

APPENDIX 3B.2

BIRD MODELLING: PREDICTIVE MODELS

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THE GENERALITY OF HABITAT SUITABILITY MODELS PRODUCED USING INFORMATION-THEORETIC TECHNIQUES IN A COMPLEX SEMI-NATURAL ENVIRONMENT.

Statistical models relating spatial variation in distribution or abundance to environmental parameters are widely used in ecology to quantify the habitat and management requirements of particular species (Ormerod et al. 2002, Rushton et al. 2004). Assuming that spatial models reflect underlying mechanistic relationships linking changes in abundance to environmental parameters (i.e. Green 1996), they can be used to identify actions to achieve particular management objectives, such as reversing the decline of a threatened species (i.e. O'Brien et al. 2006). Alternatively, such models can be used to predict species distributions across extensive areas of unsurveyed ground (Buchanan et al. 2005). However, consideration must be given to the geographical area from which those models are derived, relative to the area across which the predictions will be applied. For example, if model results are to be used to inform management elsewhere, then the generality of those models must be tested. Agri-environment schemes vary considerably in their effectiveness (Kleijn & Sutherland 2003), which may result from some being based on models that have little generality. The few studies that have examined this issue highlight the mixed predictive power of statistical models developed in specific locations, when applied to others (e.g. Fielding & Haworth 1995, Rodrigues & Andren 1999, Whittingham *et al.* 2003, Graf et al. 2006, Randin et al. 2006).

Within the UK, upland moorland and blanket bog (hereafter termed moorland) are some of the most internationally important habitats (Thompson et al. 1994). Declines in the distribution and abundance of a range of upland bird species (Gibbons *et al.* 1993, Gregory et al. 2002, Sim *et al.* 2005), have been variously related to increasing grazing pressure by both sheep and red deer, declines in the intensity of grouse moor management, and the afforestation of extensive areas of moorland (Tharme et al. 2001, Calladine et al. 2002, Buchanan et al. 2003, Pearce-Higgins & Grant 2006, Pearce-Higgins et al. 2006, Sim et al. in press). Recent work suggests areas with heterogeneity in

both vegetation composition and structure at a range of spatial scales may provide the most favourable habitat conditions for the widest range of moorland species (Pearce-Higgins et al. 2006, Buchanan et al. unpubl.). Current restructuring of Europe-wide support for agriculture, if associated with large-scale reductions in the intensity of active management, is likely to result in a reduction of habitat heterogeneity (Vandvik et al. 2005). Therefore, the potential for large-scale reductions in livestock numbers in less-favoured upland areas in the UK, may therefore be detrimental to the future conservation status of moorland birds, reflecting negative changes to grassland bird populations in other European upland ranges that have occurred following land abandonment (i.e. Laiolo et al. 2004).

Where they produce good predictions of species abundance, correlative studies can be used to inform moorland management decisions within the regions from which the data are collected (Pearce-Higgins & Grant 2006). However, if large-scale policy decisions and future management schemes are to be effective at the national level, it is important to quantify the generality of these models more widely. We therefore model spatial variation in moorland bird abundance as a function of environmental, habitat and management variables in two upland regions in the UK, and then test the generality of those models using independent data from a further two regions. This study therefore adds to the small number of studies that have examined the geographical transferability of such spatial models, a key issue if such models are to be widely used to inform successful conservation management.

METHODS

Site selection

Data were collected from four upland regions of the UK (Wales, South Pennines, North Pennines and South Scotland) that have each undergone substantial increases in sheep stocking densities over the last 60 years (Fuller and Gough 1999). Twenty-nine plots were from the north Pennines, (surveyed in 1999 and 2003), 37 from the south Pennines (surveyed in 2002), 72 were located in south Scotland (surveyed in 1999 and 2000) and 21 plots

in Wales (surveyed in 2002). Within each region, plots were located from a random sample stratified by heather cover (Buchanan et al. unpubl.), although due to access refusals, 13 plots in the north Pennines and 22 plots in south Scotland were located within areas where access was assured (Pearce-Higgins & Grant, 2006). Plots were located a minimum of 200 m from the nearest forest edge and did not include enclosed land.

Bird surveys

Breeding grouse, waders and passerines (excluding meadow pipits *Anthus pratensis* and skylarks *Alauda arvensis*) were surveyed using a standard three-visit census method following Pearce-Higgins & Grant (2006). Each plot was visited once in each three-week period from 17 April –20 June, with visits in consecutive periods made at least 7 days apart. Surveys did not take place in rain or strong winds, and each plot was surveyed by at least two different observers to minimise bias. The location and behaviour of all birds, except meadow pipits and skylarks, was recorded to the nearest 100 m. The maximum count of breeding pairs over the three visits was used as a measure of abundance for species, except curlew *Numenius arquata*, for which mean count was used (Pearce-Higgins and Grant, 2006.).

Skylarks and meadow pipits were surveyed using two, 1 km transects within each plot, 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 perpendicular distance from where each bird was initially detected to the transect was estimated by eye. The count of meadow pipits within 25 m of transects and the total count of skylarks were used as indices of abundance, as these were least prone to observer effects (Buchanan *et al.* 2006a).

Vegetation data

Vegetation data were collected from points distributed evenly across each plot, following Pearce-Higgins and Grant (2006). Structural measurements were made from 50 points during the first bird survey, whilst measures of

structure and composition were made at 100 points during an additional late visit between 21 June and the end of July.

In relation to structure, three measures of vegetation height and density were made at each point. Where present, the heights of dwarf shrubs, grass leaves, grass flowers, tall rushes and bracken were separately recorded, whilst the visibility of white marks at 0, 10, 20, 30 and 40 cm from the ground provided an index of vegetation density. Height measurements were averaged for each sampling point and summarised into three classes (0 - 15 cm, 15 - 30 cm, > 30 cm) for all vegetation, and separately for graminoid leaves and dwarf shrubs. The proportion of points at which all three 10 cm marks were visible was used as a measure of the availability of open habitat. The composition of vegetation along a 1 m bamboo cane randomly placed on the ground at each point was used to calculate mean cover values of separate plant taxa within each plot. Variation in vegetation height (height variability) was assessed as the mean change in maximum vegetation height between successive sampling points from the late visit, whilst variation in dwarf shrub cover (VDSC) was derived from the change in the log-ratio of dwarf shrubs to graminoid (grasses, sedges and rushes) cover between adjacent sampling points (Pearce-Higgins & Grant, 2006).

Physical, landscape and management data

It was important to measure as many potentially confounding environmental variables not directly amenable to management as possible, to reduce the risk of Type I errors (Pearce-Higgins & Grant 2006; Table 1). Peat depth was recorded during the late sampling period, whilst soil cover was assessed from 1:250 000 soil maps (Soil Survey of England and Wales 1983; Walker et al 1982). Topographical data were obtained from 50 m digital elevation models (Panorama, Ordnance Survey, UK). To assess the effects of adjacent land-use, measures of forest cover and enclosed farmland surrounding each plot were obtained from LCM2000 (CEH 2001). Following Tharme et al (2001) the intensity of game management was assessed from an index of gamekeeper density, the abundance of crows recorded from bird surveys, and muirburn intensity recorded during the late sampling period. Unlike Pearce-Higgins &

Grant (2006), we did not include climatic variables in the analysis, as currently available gridded data-sets were not of sufficiently high resolution to produce independent values for individual study plots. Measures of longitude and latitude were also not considered, due to the different range of values in different regions. We therefore assume that any variation in bird abundance resulting from large-scale climatic and geographical processes will be manifest through changes in habitat, and thus identified by variation in vegetation variables.

Statistical analysis

Nine species were sufficiently abundant to produce predictive models of abundance, being present on > 20 % of plots (Pearce-Higgins & Grant 1996, Buchanan et al. in prep.); red grouse *Lagopus lagopus scotica*, golden plover *Pluvialis apricaria*, Curlew *Numenius arquata*, Snipe *Gallinago gallinago*, Meadow Pipit *Anthus pratensis*, Skylark *Alauda arvensis*, Whinchat *Saxicola rubricollis* Stonechat *Saxicola torquatus* Wheatear (*Oenanthe oenanthe*). We make use of recent advances in analytical techniques to model variation in bird abundance using the Information-theoretic approach of model averaging advocated by Burnham & Anderson (2002). Due to computational constraints, this restricts the number of variables that can be examined in any one model (we found a maximum of sixteen independent terms was possible when considering all possible combinations). Where there is good ecological knowledge concerning the factors affecting the distribution of a particular species, then the terms within these models can be identified from previous studies (e.g. Whittingham *et al.* 2005, 2006), although this restricts the ability of such models to identify novel relationships. Where such ecological information is lacking, as for many rare and poorly studied species, then models have previously been based on a relatively simple suite of variables (e.g. Gibson *et al.* 2004). However, such studies are at risk from Type I errors, due to the existence of unmeasured, but causal, confounding variables (Lawlor et al. 2004a, b). There is a difficult balance to be struck between the dangers of over-fitting as a result of considering too high a number of candidate variables, whilst ensuring that all appropriate measures of environmental variation are included within a particular analysis to reduce the

risk of Type I errors. This problem is acute when modelling species distributions within complex natural or semi-natural environments, or where good ecological knowledge about a particular species is lacking, conditions which both apply to our data. We therefore follow the recommendation of Lawlor et al. (2004a) that '*Future observational studies, in this and other areas, should aim to collect information...in order to be able to adjust as fully as possible for potential confounding factors*', and measure a wide range of terms thought to influence upland bird abundance. By combining model averaging with a variable reduction process to decrease the number of terms considered, we reduce the potential problems of co-linearity between predictor variables, inappropriate model selection and overfitting of variables to produce non-robust models. Model predictions are compared with those from a simple backwards deletion approach, to assess the level of improvement in predictive power gained using model averaging.

Variables were divided into three groups, describing either variation in vegetation composition, vegetation structure, or non-vegetation (other aspects of the plot, its management, or the survey itself) variables. Vegetation composition variables were limited to the 20 plant taxa recorded on at least 40 % of the plots, plus VDSC. There were 23 vegetation structure variables relating to the cover of different height classes of graminoids, dwarf shrubs and all vegetation, plus vegetation structure measures, taken both in April and July, and the measure of height heterogeneity. Finally, there were a total of 44 non-vegetation variables (Table 1). While some of these may have represented vegetation-related characteristics (e.g. muirburn) they were classed as 'non-vegetation' due to their strong association with managements that also influence bird abundance. The number of potential predictor variables was reduced by performing a series of initial correlations between bird abundance and variables within separate sub-groups that describe the same environmental component (i.e. slope, soil, vegetation density) in different ways (Table 1). Within each subgroup, only the linear plus quadratic (first rescaled to a mean of 0 and standard deviation of one) term associated with the greatest reduction in deviance, or for vegetation cover, the top eight most strongly correlated variables, plus VDSC as a measure of heterogeneity,

were then used for modelling. The final list of variables considered for each species was reduced to 9 non-vegetation, 9 vegetation cover and 5 vegetation structure variables, plus their associated, rescaled, quadratic terms.

Due to the large number of variables remaining (46 including quadratic terms), additional steps were necessary to reduce the number of terms to a final list of sixteen, the maximum possible for model averaging (see above). Firstly, all possible one to six variable combinations (treating linear and quadratic terms separately) were determined, and used to rank the variables by the level of statistical support. A maximum of 18 variables only could be considered at this stage, so six-variable subsets were created separately for the three variable groups of vegetation composition, vegetation structure, and non-vegetation. Each of these variable combinations were inserted into a Generalised Linear Model (GLM), specifying a Poisson error and log link-function, and fixing the scale parameter for each model to one (Burnham & Anderson 2002). Region was included as a two-level factor. The support for each model was assessed using Akaike's Information Criterion (AIC). We calculated the Akaike weight for each model, and summed these weights across all the models containing each variable to produce a probability of each variable being included in the best fitting model (Burnham & Anderson 2002). Variables were then ranked within each group according to their Akaike weight. Because of the greater number of vegetation, compared to non-vegetation, measures, this process was then repeated using the top 2/3rds of the ranked vegetation composition and structure variables (12 and 6 respectively) to produce a ranked list of 18 vegetation variables comparable with the 18 non-vegetation variables.

All possible combinations of the eight vegetation and eight non-vegetation variables with the greatest Akaike weights were then modelled, and the relative Akaike weights, parameter estimates and standard errors calculated using model averaging to produce the final predictive model (Burnham & Anderson 2002). Following Burnham & Anderson, the scale parameter was fixed to the Pearson's scale parameter for a full model containing all sixteen terms. Terms whose 95% confidence intervals did not cross zero were

nominally regarded as significant. Although limiting the number of variables in each group to eight may have resulted in important variables not being considered, this is unlikely given that final significance of each term was correlated with rank ($r_s = -0.51$, $n=114$, $P < 0.001$) with no variables ranked eight, and only one ranked seven being highlighted as significant in the final models.

Due to the large number of 46 terms (including quadratics) to be initially considered, it was not possible to produce a full model containing all terms for backwards deletion. Thus, following the initial variable reduction process to 46 terms in three groups, backwards deletion was used to reduce full models containing either non-vegetation, vegetation-structure or vegetation-composition variables to minimum adequate models (MAMs) of only significant ($P < 0.05$) terms. The variables in these three MAMs were then combined to produce a full model that was simplified to a final MAM predicting bird abundance, using backwards deletion.

It is important to be able to assess the accuracy of model predictions with an independent data set (Vaughan & Ormerod 2005). As previous attempts to model bird abundance using equivalent data have generally found good predictive ability within an upland region using stepwise selection procedures (Pearce-Higgins & Grant 2006), we focus on testing the predictive abilities of our models using data from two novel geographical regions, a very rigorous test. Thus, data from the two largest regions, south Scotland and the South Pennines (totalling 109 plots), were used to produce the final predictive models, whilst the fifty plots from Wales and the North Pennines formed a completely independent test data set with which to identify those models most likely to exhibit generality across the UK uplands. When making predictions, values of explanatory variables were constrained to the range of values from south Scotland and the South Pennines used to build the models.

Predictive ability was tested separately for each species and region. Count was modelled as a function of predicted density (\log_e transformed) within a GLM, specifying a Poisson error structure and log-link function (Crawley

1993). Performance was summarised as the proportional change in deviance associated with the inclusion of predicted density. Secondly, the slope of the regression between predicted and observed density was used to indicate whether the model predicted absolute abundance (a slope of 1), or consistently under- (slope < 1) or over- (slope > 1) estimated abundance. To see whether models could be used to broadly assess the best and worst sites for a species in any one region, we thirdly assessed the ability of the models to correctly rank sites into four quartiles. Thus, the relative concordance between the observed and predicted rankings into the four quartiles of abundance was assessed using the formula of (Jeganathan et al. 2004).

$$\text{Concordance} = (\text{concordance} - \text{concordance}_{\text{null}}) / (1 - \text{concordance}_{\text{null}})$$

Factors associated with variation in model performance were tested using a GLM with normal errors, reflecting the distributions of the data. For three cases with a negative correlation between observed and predicted abundance, the proportional change in deviance was given a negative value to reflect the fact that predictive performance was worse than random. A unique identifier for each species-by-region combination was included as an 18-level factor to account for region- and species-specific differences in model performance, and significant differences in performance between the two statistical methods tested by the inclusion of a two-level factor. Analysis of variation in the slope of the regression between observed and predicted abundance was weighted by the reciprocal of the standard error of the slope, so that species-by-region combinations where the slope was poorly estimated had only a small weight. Given the considerable variation in predictive performance between different species and regions (see below), we investigate the effects of mean abundance (natural log transformed for normality) and prevalence (arcsin square-root transformed for normality) on predictive performance on the model averaged predictions. Each of the three tests of model performance; change in deviance, slope, and concordance, were regressed separately against both abundance and prevalence, with each species-by-region combination being the unit of analysis.

Where relevant, means are presented with standard errors.

RESULTS

Model construction

Model averaged outputs contained an average of 4.7 significant terms highlighted per species (Table 2), compared with 6.9 in backwards deletion models (Table 3). Model averaging, where significance was assessed by the overlap of 95% confidence limits of parameter estimates with zero, therefore provided a more conservative test of significance, although there were considerable similarities in the significant terms highlighted between the two approaches. Thus, 64 % of the variables highlighted as significant using model averaging were selected in the final backwards deletion MAMs; 83% if linear and quadratic terms of the same variable are regarded as equivalent. Conversely, 44 % of variables in the final backwards deletion MAMs were highlighted as significant by model averaging and 85% were contained within the final model averaged output.

Model performance

The three measures of model performance were all strongly correlated (slope vs deviance $r = 0.716$, deviance vs concordance, $r = 0.848$, slope vs concordance $r = 0.655$; $n=18$). The performance of the final models varied between species and regions (Table 4). Model averaged models explained on average $54 \% \pm 4.7$ of the deviance in bird abundance in the two training regions (South Pennines and South Scotland), whereas backwards deletion explained $52\% \pm 5.4$ ($F_{1,17} = 0.80$, $P = 0.38$). The slope of the regression between observed and expected counts was significantly lower with model averaging ($F_{1,17} = 53.58$ $P < 0.001$) averaging 0.73 ± 0.06 , whilst backwards deletion models provided a close description of abundance, with a mean slope of 0.99 ± 0.04 . Levels of concordance were, however, slightly greater using model averaging ($F_{1,17} = 4.57$, $P = 0.047$), averaging 0.37 ± 0.04 and 0.33 ± 0.04 respectively. Thus, although a model built using model averaging was likely to produce a slightly closer fit to the data, and better differentiate between the best and worst sites for a particular species, when estimating abundance, model averaging was more likely to under-predict the true values than backwards deletion.

When applied to the test data-set of the North Pennines and Wales, mean predictive performance ranged from 24.7 % \pm 6.3 using model averaging and 12.0% \pm 4.9 using backwards deletion ($F_{1,17} = 8.54$, $P = 0.009$). Half of the model averaged predictions showed significant predictive power, compared to 44% of the backwards deletion models. Where predictions had significant explanatory power, they accounted for 46% of the deviance in bird abundance using model averaging, but only 33% of the deviance using backwards deletion. There was, however, no significant difference in the regression slopes between the two methods due to wide variability in performance ($F_{1,15} = 0.93$, $P = 0.349$); both model-averaging (slope = 0.51 ± 0.17) and backwards regression (slope = 0.29 ± 0.16) tended to under-estimate abundance. Levels of concordance were also similarly low between the two methods across the test data ($F_{1,17} = 0.11$, $P = 0.741$; model averaging = 0.13 ± 0.05 , backwards deletion = 0.11 ± 0.05). Thus, predictions of abundance based on model averaging appeared to show a closer fit to the observed data, particularly when estimating abundance, although predictions continued to under-predict observed values.

Factors associated with good performance

Mean abundance was not significantly correlated with the proportion of deviance explained ($F_{1,17} = 3.01$, $P = 0.102$) or concordance ($F_{1,17} = 1.32$, $P = 0.267$), but was weakly negatively correlated with slope ($F_{1,17} = 3.99$, $P = 0.063$). Species prevalence was much more strongly negatively correlated with both the proportion of deviance explained ($F_{1,17} = 5.51$, $P = 0.032$) and slope ($F_{1,17} = 8.77$, $P = 0.009$), but not concordance ($F_{1,17} = 3.00$, $P = 0.102$). The lack of a significant relationship with the latter was due to two data points (golden plover in Wales, and whinchat in the North Pennines), where the distributions of species' with low prevalence were poorly predicted (Figure 1c). Overall, models were therefore more likely to show good predictive power in regions where that species occurred on only a few plots (Figure 1).

Production of final predictive models

Based upon the findings from the above analyses final predictive models were produced using the model averaging approach outlined above, with full data set from all four study regions. Details of these models for each of the nine bird species studied are given in table 4.

DISCUSSION

There was a high degree of similarity between the variables specified in either the model averaging or backwards deletion models for a particular species. As a result, the predictive abilities of the two approaches were fairly similar, although predictions based on model averaging tended to show a tighter fit to the observed data across the two test regions, but still significantly under-predicted abundance. This work therefore supports that of others (i.e. Whittingham et al. 2003, 2006) indicating that using information-theoretic techniques to construct habitat suitability models produces more accurate predictions than a more 'traditional' backwards deletion approach, although suggests that in some cases, the improvement in model performance is insignificant. The much quicker and less computationally intensive stepwise techniques for variable selection (models took about 2 working days to be produced using model averaging, but only a few minutes using backwards deletion) can still, therefore, provide a reasonable description of a particular system, and should not automatically be rejected.

Importantly, we have been able to successfully apply model averaging techniques to a complex semi-natural environment measured with a wide-range of variables. By using a multi-stage variable reduction technique, we have reduced this large number of variables to a small number of relevant terms for each species, without the need to refer to existing literature (cf. Whittingham et al. 2005, 2006). Thus, unlike other studies using model averaging, we have reduced the risk of Type I errors due to the existence of unmeasured confounding variables (Lawlor et al. 2004a, b). Therefore, practitioners that wish to use model averaging do not necessarily have to undergo an *a priori* selection of a narrow number of predictor variables to

model (Whittingham et al. 2005, 2006), or restrict their analysis to only broad measures of habitat (Gibson et al. 2004).

We were able to produce models that produced a significant correlation between observed and predicted abundance for about half of the test species-by-region combinations. Models were able to account for, on average, 25 % of the variation in breeding density, or 46 % in the half of cases where model outputs had significant predictive power. Thus, models to predict moorland bird abundance, for example to map distributions in unsurveyed areas (e.g. Buchanan et al. 2005), or to inform conservation management (e.g. Pearce-Higgins & Grant, 2006), are likely to show some generality to novel regions on about fifty percent of occasions. Unfortunately, it is difficult to compare this performance with most other studies of the generality of habitat suitability models, as these generally predicted only presence / absence, and with varying success (Fielding & Haworth 1995, Graf 2006, Randin et al. 2006, Vanruesel et al. 2007), although our measures of concordance were, on average, lower (Fielding & Haworth 1995, Graf 2006). The only other study where the generality of models to predict abundance were applied to novel regions is Whittingham et al. (2003), where predictions of skylark abundance achieved an average correlation of $r^2 = 0.22$ between observed and expected values.

In general, the best predictions appear to result from models with a few, strong, predictor variables that directly measure key resources (i.e. Graf 2006, Vanruesel et al. 2007), with many of the errors resulting from inter-regional differences in environmental predictors (Fielding & Haworth 1995, Randin et al. 2006). Our errors are unlikely to result from differing habitat associations between the different regions, as the slopes of individual relationships between abundance and habitat show wide generality (Buchanan et al. in prep.), although it is possible that when such errors are additive, as in a multivariate model, they may be sufficient to reduce predictive ability in some cases. The accuracy of predictions would probably be improved if it were possible to measure the availability of specific resources, such as invertebrate prey (i.e. Pearce-Higgins & Yalden 2003), rather than indirect environmental

surrogates of these resources (Vanruesel et al. 2007). This may explain why red grouse was the species for which our models produced the most accurate predictions, as the models included measures relating to the availability of Heather (*Calluna vulgaris* Hull), a key food resource (*M. caerulea* cover, VDSC, Table 2; *C. vulgaris* cover, *M. caerulea* cover, VDSC, Table 3). However, to do so for other species, across such extensive areas, would be logistically very difficult, particularly as, in many instances, it is not clear what the key resources should be (for example see Buchanan et al. (2006b) to highlight variation in upland bird diets). Some of the variability in model performance may also result from survey error. For example, the two species that failed to produce a significant correlation between predicted and observed in either of the test regions, meadow pipits and snipe, are known to be particularly difficult to survey accurately (Buchanan et al. 2006a, Hoodless et al. 2006), and have previously yielded poor correlations between observed and predicted abundance (Pearce-Higgins & Grant 2006).

Our data also highlighted the importance of species prevalence in determining predictive ability (Figure 1), which to our knowledge, has not previously been identified. Predictions of abundance were more likely to be accurate in regions where a species was rare, despite the fact that such measures of predictive ability are likely to be more variable in regions with a small sample size. This finding probably results from the buffer effect, where increases in population size result in a greater occupancy of poor quality sites (Kluyver & Tinbergen 1953). Thus, when a species is rare, only the highest quality habitats will be occupied, and abundance will be strongly linked to a particular environmental variable that best describes that occupied niche. However, as prevalence increases, then poorer quality habitats are likely to support a greater number of birds, reducing the strength of the relationships between the environment and abundance. This may be a useful artefact of such modelling approaches for conservationists, which makes them particularly informative when modelling the distribution of particularly rare and threatened species.

To conclude, the use of model averaging significantly improved the predictive accuracy of models describing moorland bird abundance over more traditional backwards deletion approaches, although the latter still produced significant predictions in some instances. Predictions of moorland bird abundance obtained using model averaging were likely to exhibit generality to other regions on about half of occasions. Those predictions were likely to be most accurate for species that are the easiest to survey, where the environmental variables most closely represent key resources, and for regions where the target species are relatively rare, and therefore exhibit a high degree of habitat selectivity. However, in common with other studies of habitat suitability models, this study also highlights the value of collecting data from across the geographical range to which predictions based on those data will be applied, if one is to be sure of the applicability of the model across this range (Fielding & Haworth 1995, Whittingham et al. 2003, Randin et al. 2006). Thus, policy and management decisions should ideally be based upon information from across the area to which those decisions will be applied, and it is possible that some of the failures of agri-environment schemes (Kleijn & Sutherland 2003) have resulted from them being based on models with little generality.

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Table 1 List of variables considered in the analysis

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

Variable	<i>Definition</i>
Region	Fixed effect for the four regions. Includes potential observer and year effects
Altitude	Mean altitude of plot (m)
Slope	Percentage of plot covered by 3 categories of slope (0° - 5°; 5°-10°, >10°)
Soil cover	Percentage of vegetation sample points located on mineral soil, shallow (0-50 cm) and deep (>50 cm) peat, and proportional cover by 6 soil categories from (Soil Survey of England and Wales 1983; Walker et al 1982).
Muirburn	Mean number of separate muirburns located between sample points and percentage of sample points located in muirburn
Keeper density	Density of gamekeepers per 1000 acres, obtained from landowners.
Predator index	Mean number of crow groups recorded during three bird surveys
Proximity of in-bye	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 Model averaged output for each species

Variables are divided into non-management (top), vegetation structure (middle) and vegetation composition (bottom). Terms with confidence intervals that do not overlap zero are regarded as significant (bold). Quadratic terms are denoted by a superscript 2. ^A indicates vegetation structure measures from April, and ^J from the late visit in July. In relation to forest cover ¹ = cover of forest within 1km buffer of plot, and ⁴ = proportion of plot within 400m of forest. In relation to slope, ⁵ = proportion cover of slope of 5°-10°, and ¹⁰ = cover of slope > 10°. The significance of each term is given as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$.

	Red Grouse		Curlew		Golden Plover		Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	0.576	0.881	1.872	0.482	-0.950	1.152	0.794	0.893
South Pennines	0.839	0.849	-0.129	0.261	0.534	0.567	-0.209	0.363
Altitude	0.002	0.001	-0.001	0.001	0.003	0.002	-0.003	0.002
Altitude ²	-0.080	0.085						
Slope					1.051 ⁵	0.619		
Slope ²			0.154⁵	0.068	0.251⁵	0.105	0.067 ⁵	0.077
Mineral Soil cover	-1.767	0.588						
Mineral Soil cover ²	-0.089	0.121						
All peat cover							-0.557	0.286
Deep Peat cover			-0.695	0.536				
Burn cover	1.106	1.207						
No. burns			0.340	0.287	0.483	0.446		
No. burns ²					0.059	0.033		
Game keeping	3.110	1.308	1.750	0.812			-0.085	0.956
Game keeping ²	0.102	0.102						
Forest cover					-4.751 ¹	2.899	0.629 ⁴	0.644
Inbye cover	-1.960	0.885	0.492	0.857	-2.241	1.079		
Inbye cover ²			-0.058	0.110	-0.117	0.176		
Crow Groups			0.017	0.032			0.027	0.027
First survey date ²							-0.302	0.123
Open structure cover					1.898^A	0.779		
Open structure cover ²					-0.119 ^A	0.202		
Short dwarf shrub cover ²			-0.189 ^A	0.101				
Medium dwarf shrub cover	1.124 ^J	1.093						
Medium dwarf shrub cover 2	-0.097 ^J	0.079						
Short vegetation cover					1.711 ^J	0.884		
Tall vegetation cover ²			-0.242^J	0.104			-0.153 ^J	0.090
Height variability	0.0002	0.035					0.024	0.040
Bare cover ²					-0.057	0.027		
C. vulgaris cover								
C. vulgaris cover ²								
E. angustifolium cover			-0.222	0.111			-0.117	0.085
E. angustifolium cover ²			0.088	0.181				
Fine leaved grass cover					-0.020	0.012		
J. acutifloris cover	-0.108	0.087					0.042	0.040
J. acutifloris cover ²					-0.134	0.129		
J. effusus cover			0.072	0.054				
J. effusus cover ²			0.157	0.116				
M. caerulea cover	-0.024	0.011			-0.026	0.011		
S. cespitosus cover			-0.140	0.051				
Sedge spp. Cover							0.136	0.059
Sedge spp. Cover ²			0.056	0.032			0.082	0.047
V. myrtillus cover							-0.064	0.034
VDSC	0.432	0.115			0.065	0.115	0.314	0.100
VDSC ²	-0.022	0.100					-0.140	0.095

	Meadow pipit		Skylark		Sontechat		Wheatear		Whinchat	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	2.528	0.228	2.352	0.632	1.117	0.989	-1.384	1.564	-0.089	3.512
South Pennines	0.130	0.176	0.243	0.300	-1.573	1.722	-0.180	0.256	-0.370	0.525
Altitude					-0.005	0.003	-0.004	0.002	-0.009	0.004
Altitude ²	-0.115	0.061	-0.002	0.001						
Slope					2.070 ¹⁰	1.326			-2.957⁵	1.298
slope ²					-0.127 ¹⁰	0.188				
Peat cover ²									-0.298	0.242
Shallow peat cover					0.820	1.080				
Deep peat cover			-1.521	0.583			-1.266	0.630		
Deep peat cover ²			-0.194	0.118						
Surface-water Gley cover ²	0.067	0.032								
Burn cover	1.233	1.203							3.625	2.721
Burn cover ²	-0.028	0.040							0.036	0.068
No. burns			0.023	0.030	0.285	0.718	-0.802	0.605		
No. burns ²					-0.034	0.051	-0.120	0.085		
Game keeping							-0.440	0.964	-0.092	2.044
Forest cover	-0.610 ⁴	0.686	-0.080 ⁴	0.061					0.544 ¹	1.500
Forest cover ²	0.022 ⁴	0.041					0.053	0.034		
Inbye cover					-3.042	1.926				
Inbye cover ²	-0.055	0.058	0.107	0.074			-0.204	0.098		
Crow groups			0.074	0.030	-0.063	0.069				
Third survey date			-0.003	0.012			0.049	0.018	0.009	0.036
Third survey date ²	-0.017	0.018								
Open structure cover							1.791^J	0.645		
Short dwarf shrub cover									-2.288	1.498
Short dwarf shrub cover ²										
tall dwarf shrub cover					1.955 ^A	1.903				
Short grass cover							0.921 ^A	0.703		
Short grass cover ²			-0.045 ^J	0.114					-0.812^J	0.367
short vegetation cover	-0.814^A	0.341								
short vegetation cover ²			-0.135 ^A	0.130						
Tall vegetation cover					1.902 ^A	1.482				
Bare cover					0.165	0.043				
Bare cover ²			-0.070	0.054						
C. vulgaris cover ²					-0.728	0.275				
E. nigrum cover ²							-0.159	0.279		
E. angustifolium cover	-0.043	0.044	-0.094	0.093						
E. angustifolium cover ²	-0.059	0.049	0.065	0.107						
E. vaginatum cover					-0.133	0.056	-0.024	0.028		
E. vaginatum cover ²					0.396	0.157	-0.222	0.120		
Fine leaved grass cover ²					-0.392	0.158				
J. acutifloris cover									0.110	0.073
M. caerulea cover									0.068	0.033
M. caerulea cover ²									-0.320	0.184
Moss spp. cover	0.029	0.028			-0.045	0.075				
Moss spp. cover ²	-0.158	0.103								
N. stricta cover			0.020	0.019						
N. stricta cover ²			0.023	0.041						
P. aquilinum cover	0.033	0.031					0.023	0.047	0.412	0.160
P. aquilinum cover ²	0.071	0.051					0.014	0.080	-0.487	0.228
Sedge spp. cover	0.076	0.036								
V. myrtillus cover			-0.026	0.021						
VDSC									0.512	0.217

Table 3 Backwards deletion model output for each species

Variables are divided into non-management (top), vegetation structure (middle) and vegetation composition (bottom). Quadratic terms are denoted by a superscript 2. ^A indicates vegetation structure measures from April, and ^J from the late visit in July. In relation to forest cover ¹ = cover of forest within 1km buffer of plot, and ⁴ = proportion of plot within 400m of forest. In relation to slope, ⁵ = proportion cover of slope of 5°-10°, and ¹⁰ = cover of slope > 10°. The significance of each term is given as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$.

	Red Grouse		Curlew		Golden Plover		Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	0.048	0.505	2.181	0.184	-1.052	0.630	0.386	0.277
South Pennines	1.420	0.133****	-0.175	0.206	0.921	0.182	-0.399	0.311
Altitude	0.0016	0.0007*			0.001	0.001**		
Slope 5					1.141	0.358**		
Slope 5 ²			0.199	0.047****				
Mineral soil cover	-1.034	0.334**						
All peat cover							-0.708	0.233**
No. burns					0.568	0.221*		
Game keeping	2.105	0.513****	1.879	0.465****				
Forest cover					-5.708	2.339**		
Inbye cover ²					-0.209	0.113*		
First survey date ²							-0.361	0.108***
Short grass cover	-0.162 ^J	0.086*						
Short dwarf shrub cover ²			-1.963 ^A	0.497****				
Short dwarf shrub cover ²			-0.210 ^A	0.085**				
Tall grass cover			-1.431 ^J	0.489**				
C. vulgaris cover	0.007	0.003*						
E. angustifolium cover			-0.140	0.056**				
M. caerulea cover	-0.013	0.007*			-0.024	0.009**		
S. cespitosus cover			-0.101	0.035**				
sedge spp. cover ²							0.112	0.023****
V. myrtillus cover							-0.074	0.025**
VDSC	0.333	0.059****					0.333	0.074****

	Meadow pipit		Skylark		Stonechat		Wheatear		Whinchat	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	2.733	0.119	2.051	0.170	1.755	0.654	-2.665	1.345	6.519	1.955
South Pennines	0.483	0.119****	0.744	0.191	-3.554	0.827****	-0.600	0.284	-2.210	0.711***
Altitude					-0.004	0.002*	-0.005	0.001****	-0.014	0.003****
slope					1.445 ¹⁰	0.646*			-6.371 ⁵	1.146****
Peat cover ²									-0.732	0.224***
Deep peat cover							-1.831	0.555***		
Deep peat cover ²			-0.233	0.082**						
Surface-water Gley cover ²	0.063	0.019**								
Game keeping									8.170	2.697**
Game keeping ²									-1.650	0.487***
Inbye cover ²							-0.291	0.102***		
Crow groups			0.053	0.018**						
Survey date							0.059 ³	0.017***		
Open structure cover									-3.036 ^J	1.054**
Short dwarf shrub cover ²									-0.912 ^A	0.326**
Short grass cover							2.006 ^a	0.599***		
Short grass cover ²			0.134 ^J	0.046**					-0.928 ^J	0.328***
short vegetation cover	-1.023 ^A	0.231****								
short vegetation cover ²			-0.213 ^A	0.090*						
Height variability									0.229	0.070***
Bare cover					0.186	0.035****				
Bare cover ²			-0.081	0.039*						
C. vulgaris cover ²					-0.724	0.220***				
E. angustifolium cover	-0.066	0.025**	-0.230	0.065***			0.354	0.104***		
E. angustifolium cover ²			0.225	0.070**			-0.433	0.135***		
E. vaginatum cover					-0.138	0.041***				
E. vaginatum cover ²					0.384	0.140*				
Fine leaved grass cover ²					-0.504	0.150****				
Moss spp. cover ²	-0.198	0.070**								
N. stricta cover			0.024	0.009**						
Sedge spp. cover	0.091	0.025***								
V. myrtillus cover			-0.029	0.013*						

Table 4 Details of final predictive models based upon data from all four study regions and model averaged output for each species

Variables are divided into non-vegetation (top), vegetation structure (middle) and vegetation composition (bottom). Terms with confidence intervals that do not overlap zero are regarded as significant (bold). Quadratic terms are denoted by a superscript 2. ^A indicates vegetation structure measures from April, and ^J from the late visit in July. In relation to forest cover ¹ = cover of forest within 1km buffer of plot, and ⁴ = proportion of plot within 400m of forest. In relation to slope, ⁵ = proportion cover of slope of 5°-10°, and ¹⁰ = cover of slope > 10°, and date, the superscript relates to the visit number the date refers to.

	Red Grouse		Curlew		Golden Plover		Snipe	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	-0.491	0.963	-0.583	1.062	-0.650	1.438	-0.831	0.867
South Pennines								
Altitude	0.002	0.001	-0.002	0.001	0.002	0.001	-0.002	0.001
Altitude ²	-0.082	0.084						
Slope	-0.192 ¹⁵	0.398			-1.884¹⁵	0.579	0.506 ⁵	0.360
Slope ²							0.042 ⁵	0.065
Mineral Soil cover	-1.102	0.523						
Mineral Soil cover ²	-0.053	0.113						
All peat cover ²							0.191	0.121
Deep Peat cover			-0.628	0.486				
Burn cover	1.435	1.353						
Burn cover ²	0.008	0.039						
No. burns			0.603	0.279	0.634	0.337		
Game keeping			1.613	1.070	3.308	1.742	0.750	0.783
Game keeping ²			-0.062	0.070	-0.112	0.131	-0.022	0.052
Forest cover			-1.678 ¹	1.511	-0.382 ⁴	0.833		
Forest cover ²			-0.051 ¹	0.052				
Inbye cover	-1.980	0.658						
Inbye cover ²					-0.111	0.082		
Crow Groups			0.024	0.036			0.030	0.028
First survey date ²							-0.211	0.103
Open structure cover					2.309^A	0.837		
Open structure cover ²			-0.175 ^J	0.097	-0.195 ^A	0.183	-0.139	0.585
Short dwarf shrub cover ²			-0.136 ^A	0.084				
Medium dwarf shrub cover ²							-0.113	0.099
Short graminoid cover							1.308^J	0.585
Tall graminoid cover			-1.059 ^J	0.709				
Short vegetation cover ²	0.025	0.033						
Tall vegetation cover					-2.175	0.864		
Height variability							0.026	0.030
Bare cover			0.030	0.051	0.009	0.004		
Bare cover ²			-0.130	0.092	-0.077	0.045		
C. vulgaris cover	0.012	0.004						
E. angustifolium cover			-0.109	0.061				
J. acutifloris cover	-0.119	0.086					0.037	0.036
N. stricta cover					-0.042	0.021		
M. caerulea cover	-0.023	0.011						
P. aquilinum cover					-0.120	0.068		
S. cespitosus cover			-0.102	0.041				
Carex spp. Cover			0.106	0.041			0.145	0.039
VDSC	0.407	0.093			0.056	0.118	0.184	0.080
VDSC ²	-0.094	0.087						

	Meadow pipit		Skylark		Stonechat		Wheatear		Whinchat	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	3.788	0.372	3.123	0.557	2.803	0.696	1.144	1.386	3.953	1.347
South Pennines										
Altitude	-0.001	-0.001			-0.006	0.001	-0.004	0.001	-0.005	0.001
Altitude ²	-0.131	0.049								
Slope	0.224 ¹⁰	0.313			-2.558⁵	0.327			-2.124⁵	0.495
slope ²	-0.043 ¹⁰	0.038			0.139⁵	0.066				
Mineral soil	-0.304	0.293								
Shallow peat cover					0.196	0.500	1.333	0.636		
Shallow peat cover ²							-0.114	0.125		
Deep peat cover			-1.263	0.826						
Deep peat cover ²			-0.215	0.178						
Burn cover					-1.080	1.427			-1.458	2.322
Burn cover ²					0.047	0.042	-0.246	0.092	0.091	0.039
No. burns			-0.810	0.773						
No. burns ²			0.046	0.091						
Game keeping ²					0.192	0.042				
Forest cover ²	0.021 ⁴	0.017								
Inbye cover					-2.636	0.717	-1.206	0.578	-0.349	0.832
Inbye cover ²	-0.057	0.038							-0.035	0.137
Crow groups			0.078	0.053			0.090	0.064	0.015	0.058
Crow groups ²			0.026	0.053			-0.097	0.062	-0.172	0.061
Survey date	-0.008 ¹	0.007	0.024 ¹	0.021			0.026³	0.013		
Survey date ²			-0.181 ¹	0.169						
Open structure cover							1.445^J	0.526		
Open structure cover ²	-0.103^A	0.049								
Density					0.556 ^J	0.285				
Short dwarf shrub cover							2.034^J	1.024	-5.127^A	1.551
Short dwarf shrub cover ²							-0.221^J	0.094	-0.857^A	0.264
Medium dwarf shrub cover			0.069 ^J	0.064						
Medium dwarf shrub cover ²			-1.440 ^J	1.133						
tall dwarf shrub cover					3.867^A	1.091				
tall dwarf shrub cover ²					-0.156^A	0.059				
Short grass cover							0.507 ^A	0.582		
Short grass cover ²									-0.436^J	0.083
short vegetation cover	-0.548^A	0.219								
Tall vegetation cover									1.323^J	0.471
Bare cover					0.155	0.021				
C. vulgaris cover ²	-0.075	0.049	-0.118	0.154	-0.256	0.092	-0.155	0.102		
D. flexuosa cover ²			0.107	0.086						
E. nigrum cover ²							-0.130	0.162		
E. angustifolium cover ²									-0.833	0.338
E. vaginatum cover							-0.042	0.015		
Fine leaved grass cover ²			0.051	0.090	-0.293	0.068			-0.194	0.063
J. effusus cover	0.043	0.037								
J. effusus cover ²	-0.054	0.029								
Moss spp. cover	0.020	0.015			-0.052	0.034				
Moss spp. cover ²					0.138	0.030				
P. aquilinum cover	0.023	0.017					0.043	0.026	0.422	0.063
P. aquilinum cover ²									-0.375	0.093
Spagnum spp. cover ²	0.015	0.013								
V. myrtillus cover			-0.035	0.030						
V. myrtillus cover ²			-0.050	0.104						
VDSC ²			0.133	0.116						

Figure 1 The effects of species prevalence (the proportion of plots in a region where that species was recorded) on the predictive accuracy of the models

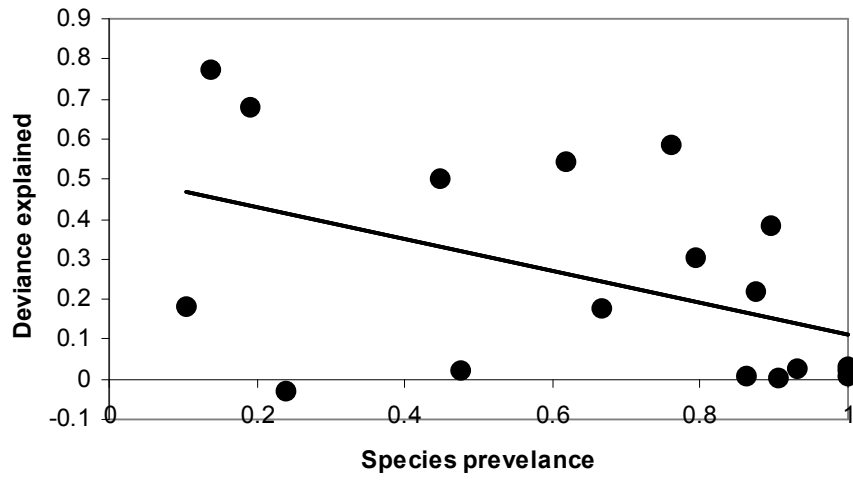
Predicted accuracy assessed using the proportion of deviance in observed abundance explained by predicted abundance, the slope of the relationship between observed and predicted abundance, and the ability of the model to rank sites into quartiles (concordance). The size of points in relation to slope is proportional to the weight in the analysis, based upon the reciprocal of the standard error of estimated slope. Fitted regression lines are as follows.

a) Deviance explained = $-0.3966 \cdot \text{prevalance} + 0.509$

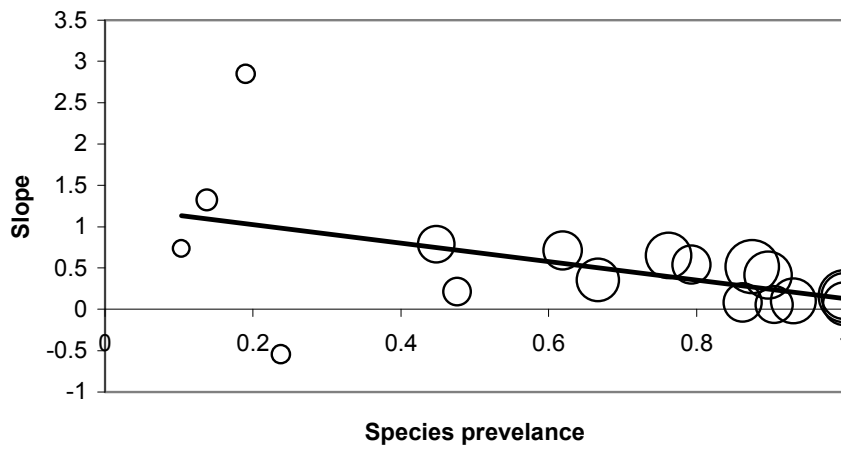
b) Slope = $-1.1226 \cdot \text{prevalance} + 1.2512$

c) Concordance = $-0.2675 \cdot \text{prevalance} + 0.3053$

a)



b)



c)

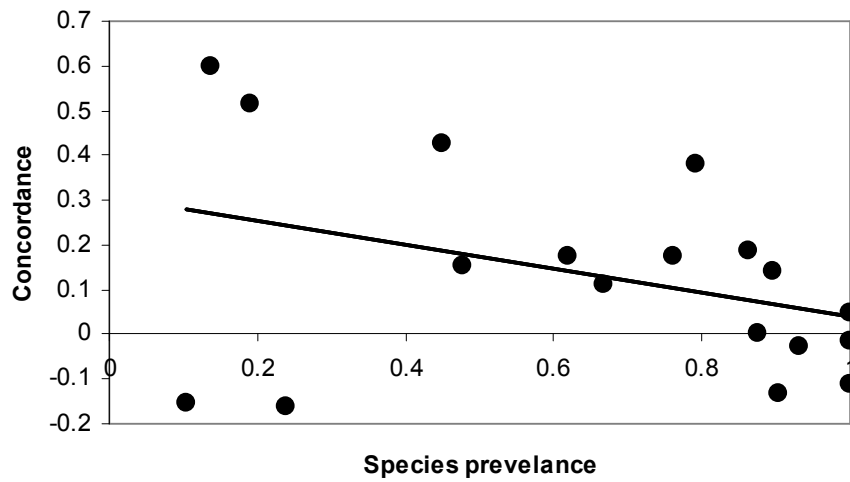


Table 5 A comparison of model performance for each species and region between model averaging and backwards deletion
Performance is measured by the proportion of deviance explained by the observed count (prop dev), the significance of which is indicated as follows (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$), by the slope of the relationship between observed and predicted count from the model (\pm standard error), and the concordance between observed and predicted ranks of four quartiles of abundance.

	Model averaging				Backwards deletion			
	N. Pennines	Wales	S. Pennines	S. Scotland	N. Pennines	Wales	S. Pennines	S. Scotland
Red grouse								
Prop dev	0.383****	0.545****	0.842****	0.652****	0.256***	0.481****	0.808****	0.724****
Slope	0.41 \pm 0.11	0.71 \pm 0.17	0.58 \pm 0.06	0.62 \pm 0.06	0.58 \pm 0.21	1.03 \pm 0.27	0.89 \pm 0.10	1.14 \pm 0.10
Concordance	0.139	0.175	0.748	0.407	0.139	0.492	0.676	0.537
Curlew								
Prop dev	0.028	0.678****	0.318****	0.643****	0.672	0.650	0.926***	0.820****
Slope	0.09 \pm 0.12	2.85 \pm 0.68	0.67 \pm 0.18	0.67 \pm 0.06	0.22 \pm 0.17	1.07 \pm 0.66	0.58 \pm 0.23	1.08 \pm 0.09
Concordance	-0.026	0.515	0.171	0.426	0.179	0.273	0.171	0.426
Golden plover								
Prop dev	0.305***	0.030	0.647****	0.571****	0.306***	0.374***	0.534****	0.490****
Slope	0.54 \pm 0.16	-0.55 \pm 0.70	0.54 \pm 0.08	0.69 \pm 0.08	1.05 \pm 0.34	-1.88 \pm 0.57	0.83 \pm 0.15	1.26 \pm 0.18
Concordance	0.378	-0.161	0.387	0.497	0.187	-0.419	0.351	0.429
Snipe								
Prop dev	0.009	0.024	0.224***	0.497****	0.000	0.000	0.153*	0.449****
Slope	0.08 \pm 0.16	0.21 \pm 0.31	0.74 \pm 0.24	0.66 \pm 0.08	-0.00 \pm 0.30	0.04 \pm 0.56	0.87 \pm 0.38	1.01 \pm 0.14
Concordance	0.187	0.154	0.136	0.278	0.044	0.154	0.091	0.222
Meadow pipit								
Prop dev	0.007	0.030	0.517****	0.190****	0.068	0.008	0.462****	0.255****
Slope	0.07 \pm 0.13	0.16 \pm 0.11	0.60 \pm 0.06	0.52 \pm 0.10	0.20 \pm 0.13	0.06 \pm 0.08	1.07 \pm 0.12	0.87 \pm 0.15
Concordance	-0.111	-0.016	0.171	0.167	0.111	0.048	0.099	0.104
Skylark								
Prop dev	0.217****	0.021	0.638****	0.229****	0.041***	0.025	0.715****	0.224****
Slope	0.51 \pm 0.09	0.16 \pm 0.09	0.65 \pm 0.05	0.52 \pm 0.07	0.31 \pm 0.12	0.16 \pm 0.09	1.19 \pm 0.10	0.77 \pm 0.10
Concordance	0	0.048	0.604	0.208	0	0.302	0.495	0.104
Stonechat								
Prop dev	0.773****	0.178***	0.688****	0.698****	0.313*	0.009	0.447***	0.650****
Slope	1.32 \pm 0.54	0.35 \pm 0.13	1.76 \pm 0.83	0.79 \pm 0.10	0.78 \pm 0.33	0.09 \pm 0.15	0.99 \pm 0.44	1.00 \pm 0.13
Concordance	0.600	0.111	0.349	0.632	0.283	-0.079	0.349	0.586
Wheatear								
Prop dev	0.501****	0.006	0.476****	0.399****	0.378****	0.005	0.524****	0.327****
Slope	0.79 \pm 0.18	0.06 \pm 0.17	0.76 \pm 0.17	0.70 \pm 0.11	1.04 \pm 0.31	0.07 \pm 0.22	1.28 \pm 0.22	0.87 \pm 0.17
Concordance	0.429	-0.132	0.385	0.241	0.302	-0.057	0.253	0.259
Whinchat								
Prop dev	0.180	0.586****	0.762****	0.736****	0.051	0.461****	0.933****	0.756****
Slope	0.74 \pm 0.83	0.65 \pm 0.12	0.84 \pm 0.19	0.83 \pm 0.11	0.16 \pm 0.29	0.33 \pm 0.07	1.18 \pm 0.37	0.97 \pm 0.13
Concordance	-0.153	0.175	0.349	0.442	-0.153	0.238	0.349	0.512