crow groups recorded during three bird surveys
<i>Proximity of in-bye</i>	Percentage of plot located within 400 m buffer of in-bye
Forest	Percentage of plot within 400 m buffer of forest, and proportion of a 1km buffer around the plot containing forests
Observer	Percentage of bird surveys conducted by each observer - only 1 observer worked in multiple regions
Survey date	Date of each of three bird survey visits, as counted from 1 April
Vegetation height	Percentage of sample points in each of three height classes (short, 0 – 15 cm; medium, 15 – 30 cm; tall, > 30 cm) for dwarf shrubs, graminoids and all vegetation. Measurements made at start (April) and end (July) of season.
Vegetation density	Density. Mean number of white marks at 0, 10, 20, 30 and 40 cm on vertically held bamboo cane visible across all sample points. Openness. Percentage of sample points with the 10 cm white marks visible at each of the three measures at that point. Measurements made at start (April) and end (July) of season
Height variability	Mean difference in mean maximum vegetation height between adjacent sample points in late visit
VDSC	Mean change in ratio of dwarf shrubs to graminoids between adjacent sample points in late visit
Vegetation composition	Percentage of sample points composed of each of the 21 plant taxa recorded in 40% of study plots.

Table 2 Mean abundance (\pm SE) and percentage of plots occupied for each region for the nine most frequently recorded species

Abundances indicates breeding pairs per 2 km² plot for all species except meadow pipit and skylark for which abundance is the number of individuals recorded from line-transects (see text). Meadow pipits and skylark were not surveyed on 8 plots in South Scotland and 1 plot in the North Pennines.

	North Pennines (n=25)		South Pennines (n=37)		South Scotland (n=71)		Wales (n=21)	
	Abundance	% plots occupied	Abundance	% plots occupied	Abundance	% plots occupied	Abundance	% plots occupied
r grouse	12.92 (1.92)	92	25.16 (4.14)	92	7.06 (0.81)	80	1.76 (0.47)	62
curlew	5.56 (0.76)	92	2.97 (0.46)	87	4.62 (0.55)	79	0.29 (0.14)	24
g plover	12.80 (2.76)	88	5.05 (0.77)	87	1.41 (0.27)	42	0.52 (0.24)	24
snipe	2.32 (2.32)	84	0.59 (0.15)	38	2.45 (0.28)	78	0.71 (0.18)	48
skylark	6.85 (1.40)	88	9.32 (1.39)	78	7.54 (0.61)	97	23.57 (2.90)	100
m pipit	10.15 (0.86)	100	12.11 (1.28)	95	11.13 (0.54)	100	25.38 (1.94)	100
wheatear	0.72 (0.22)	36	0.89 (0.25)	55	1.58 (0.20)	70	2.19 (0.34)	91
whinchat	0.04 (0.04)	4	0.22 (0.13)	8	0.80 (0.17)	39	2.10 (0.63)	16
stonechat	0.16 (0.09)	12	0.08 (0.05)	8	0.80 (0.14)	42	1.62 (0.41)	67

Table 3 Mean (and range) of vegetation characteristics that were correlated with bird abundance across North Pennines, South Pennines, South Scotland and Wales

Values for composition indicate percentage cover except for *D. flexuosa* which is proportion of sample points where it occurred. Vegetation height is mean proportion cover of each vegetation type. Openness and density are indices (see methods). Differences among regions (Kruskall Wallis test) indicated by the number of symbols - P < 0.05 *, P < 0.01**, P < 0.001 ***

	N Pennines	S Pennines	S Scotland	Wales
bare soil **	4.20 (0 - 20.1)	7.21 (0 - 31)	1.96 (0 - 12.7)	1.87 (0 - 8.3)
<i>C. vulgaris</i> ***	33.2 (0.10 - 72.2)	16.7 (0 - 71.9)	30.7 (0.10 - 72.3)	26.7 (0 - 78.3)
<i>Carex</i> spp. ***	1.20 (0 - 5.4)	0.39 (0 - 7.35)	1.79 (0 - 8.80)	2.30 (0 - 7.45)
<i>D. flexuosa</i> **	0.23 (0 - 0.69)	0.36 (0 - 0.78)	0.20 (0 - 0.66)	0.15 (0 - 0.42)
density ***	0.92 (0.44 - 1.68)	0.79 (0.33 - 1.37)	1.07 (0.49 - 1.92)	1.09 (0.69 - 1.94)
density (e) ***	0.69 (0.20 - 1.12)	0.59 (0.24 - 1.27)	0.86 (0.57 - 1.4)	0.81 (0.32 - 1.70)
<i>E. angustifolium</i> ***	1.80 (0 - 11.9)	3.10 (0 - 8.46)	0.95 (0 - 7.31)	1.16 (0 - 4.25)
<i>E. nigrum</i> ***	0.38 (0 - 1.35)	9.22 (0 - 69.2)	0.22 (0 - 2.78)	0.60 (0 - 2.17)
<i>E. vaginatum</i> **	10.8 (0 - 27.8)	12.3 (0 - 51.1)	5.93 (0 - 31.5)	5.83 (0.57 - 15.3)
<i>Erica</i> spp ***	1.10 (0 - 6.17)	0.45 (0 - 8.40)	0.90 (0 - 7.57)	0.47 (0 - 1.95)
Fine-leaved grass ***	16.3 (1.78 - 40)	11.4 (0 - 38.8)	21.7 (2.52 - 59.2)	10.1 (2.42 - 26.1)
<i>G. saxatile</i> **	0.51 (0 - 2.92)	0.61 (0 - 8.47)	0.36 (0 - 3.91)	0.85 (0 - 3.40)
height variation **	13.5 (6.92 - 24.5)	11.3 (4.57 - 19.6)	11.6 (4.56 - 19.3)	14.5 (8.05 - 19.9)
<i>J. acutifloris</i> ***	0.32 (0 - 2.3)	0.09 (0 - 1.14)	1.86 (0 - 13.7)	0.15 (0 - 1.7)
<i>J. squarrosus</i> ***	5.20 (0.1 - 29.1)	0.68 (0 - 6.28)	1.68 (0 - 8.88)	7.41 (0 - 20)
<i>M. caerulea</i> ***	0.84 (0 - 9.41)	15.2 (0 - 75.8)	10.6 (0 - 60.6)	12.7 (0 - 65.8)
moss spp ***	6.10 (0.5 - 22.1)	1.40 (0 - 6.15)	4.88 (0.21 - 17.1)	7.33 (2.1 - 21.9)
openness **	0.47 (0.1 - 0.9)	0.47 (0.05 - 0.88)	0.34 (0.05 - 0.72)	0.36 (0.05 - 0.66)
openness (e) **	0.64 (0.16 - 1.35)	0.64 (0.00 - 0.96)	0.48 (0.1 - 0.91)	0.49 (0.06 - 0.88)
<i>P. aquilinum</i>	1.99 (0 - 25.6)	1.10 (0 - 11.8)	1.96 (0 - 10.2)	0.71 (0 - 4.77)
<i>S. cespitosus</i> ***	1.99 (0 - 22.1)	0.14 (0 - 2.82)	3.40 (0 - 18.3)	1.73 (0 - 9.7)
short grass (e)	0.65 (0.12 - 1)	0.56 (0 - 1)	0.59 (0.04 - 0.98)	0.61 (0.04 - 0.9)
short vegetation (e)	0.50 (0.02 - 0.97)	0.49 (0 - 1)	0.38 (0.04 - 0.86)	0.45 (0.04 - 0.86)
short dwarf shrub	0.21 (0.01 - 0.42)	0.21 (0 - 0.61)	0.16 (0 - 0.70)	0.12 (0.01 - 0.39)
short vegetation **	0.19 (0.02 - 0.44)	0.19 (0 - 0.64)	0.12 (0 - 0.74)	0.19 (0.02 - 0.42)
<i>Sphagnum</i> spp ***	2.37 (0 - 4.6)	0.67 (0 - 3.65)	1.96 (0 - 11.3)	2.91 (0 - 11.8)
tall dwarf shrub (e) *	0.09 (0 - 0.38)	0.08 (0 - 1)	0.10 (0 - 0.44)	0.20 (0 - 0.73)
tall grass (e)	0.01 (0 - 0.14)	0.02 (0 - 0.24)	0.02 (0 - 0.19)	0.00 (0 - 0.04)
tall vegetation (e) **	0.16 (0 - 0.68)	0.13 (0 - 1)	0.18 (0 - 0.54)	0.27 (0.02 - 0.76)
tall grass ***	0.14 (0 - 0.53)	0.07 (0 - 0.41)	0.24 (0 - 0.77)	0.11 (0 - 0.4)
tall rush ***	3.53 (0 - 11.3)	1.41 (0 - 6.09)	1.56 (0 - 7.35)	4.47 (0.5 - 15.2)
tall vegetation ***	0.38 (0.09 - 0.88)	0.31 (0.02 - 0.75)	0.49 (0 - 0.98)	0.44 (0.15 - 0.81)
VDSC *	3.19 (0.73 - 5.30)	2.36 (0.28 - 4.64)	3.06 (0.47 - 6.04)	2.42 (0.97 - 4.19)

Table 4 Shape of significant relationships (see methods) between bird abundance and vegetation composition, after controlling for non vegetation effects

Details of regional differences in relationships, indicated by #, are given Figure 4. Significance of relationships is denoted by number of symbols: P<0.05 - 1 symbol, P<0.01 - 2 symbols, P<0.001 - 3 symbols.

Vegetation	r grouse	g plover	curlew	snipe	skylark	m pipit	wheatear	whinchat	stonechat
VDSC	(((-	+	(+++	+++
bare soil			∩						
<i>P. aquilinum</i>		--				#6	+	(((+
<i>C. vulgaris</i>	(((#1			-	∩∩∩		∩∩	(((
<i>D. flexuosa</i>		#2			+				
<i>E. angustifolium</i>							∩	---	
<i>E. nigrum</i>	(((
<i>Erica</i> spp	((
<i>E. vaginatum</i>		+		+					
fine-leaved grass		#3						∩∩∩	
<i>G. saxatile</i>	((∩∩			
<i>J. acutifloris</i>			+						
Tall rushes		-				∩∩∩			
<i>J. squarrosus</i>								-	
<i>M. caerulea</i>	---	#4			#5				
moss spp	(((∩			
<i>S. cespitosus</i>	-	(((((
<i>Carex</i> spp	-		+	+++	+	+			-
<i>Sphagnum</i> spp				∩		+		-	

Table 5 Shape of significant relationships (see methods) between bird abundance and vegetation height and structure, after controlling for non-vegetation effects. e denotes measurements made on the first visit (late April – early May) as opposed to late season vegetation survey (see methods)

Details of regional differences in relationships, indicated by #, are given in figure 6. Significance of relationships is denoted by number of symbols: P<0.05 - 1 symbol, P<0.01 - 2 symbols, P<0.001 - 3 symbols.

Vegetation	r grouse	g plover	curlew	snipe	skylark	m pipit	wheatear	whinchat	stonechat
short dwarf shrub	∩∩∩	∩∩∩	#7		++		∩∩		
tall dwarf shrub									((((e
short grass)])e
tall grass			#8					((e	
short vegetation			∩		+e	-e			
tall vegetation		---						++	((((e
density					---e	∩		++	((
openness	-e	+++e		++					
height variation		---	(+	+++	++

Annex 1a Spearman ranks correlations between non vegetation variables

Only variables with correlations > 0.6 are shown.

	spring rain	forest 400m	crows (individuals)	shallow peat	deep peat	% muirurn	slope 5°-10°
annual rain	0.95						
forest 1km		0.81					
crows (groups)			0.93				
peat hags					0.62		
% mineral soil				-0.64			
number of muirburns						0.84	
slope 0° - 5°							-0.65

Annex 1b Spearman ranks correlations between vegetation variables

Only variables with correlations > 0.6 are shown. ^e denotes measure from the early (April) vegetation survey. Dwarf shrub is abbreviated to ds, grasses to gr and all vegetation to veg. VDSC is index of variation in dwarf shrub cover.

	Medium ds ^e	medium ds	tall ds ^e	tall ds	tall gr	short veg ^e	short veg	medium veg ^e	medium veg	tall veg ^e	tall veg	density ^e	openness ^e	openness	VDSC
Bare							0.65								
C.vulgaris	0.71	0.64	0.74	0.79		-0.62				0.64		0.62			0.63
medium ds	0.75														
tall ds										0.81					
tall ds	0.75		0.85						0.73	0.76					
short gr ^e						0.78				-0.64					
short gr					-0.66		0.71								
medium gr ^e								0.69							
medium gr									0.65						
tall gr											0.64				
short veg ^e	-0.68		-0.67	-0.67				-0.63		-0.75				0.62	
short veg											-0.61				
medium veg											-0.76				
density ^e	0.64		0.71	0.65		-0.74				0.78			-0.84	-0.65	
density				0.65						0.70	0.67	0.71	-0.61	-0.85	
openness ^e	-0.66		-0.68	-0.70		0.75				-0.71				0.67	
openness										-0.63					

Annex 2 Summary of the non vegetation minimum adequate models, incorporating non-vegetation variables

Parameter estimates and significance values ($P < 0.05$ *, $P < 0.01$ **, $P < 0.001$ ***) calculated with all significant non vegetation variables in MAM.
(NP – North Pennines, SP – South Pennines, SS – south Scotland, W – Wales)

Species	Parameter	Estimate (\pm se)	Sig
r grouse	Intercept	0.5401 \pm 0.3834	
	Keeper dens.	7.0954 \pm 1.257	***
	Keeper dens. ²	-10.1893 \pm 2.8226	
	Deep peat	1.1296 \pm 0.3085	***
	Region - NP	1.7109 \pm 0.4034	***
	Region - SP	1.9319 \pm 0.4071	
	Region - SS	0.9179 \pm 0.3911	
	In-bye	-2.3912 \pm 0.505	***
	Peat hags	-0.9604 \pm 0.2909	**
	Explained Deviance	69%	
g plover	Intercept	-6.8791 \pm 1.5523	
	Slope > 15	-1.0380 \pm 0.4066	*
	Keeper dens.	6.0309 \pm 1.1434	***
	Keeper dens. ²	-8.9828 \pm 2.0155	
	Peat hags	0.9507 \pm 0.3366	**
	Region - NP	0.3840 \pm 0.6357	***
	Region - SP	-1.2734 \pm 0.7446	
	Region - SS	0.3061 \pm 0.5366	
	Easting	2.11 $\times 10^{-5}$ \pm 0.48	***
	Forests (1km)	-4.8276 \pm 1.8831	**
Explained Deviance	72%		
curlew	Spring rain	-0.0151 \pm 0.0047	**
	Region - NP	1.9716 \pm 0.5938	***
	Region - SP	1.1995 \pm 0.6165	
	Region - SS	2.0158 \pm 0.5651	
	Easting	0.99 $\times 10^{-5}$ \pm 0.24	***
	Peat hags	-1.6442 \pm 0.3616	***
	Observer	1.0903 \pm 0.2883	***
	Forests (1km)	-2.6523 \pm 0.8427	**
	Explained Deviance	60%	

Species	Parameter	Estimate (\pm se)	Sig
snipe	Intercept	-1.4128 \pm 0.8190	
	Region - NP	0.4593 \pm 0.4031	***
	Region - SP	-1.2935 \pm 0.4829	
	Region - SS	0.8430 \pm 0.3445	
	Easting	0.88 x 10 ⁻⁵ \pm 0.22	***
	Altitude	-0.0032 \pm 0.0009	***
Explained Deviance	34%		
skylark	Intercept	-0.3602 \pm 1.1059	
	Region - NP	-0.9006 \pm 0.1934	***
	Region - SP	-0.3919 \pm 0.1652	
	Region - SS	-0.9627 \pm 0.1358	
	Crow groups	0.0520 \pm 0.0201	***
	Deep peat	1.3242 \pm 0.9752	***
	Deep peat ²	-4.2495 \pm 1.7847	
	Number of muirburns	-1.8490 \pm 0.4924	***
	Number of muirburns ²	1.2476 \pm 0.4044	
	Date	0.2357 \pm 0.0829	*
	Date ²	-0.0042 \pm 0.0015	
	Observer	-1.3766 \pm 0.6774	*
	Explained Deviance	59%	
m pipit	Intercept	2.3753 \pm 1.3256	
	Region - NP	0.9543 \pm 0.1539	
	Region - SP	-0.5931 \pm 0.1248	
	Region - SS	-1.1626 \pm 0.1509	
	Altitude	0.0140 \pm 0.0041	**
	Altitude ²	-0.0015 \pm 0.0004	
	In-bye	0.8673 \pm 0.6655	**
	In-bye ²	-2.6113 \pm 1.2478	
	Spring Temperature	-0.2416 \pm 0.0963	*
	Shallow peat	0.4760 \pm 0.2341	*
Explained Deviance	52%		

Species	Parameter	Estimate (\pm se)	Sig
wheatear	Intercept	-2.9028 \pm 1.5345	
	Crow groups	0.2172 \pm 0.0830	***
	Crow groups ²	-0.0152 \pm 0.0067	
	Peat hags	-1.1035 \pm 0.5855	*
	Number of muirburns	-0.8928 \pm 0.3521	**
	Inbye	-1.7355 \pm 0.5300	***
	Deep peat	-1.3813 \pm 0.5507	*
	Date	0.2742 \pm 0.1162	**
	Date ²	-0.0049 \pm 0.0021	
Explained Deviance	29%		
whinchat	Intercept	6.3617 \pm 0.8301	
	Region - NP	-3.9238 \pm 1.0689	***
	Region - SP	-2.9098 \pm 0.4255	
	Region - SS	-1.9587 \pm 0.2799	
	Altitude	-0.0102 \pm 0.0016	***
	Slope 0 - 5 °	-3.7221 \pm 0.6035	***
	Number of muirburns	4.0321 \pm 1.3395	**
	Explained Deviance	50%	
stonechat	Intercept	1.5314 \pm 0.2071	
	Region - NP	-1.4847 \pm 0.5060	***
	Region - SP	-2.2706 \pm 0.5719	
	Region - SS	-0.8650 \pm 0.2113	
	Peat hags	-4.9569 \pm 0.9534	***
	Inbye	-3.3568 \pm 0.8378	***
	Observer	-4.5366 \pm 1.6250	***
	Explained Deviance	50%	

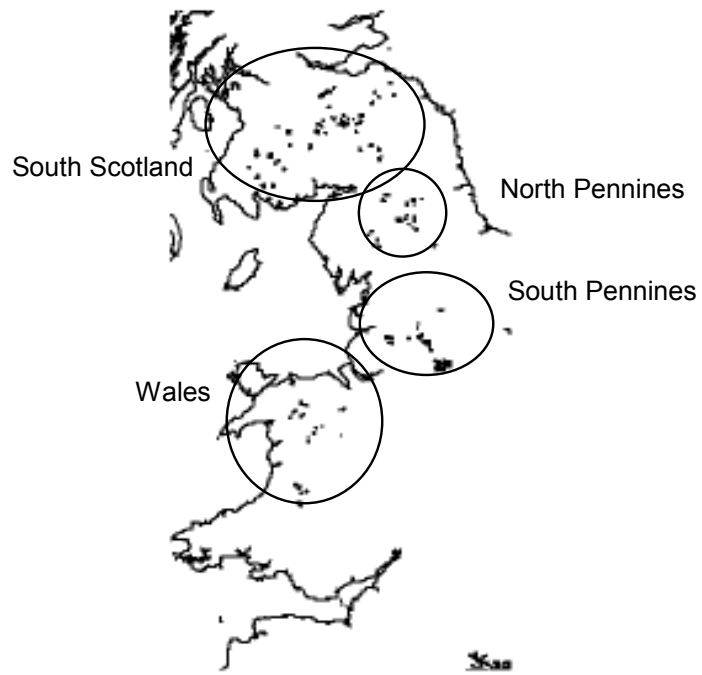


Figure 1 **Distribution of 154 2km² plots across 4 regions of Britain**

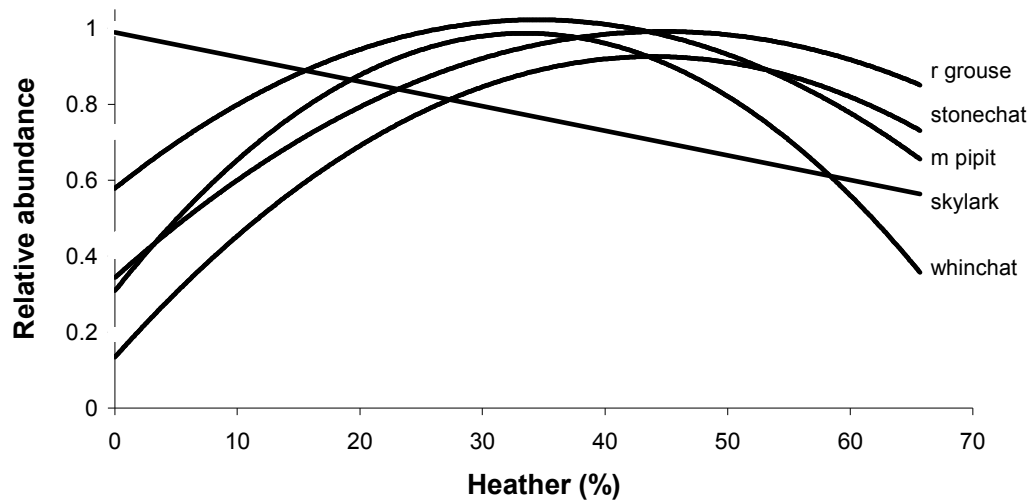


Figure 2 Modelled relationships between heather cover and relative bird abundance between approaching 0 (lowest abundance) and 1 (highest abundance) for species for which a significant correlation was detected

Relative abundance is pairs per 2km² except for meadow pipit and skylark for which indices of abundance are used. Values were calculated using mean values of variables in non vegetation MAMS, and scaled according to the maximum value for each species. Absolute abundances were not produced due to the effect of region on abundance.

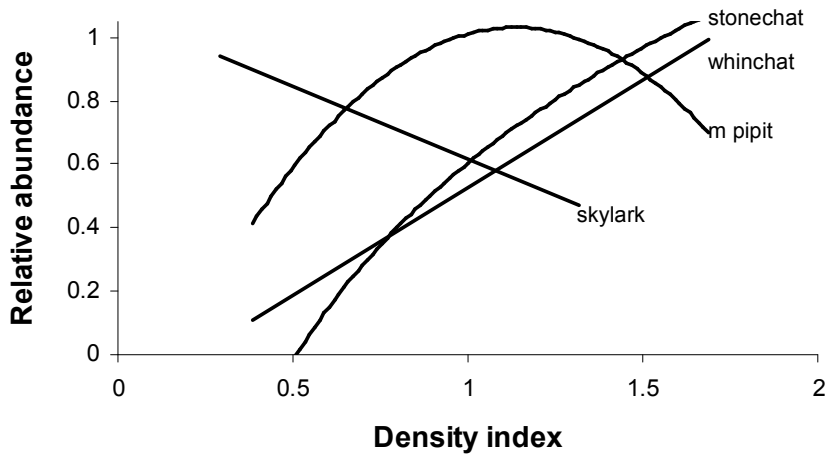
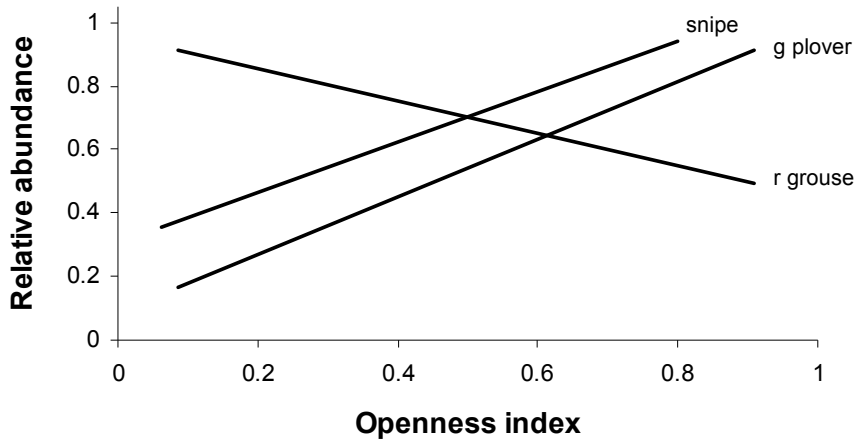


Figure 3 a and b Modelled relationships between vegetation openness (a) and density (b) and relative bird abundance between approaching 0 (lowest abundance) and 1 (highest abundance) for species for which a significant correlation was detected

Relative abundance is pairs per 2km² except for meadow pipit and skylark for which indices of abundance are used. Values were calculated using mean values of variables in non vegetation MAMS, and scaled according to the maximum value for each species. Absolute abundances were not produced due to the effect of region on abundance. Relationships for golden plover are with April measure of openness, while snipe is July. Skylark is with April density while meadow pipit, whinchat and stonechat are with July density measurements (see methods).

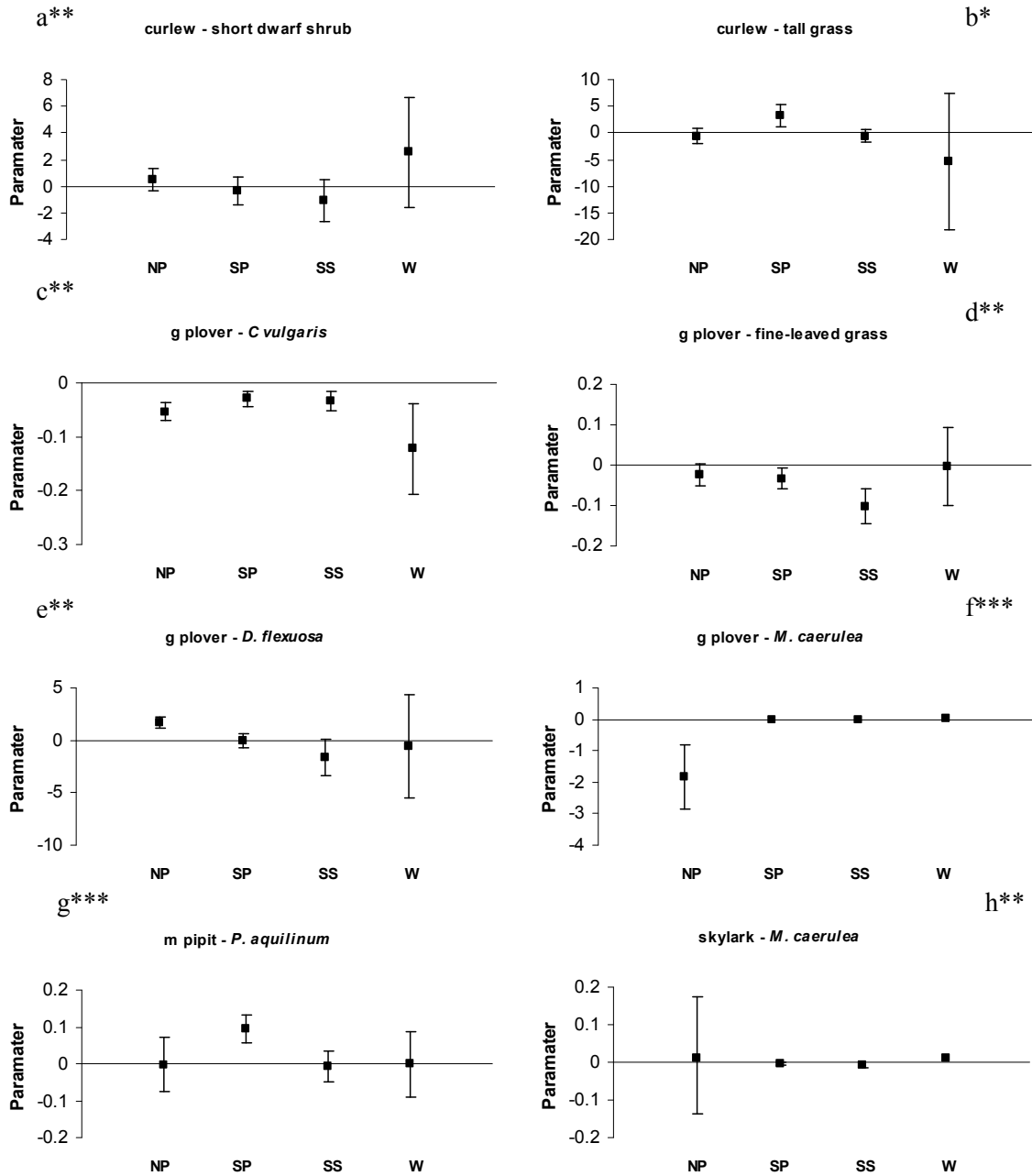


Figure 4 a-h Parameter estimates (± 95 % confidence intervals) for each region (NP – North Pennines, SP – South Pennines, SS – south Scotland, W – Wales) for the vegetation variables that significant regional interactions were detected for

Only linear parameters are shown. Strength of interaction denoted by the number of symbols ($P < 0.05$ *, $P < 0.01$ **, $P < 0.001$ ***). The sign of the parameter estimate indicates the direction of the relationship, with relationships with confidence intervals overlapping zero being non significant. Increased distance between the parameter estimates from each region and 95 % confidence intervals of the other regions indicates stronger differences between the regions in effect.

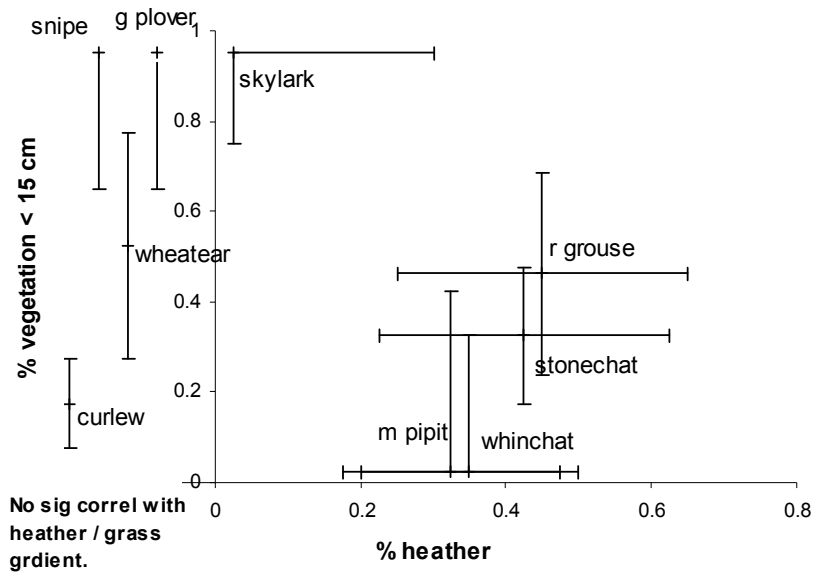


Figure 5 Schematic illustration of position of maximum species abundance along a compositional gradient of complete grass to complete heather cover, and a structural gradient from complete short vegetation cover to complete tall vegetation cover

See tables 4 and 5 for complete results. Figure shows peak modelled abundance, together with confidence intervals within which abundance remains above 75 % of the peak. The four species to the left of the figure did not display were not associated with the heather grass gradient.