

The effect of management for red grouse shooting on the population density of breeding birds on heather-dominated moorland

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Summary

1. Breeding birds, vegetation and moorland management were surveyed in 320 1-km squares on 122 estates in upland areas of eastern Scotland and northern England where red grouse shooting is a widespread land use. We assessed whether population densities of eleven species of breeding birds differed between heather-dominated moorland managed for red grouse shooting and other moorland with similar vegetation.

2. We classified estates which had a full-time equivalent moorland gamekeeper as grouse moors. The mean density of red grouse shot per year was four times higher and the mean density of gamekeepers was three times higher on grouse moors than on other moors. Rotational burning of ground vegetation covered a 34% larger area on grouse moors than on other moors.

3. Selection of heather-dominated squares resulted in similar composition of vegetation on grouse moors and other moors (about 76% heath, 12% grass, 8% bog, 2% flush and <1% bracken on both types). However, grouse moors tended to have less tall vegetation than other moors and differed significantly in some other characteristics of the vegetation, topography and soil type.

4. Densities of breeding golden plover and lapwing were five times higher and those of red grouse and curlew were twice as high on grouse moors as on other moors, whilst meadow pipit, skylark, whinchat and carrion/hooded crow were 1.5, 2.3, 3.9 and 3.1 times less abundant, respectively, on grouse moors. The differences in density between moorland types remained significant ($P < 0.001$)

for golden plover and crow and approached significance ($P < 0.10$) for lapwing and meadow pipit after allowing for variation among regions.

5. We used Poisson regression models to relate bird density to vegetation cover, topography, climate and soil type. After adjusting for significant effects of these habitat variables, significant differences in bird density between the two moorland types remained for six species, though their magnitude was reduced.

6. Correlations of adjusted bird density with measures of different aspects of grouse moor management provided evidence of a possible positive influence of predator control (assessed using crow density) on red grouse, golden plover and lapwing. The control of crows by gamekeepers is the most likely cause of the low densities of crows on grouse moors. There was evidence of a positive effect of heather burning on the density of red grouse and golden plover and a negative effect on meadow pipit. Multiple Poisson regression indicated that predator control and heather burning had significant separate effects on red grouse density. Significant relationships between adjusted breeding bird densities and the abundance of raptors and ravens were few and predominantly positive.

7. The results provide correlative evidence that moorland management benefits some breeding bird species and disbenefits others in ways that cannot readily be explained away as effects of differences in vegetation type or topography. However, experimental manipulations of numbers of some predators and heather burning are required to test these findings.

Introduction

Heather-dominated moorland in the UK is of national and international importance for nature conservation. Six European heath and mire plant communities are virtually confined to Britain and Ireland and seven others are better developed there than elsewhere. Of 40 species of breeding birds associated with UK uplands, seven occur in internationally important numbers and eight are listed in Annex 1 of the EC Birds Directive 70/409/EEC (Thompson *et al.* 1995). Heather-dominated moorland is an important component of the habitat for all of them.

The sport shooting of red grouse *Lagopus lagopus scoticus* (Latham) has been practised in the UK for over 150 years, primarily on heather-dominated moors. Estimates of the area managed for this purpose vary between 0.5 million ha (Bunce & Barr 1988) and 3.8 million ha (Hudson 1995), depending upon definitions and the methods used. Brown & Bainbridge (1995) estimated that 5-15% of the uplands was managed for grouse shooting; equivalent to about 20 - 60% of the heather-dominated area (Ball, Radford & Williams 1983).

Grouse moors and their management might contribute to nature conservation in several ways. For example, grouse shooting may restrict other land uses with which it is seen to be incompatible, such as afforestation with exotic conifers and high sheep stocking rates. Heather moorland declined from 20% of the land area of Scotland in the 1940s to 15% in the 1980s, largely because of afforestation and grassland expansion (Mackey, Shewey & Tudor 1998). Heather loss was 41% on a sample of moors which had ceased to be used as grouse moors between the 1940s and 1980s, compared with a 24% loss on moors which had continued as grouse moors (Barton & Robertson 1997).

Gamekeepers burn patches of heather in rotation to provide a mixture of areas with young shoots suitable as food for red grouse and older heather that provides cover. Upland vegetation is also burned to improve sheep grazing, but this does not result in a mixture of small patches of different growth stages and may not promote the maintenance of heather cover. It may be that patch burning results in a vegetation mosaic that is favourable to other species than red grouse. Gamekeepers also kill predators of red grouse and their eggs, especially the red fox *Vulpes vulpes* (L.) and the carrion/hooded crow *Corvus corone* (L.) (hereafter called "crow"). In addition to control of these predators by legal methods, birds of prey are illegally, shot, trapped or poisoned on many grouse moors (Etheridge, Summers & Green 1997; Potts 1998; Green & Etheridge 1999). Some are also killed accidentally by the illegal use of poison baits intended for crows and foxes. Predator control might increase the survival and breeding success of other birds and mammals.

There is little quantitative evidence of the effects of grouse moor management on the density of species other than red grouse. Hudson (1992) found a correlation between golden plover *Pluvialis apricaria* (L.) abundance and both grouse bags and gamekeeper density. Haworth & Thompson (1990) found that golden plover, curlew *Numenius arquata* (L.) and redshank *Tringa*

totanus (L.) were more frequent in upland areas managed by gamekeepers. Thompson *et al.* (1997) compared the proportion of 2-km squares within 10-km National Grid squares occupied by various bird species between upland 10-km squares with different amounts of grouse moor. In the Scottish Highlands, more bird species were more widely distributed in squares with little or no grouse moor than in squares with much grouse moor, but in southern Scotland, England and Wales the converse was true. It is unclear from these studies whether or not correlations of bird distribution and abundance with grouse moor management resulted from differences in the characteristics of the moorland used for different purposes, such as geological or vegetation features, or were due directly to the effects of heather burning and predator control to benefit red grouse (Brown & Bainbridge 1995; Thompson *et al.* 1997). A well-replicated field experiment in which heather burning, predator control and a combination of these two treatments were applied to experimental plots would resolve this problem, but this would be difficult and expensive. Moreover, movements of birds and their predators across plot boundaries might obscure effects on population density or give rise to spurious effects. Hence, correlative studies are likely to remain a useful complement to field experiments on this topic for some time to come (Manel, Buckton & Ormerod 2000).

In this paper we use surveys in the heather-dominated uplands of northern England and Scotland in a correlative study that attempts to disentangle the effects on bird density of habitat differences and grouse moor management. Study plots were selected to have broadly similar vegetation in areas managed for grouse shooting and other moorland. Possible confounding effects of remaining habitat differences were allowed for by multiple regression.

Methods

STUDY AREAS AND SELECTION OF SURVEY PLOTS

The study was conducted in the central and eastern Highlands of Scotland in 1995 and in the North Pennines, Northumberland and North York Moors in England in 1996. The study areas were subdivided into six regions; (1) North Northumberland, north of Tynedale, (2) Northumberland south of Tynedale, Durham, east Cumbria and north-west Yorkshire, (3) North York Moors, (4) Tayside west from Glen Garry to Kinloch Rannoch, (5) Grampian and Tayside east from Glen Garry to the Angus glens, (6) Grampian north of the Dee watershed to Donside (see Fig. 1).

The study was restricted to moorland dominated by heather, because red grouse are usually too scarce for driven shooting where other types of vegetation predominate. Estates with this habitat were selected so that each region included some on which the moorland was managed for the shooting of driven red grouse and others on which grouse shooting was absent or occurred at low intensity, though we were unable to survey moors that were not managed for grouse shooting in regions 3 and 6. Estates were categorised as having grouse moors if there was at least one gamekeeper equivalent (see Methods: Grouse Moor Management) working full-time on moorland management. Parts (beats) of the grouse moor area on eight large estates were independently managed by separate gamekeepers. These were treated as 27 separate estates for our purposes. On each estate, between one and six 1-km National Grid squares were selected. The number surveyed depended upon the area of moorland within the estate. Squares were considered eligible if heather covered more than 75% of their area, according to a heather map of Scotland (Macaulay Land Use Institute 1988) or if a habitat category dominated by heather covered more than 75% of their area, according to English Nature Phase 1 habitat survey maps. Where more than one square was surveyed within an estate, the squares were chosen to be no more than 3 km apart so that the observer could travel easily between them. Squares were not selected at random, but prior information on their birds and habitats did not influence selection, except as regards eligibility. In Scotland we surveyed 99 one-kilometre squares on 37 grouse moor estates and 43 squares on 20

other estates. In England, 133 squares were surveyed on 45 grouse moor estates and 45 squares on 20 other estates.

BIRD SURVEYS

Observers mapped the distribution and activities of all birds present in each 1-km square by the method of Brown & Shepherd (1993) between 07.30 and 17.00 GMT on two dates separated by about one month (first visits - 14 April to 27 May; second visits - 27 May to 2 July). In the North York Moors only waders, skylarks *Alauda arvensis* L. and meadow pipits *Anthus pratensis* (L.) were recorded and at one square in Northumberland no data were collected on meadow pipits. Meadow pipits and skylarks were only recorded during the first visit to avoid the difficulty of distinguishing adults from juveniles during the second visit (Brown & Stillman 1993). Red grouse were counted on the first visit only. Counts with pointing dogs would have been more accurate for red and black grouse *Tetrao tetrix* L., but our surveys are considered to give an acceptable index of density. The number of individuals seen was used for analysis for red grouse, black grouse, meadow pipit, skylark and crow, whereas mapped data on birds with nests or young or which sang or engaged in agonistic, alarm or distraction displays were converted to estimates of the number of breeding pairs of other species after Brown & Stillman (1993). Ideally we would have used the second method for all species, but recording details of behaviour was prohibitively time consuming for meadow pipit and skylark, whilst crows show conspicuous agonistic, courtship and parental behaviour infrequently. For the species counted twice the higher of the two counts was taken to be the best estimate of numbers.

We analysed data for the eleven species recorded in more than 20 1-km squares (Table 1). Raptors and ravens *Corvus corax* L. were recorded, but excluded because they have large home ranges and a proportion of the population is sub-adult and/or non-breeding. The density of records was therefore not considered a reliable index of local breeding density. However, because they are predators of the eggs, young or adults of other birds, the mean numbers of individuals seen per visit of buzzard *Buteo buteo* (L.), hen harrier *Circus cyaneus* (L.), kestrel *Falco tinnunculus* L., merlin *Falco*

columbarius L., peregrine falcon *Falco peregrinus* Tunstall and raven were examined as potential correlates of the densities of breeding birds.

VEGETATION COMPOSITION AND STRUCTURE

Vegetation composition data were collected at two places in each quarter (quadrant) of the 1-km square on the second survey visit. Five and 20 minutes after beginning the survey in each quadrant, the surveyor recorded the habitat composition in a 5x5 m quadrat. Five summary habitat categories: heath, bog, flush, grass and bracken were defined, based on groups of indicator plant taxa used by Brown & Stillman (1993). In each quadrat the dominant (>50% cover) and sub-dominant vegetation types and the rank order of the cover of 22 indicator plant taxa were recorded (Brown & Stillman 1993). The two indicator taxa with the highest cover were each attributed to the appropriate summary habitat category (see above). For example, a quadrat with *Calluna* and *Vaccinium* as the two highest ranking indicator taxa would be classed as Heath/Heath. For each 1-km square, the proportion of quadrats (out of eight) falling into each of the 25 possible pairwise combinations of summary habitat categories was taken as a description of the vegetation. No cases were recorded of Bog/Bracken, Flush/Bracken, Bracken/Flush and Bracken/Bog, so this procedure yielded 21 variables which were proportions.

Five measurements of vegetation height in 5 cm categories were made with a measuring stick and a mean taken for each quadrat. The proportion of quadrats with short (mean height < 10 cm), medium (10-25 cm) and long (>25 cm) vegetation was calculated for each 1-km square. The quadrat mean heights were used to subdivide the heath, bog and grass-dominated vegetation categories (see above) into short, medium and long. There were insufficient cases to do this with flush and bracken.

The evenness of the distribution of vegetation heights was calculated from the distribution of the forty individual height measurements from a 1-km square, using a modification of the formula for equitability of numbers of individuals in each of the species within a community (Pielou 1977):

$$- \sum (p_i * \log_e (p_i)) / \log_e (T)$$

where p_i is the proportion of measurements in the i th occupied 5 cm height class and T is the tallest occupied height class (numbered as 0-5 cm = 1, 5-10 cm = 2, etc). High values of the index indicate a more complex structure such as tussock vegetation and low values indicate a more even stand.

TOPOGRAPHY, SOIL AND CLIMATE

Topography was described using 1:25 000 Ordnance Survey maps. For each 1-km square, the mean altitude was calculated from the altitudes (interpolated to the nearest 5 m) of 25 points on a regular 5x5 square grid with points 200 m apart and with the outermost points 100 m from the nearest edge. Using the same grid, the slopes over the 100 m to the north and east of each point was noted. The proportion of points in each of three ranges of slope (<5°, 5-10° and >10°) was calculated. Aspect was assessed in each of the quadrants of a 1-km square. The direction of the predominant slope within each quadrant was determined by eye and its angle from north was assigned to one of four categories; NE = 1° - 90°, SE = 91° - 180°, SW = 181° - 270° and NW = 271° - 360°. These data were converted to four variables; the proportion of quadrants in each of the four aspect categories.

The proportion within each 1-km square of each of seven soil association groups, defined according to their dominant broad soil types, was estimated by eye from 1:250 000 soil maps (Soil Survey of England and Wales 1983; Walker *et al.* 1982). A transparent overlay marked with 1-km squares was used to locate the focal square on the map. Soil associations dominated by seven broad soil types (peats, podzols, stagnopodzols, crypto-podzols, stagnohumic gleys, stagnogleys and brown earths) were present in the survey squares.

The average annual rainfall (mm) for each square was obtained from Ball, Radford & Williams (1983). The mean April-June temperature (1951-1970) was determined from the climatic model derived by White & Smith (1982). The presence or absence of pools was recorded in each of the quadrants of a 1-km square and the proportion of quadrants with pools was used in the analysis

GROUSE MOOR MANAGEMENT

We measured variables that reflect the intensity and effectiveness of grouse moor management. The extent of three classes of burned heather were estimated during the vegetation survey of each 1-km square: Burn 1 = burned within one year of the survey as judged from burnt soil/burnt stems present; Burn 2 = burned at least one year before the survey as judged from the lack of blackened soil and stems, but dead stems present and little or no regeneration of heather; Burn 3 = burned at least one year before the survey as judged from the dead stems present and with moderate to good regeneration of heather (heather cover >25%, but heather height <20 cm). The area with heather that had regrown to a greater extent than this was not estimated. The cover of each category in each quadrant of a 1-km square was scored by eye as; none = score 0, 1-10% cover = score 1, 11-25% = 2, 25-50% = 3, >50% = 4. The mean of the four scores was taken to represent the cover of that burning class for the 1-km square.

Other information on grouse moor management was obtained directly from the estates. This comprised the area managed as a grouse moor, the average red grouse bag for the five years before the survey (1990-1994 for Scotland; 1991 - 1995 for England) and the number of gamekeepers employed full-time and part-time on managing the grouse moor area within the estate. Data on grouse bags were available for 104 of the 122 estates and gamekeeper numbers were available for 101 estates. Bag data were incomplete for three estates in Scotland for which records for seven estate-years were missing. For these estates, the five-year mean was calculated after imputing missing values using a two-way (ESTATES X YEARS) ANOVA on the data for all estates. The mean bag was divided by the area of grouse moor within the estate to give the mean number shot km⁻² per year. Each full-time moorland gamekeeper was considered as 1 unit and a part-time gamekeeper as equivalent to 0.5 units. Gamekeeper units were converted to densities per km² by dividing by the area of grouse moor within the estate. Grouse bag density and gamekeeper density could only be obtained for whole estates and not for individual 1-km squares. We used the mean density of crows, averaged over all the surveyed squares within an estate, from the bird survey (see above) as an index of the level of predator control.

Statistical analysis

Our main objectives were to determine whether there were differences in bird density between grouse moors and other moors and to assess whether any differences found were likely to be due to differences between the two types of moors in vegetation, climate, soils or topography (henceforward called “habitat variables”) or to predator control and patch burning of heather (henceforward called “grouse moor management variables”) specifically carried out to enhance the productivity and survival of red grouse. The analysis had five stages:

1. Test for differences in the density of each bird species between grouse moors and other moors in the entire dataset and assess whether the within-region differences are consistent.
2. Test for differences in habitat variables between grouse moors and other moors in the entire dataset and assess whether the within-region differences are consistent.
3. Build parsimonious multiple regression models relating the numbers of each bird species to habitat variables (excluding grouse moor management). Variants of these models could either allow (RH) or exclude (H) region as a factor that could be incorporated into the final model.
4. Build parsimonious multiple regression models relating the numbers of each bird species to habitat variables and heather burning (excluding grouse moor management other than burning). Variants were produced that included (RHB) or excluded (HB) region as a candidate factor.
5. Model the observed number of each bird species on an estate relative to that expected under the H and RH models in relation to estate-specific mean values of grouse moor management variables. Similar analyses were carried out using expected numbers from the HB and RHB models. Because the latter models took the influence of heather burning into account in obtaining the expected numbers, only the densities of red grouse shot and of gamekeepers were used as independent variables. The mean density of crows and the mean number of raptors and ravens seen per visit during our surveys were also included as independent variables in Stage 5.

STAGES 1 AND 2: DIFFERENCES IN BIRD DENSITY AND HABITAT VARIABLES BETWEEN GROUSE MOORS AND OTHER MOORS

We used GLIM 4 to fit linear models with a log link function and Poisson error. The total count of a particular bird species in all the squares on an estate was treated as the dependent variable.

Differences in the number of squares surveyed per estate were allowed for by declaring the logarithm of the number of squares as an offset variable. The residual deviance was rescaled to equal the residual degrees of freedom. Two models were fitted for each species, (1) whether or not the estate was a grouse moor was included as a binary independent variable and (2) in addition to the effect of grouse moor, region was included as a factor. In both tests the increase in scaled deviance when the grouse moor effect was deleted from the model was treated as χ^2 with one degree of freedom (Crawley 1993). Similar analyses were carried out for raptors and ravens with the combined count for both survey visits as the dependent variable.

Differences among means of habitat variables between grouse moors and other moors were tested using Mann-Whitney U tests with estate-specific means treated as mutually independent data. For both bird densities and habitat variables, overall weighted means and standard errors were calculated from estate-specific means with the number of squares surveyed on each estate as weights.

STAGES 3 AND 4: MODELS OF BIRD DENSITY VERSUS HABITAT

The number of a bird species in a 1-km square was treated as the dependent variable and related to habitat variables by a linear model with log link function and Poisson error. The significance of a variable or factor was tested by fitting the model including the focal variable together with others. The residual deviance was rescaled as described above. The model was then refitted after deleting the focal variable and the scaled deviance was calculated using the same scaling factor. The difference between the two scaled residual deviances was treated as χ^2 with degrees of freedom equal to the number of extra parameters needed to include the variable or factor (Rushton, Hill & Carter 1994; Crawley 1993). The square of a candidate independent variable was included in the model along with the variable itself to allow for curvilinear quadratic relationships. The quadratic term was only included if the change in deviance associated with its deletion was significant at the α

= 0.05 level or if the effect of the variable and its square were only significant if they were included together. Interactions among variables were not examined.

We adopted simple codes to describe the nature of curvilinear relationships for those variables for which the quadratic term was included in the final model. We classified such relationships into six categories according to the shape of the fitted relationship within the range of the independent variable defined by the central 90% of values observed for our sample of squares. The classes were convex increasing, convex decreasing, concave increasing, concave decreasing, maximum within the 90% range and minimum within 90% range (see Appendix 1).

Model selection was by a step-up procedure. At each step the change in scaled deviance from including and then deleting each of the variables and factors not already included in the model was calculated and the most significant of these was selected, provided that its effect was significant at $P < 0.05$. After including a new variable, the effects of all the variables already in the model, including squares, was tested by removing and replacing each in turn. Any whose effect was no longer significant at $P < 0.05$ were deleted. Hence, deletion of any variable or factor from the final model resulted in a significant increase in the scaled deviance and none of the variables and factors excluded from the model had a significant effect when included.

The number of candidate habitat variables was large (60 including burning scores and excluding the factors region and observer), so we considered summarising them before analysis using Principal Components Analysis (PCA), so that a group of variables that were strongly intercorrelated could be represented by a single PCA score. However, only 1.5% of all possible correlation coefficients between pairs of habitat variables exceeded 0.5 and the first five axes of the PCA explained only 37% of the total variance. Hence, we considered that the degree to which the PCA summarised the habitat variables was insufficient to warrant using PCA axes in place of the habitat variables.

Surveys were carried out in two years and six regions by eight observers and we included these factors as candidate explanatory variables in the bird versus habitat models. However, it was impossible to separate the effects of year, region and observer because three regions were surveyed in one year and three in the next, with none being surveyed in both. Furthermore, one region was surveyed by two observers who did not work in any of the other regions. We represented the

combination of these effects in the models using the two factors region (6 states) and observer (8 states). However, the statistical significance attributed to these factors in the analyses should be regarded with caution and only taken together to represent the combined effects of the three factors, year, region and observer. Because these effects, like the those of the habitat variables discussed above, are not of primary interest and are treated as nuisance effects.

STAGE 5: RELATIONSHIP OF ADJUSTED BIRD ABUNDANCE TO GROUSE MOOR MANAGEMENT VARIABLES

The Stage 3 (H, RH) and Stage 4 (HB, RHB) analyses resulted in up to four final models relating bird density to habitat for each bird species. In practice not all species had four different models because the effects of the factor region and the heather burning variables were not always significant. The total number of pairs or individuals N_i observed and the numbers N_i' expected from a particular bird - habitat model were obtained for each estate and the following model was fitted to data for all estates:

$$\log_e (N_i / N_i') = b_0 + b_j * X_j$$

where b_0 and b_j are constants and X_j is a grouse moor management variable, crow density or a raptor or raven sighting rate. A test of the difference in bird density between grouse moors and other moors was conducted by fitting this model using a binary independent variable in which grouse moors were scored 1 and other moors zero. The model was fitted in GLIM 4 using N_i as the dependent variable and X_j as the independent variable, with a log link function, Poisson error and with $\log_e (N_i')$ as an offset variable. The residual deviance was rescaled to equal the residual degrees of freedom and the statistical significance of the effect of variable X_j was assessed by a likelihood-ratio test using the change in rescaled deviance obtained when the focal variable was omitted from the model.

We included the burning scores both as habitat variables in the Stage 4 bird-habitat models (HB, RHB) and also to use estate-specific mean burning scores as management variables in Stage 5

analyses. Stage 5 analyses with burning scores as management variables were only undertaken in conjunction with expected bird numbers from the Stage 3 (H, RH) models, to avoid burning score appearing twice in the same analysis; in the expected number of birds and as a management variable. Including burning scores in the Stage 4 models allowed within-estate variation in burning among the squares within an estate to contribute to the bird-habitat models. The Stage 5 analyses that used expected numbers of birds from these models allowed the effects of management other than burning to be evaluated after effects of burning had been allowed for.

We fitted multiple regression Stage 5 models in which expected numbers of pairs or individuals were taken from the Stage 3 models and gamekeeper density, heather burning scores and crow density were used as multiple independent variables. Grouse bag density was excluded because it indicates the combined effects of all the management variables and unmeasured influences, whereas the other variables represented components of management itself (predator control and burning) that could vary independently. These multiple regressions were only fitted to data from the 92 estates for which gamekeeper density, burning scores and crow density were all available.

To illustrate relationships between observed:expected bird numbers and grouse moor management variables, estates were first grouped into bins according to the value of each management variable. The combined total number of pairs or individuals was obtained for all the estates within each bin. Each Stage 3 and Stage 4 model was used to calculate expected combined totals of pairs or individuals from the habitat information for the estates in each of the same bins. Boundaries were chosen so that expected numbers of birds or pairs within a bin did not fall below ten. Ratios of observed to expected totals within the bins were calculated and plotted against the mean value of the management variable for the bin. These results were not used for testing statistical significance, but only for displaying the results in graphical form.

Results

STAGE 1: DIFFERENCES IN BREEDING BIRD DENSITY BETWEEN GROUSE MOORS AND OTHER MOORS

Red grouse, golden plover, curlew and lapwing *Vanellus vanellus* (L.) occurred at significantly higher density and meadow pipit, skylark, whinchat *Saxicola rubetra* (L.) and crow at significantly lower density on grouse moors than on other moors (Table 1). There was no significant difference in density for black grouse, common snipe *Gallinago gallinago* (L.) and wheatear *Oenanthe oenanthe* (L.). There might be differences in bird density among regions, unrelated to grouse moor management, that could obscure the true pattern, so a further analysis that including regional effects was carried out (see Statistical Analysis, Stage 1). When this was done, the difference in density between grouse moors and other moors remained significant for golden plover and crow ($P < 0.001$) and approached significance for lapwing and meadow pipit ($0.05 < P < 0.10$). For meadow pipit and crow the difference in mean density between grouse moors and other moors was consistent across all four regions in which moors of both types were surveyed (Table 1).

STAGE 2: DIFFERENCES IN HABITAT BETWEEN GROUSE MOORS AND OTHER MOORS

A comparison of the of the mean cover of the five main categories of vegetation shows that our selection procedure produced a good match in the vegetation in the two types of moors (Table 2). However, there were significant differences between grouse moors and other moors for seven of the detailed habitat variables and differences which approached significance ($0.05 < P < 0.10$) for six variables (Table 2). The differences between the two types of moors within regions was in the same direction in all four of the regions where both types could be compared for three of these thirteen variables. Even though a large number of habitat variables (56) was tested, the number of significant differences exceeded that expected by chance (7 observed *cf.* 2.8 expected for $P < 0.05$ and 13 *cf.* 5.6 for $P < 0.10$).

DIFFERENCES IN MANAGEMENT BETWEEN GROUSE MOORS AND OTHER MOORS

Because we used the presence of a full-time equivalent moorland gamekeeper to define grouse moors, it is not surprising that gamekeeper density was significantly higher on grouse moors than

on other moors (Table 3). Some red grouse were shot on moors without a full-time gamekeeper, but the grouse bag density on grouse moors was more than four times higher than on other moors. This ratio was greater than the two-fold difference in density of adult grouse (Table 1). The mean area of burned heather was higher on grouse moors than other moors for all burning classes, but the differences were small (34% more burning of all classes on grouse moors) and only significant for the Burn 3 class and the combined total of all burning classes.

DIFFERENCES IN THE ABUNDANCE OF RAPTORS AND RAVENS BETWEEN GROUSE MOORS AND OTHER MOORS

Significantly more buzzards and significantly fewer hen harriers were seen on grouse moors than on other moors (Table 4). These differences persisted when the effect of region was taken into account and it then also appeared that merlins were seen significantly less frequently on grouse moors.

STAGE 3: MODELS OF BIRD DENSITY VERSUS HABITAT

The analyses carried out in Stage 2 provided enough evidence of habitat differences between grouse moors and other moors to require that they should be allowed for in the analysis of differences in bird densities. Therefore we used Poisson regression models relating bird density to habitat variables as described in Statistical Analysis. Details of the final models are presented in Appendix 1 (models H and RH), but their details will not be examined in this paper because our principal objective is to assess the effects of grouse moor management. Pearson correlation coefficients between estate-specific means of observed and expected bird density were high (mean $r = 0.815$; range 0.618 to 0.953) for most models, indicating good performance. The factor Region occurred in the final model in nine of the eleven bird species examined when it was eligible for selection (RH models). When Region was not eligible for selection (H models), the factor Observer, which is confounded with Region, occurred in the final model for eight species.

STAGE 4: MODELS OF BIRD DENSITY VERSUS HABITAT AND HEATHER BURNING

When the cover of burned moorland was eligible for inclusion in the bird-habitat model (models HB and RHB), at least one burning variable occurred in the final model for nine of the eleven bird species when the factor Region was not eligible for inclusion (HB models) and for eight species when Region was eligible (RHB). There were significant positive effects of burning for red grouse, golden plover, curlew and whinchat, a positive effect or an optimum level for lapwing and a negative effect for meadow pipit, crow and wheatear (Appendix 1). Both positive and negative effects were found for black grouse depending upon the stage of regrowth after burning (Appendix 1). Pearson correlation coefficients between estate-specific means of observed and expected bird density were similar (mean $r = 0.815$; range 0.591 to 0.953) to those for the Stage 3 models. Region occurred in the final model when it was eligible for selection (RHB models) for seven species. When Region was not eligible for selection (HB), Observer occurred in the final model for six species.

STAGE 5: RELATIONSHIP OF ADJUSTED BIRD ABUNDANCE TO GROUSE MOOR MANAGEMENT

After adjustment for the habitat effects described by the Stage 3 and 4 models, golden plover occurred at significantly higher density on grouse moors than other moors regardless of which of the four habitat models was used to make the adjustment (Table 5). Adjustment reduced the difference in density between the two moor types, especially for the models that took region into account. The adjusted densities of curlew and lapwing were significantly higher on grouse moors than other moors with the H and HB models, but the difference was not significant when the adjustment took region into account. The adjusted density of red grouse was significantly higher on grouse moors than other moors with the H model, but the difference was not significant when the adjustment took region and burning into account. Crows occurred at significantly lower density on grouse moors than on other moors after adjustment for habitat effects, regardless of which habitat model was used. The adjusted density of meadow pipit was significantly lower on grouse moors than other moors with the H and HB models, but not when Region was taken into account. There

was no significant difference between grouse moors and other moors in the adjusted densities of skylark and whinchat.

Univariate regression analysis of bird density, adjusted for habitat effects, on moorland management variables and crow density identified significant relationships with at least one variable in conjunction with at least one of the four adjustment models for six of the eleven bird species (red grouse, black grouse, golden plover, curlew, lapwing and meadow pipit; Table 5).

Adjusted red grouse density was significantly negatively related to crow density in all four model variants (Table 5 ; Fig. 2(c)) and was also positively related to the area of heather burning in classes 2 and 3 and to the sum of all burn classes for both the H and RH adjustments (Table 5 , Fig. 2(a,b)). For both the H and RH adjustments, the effect of the area of Burn class 2 was non-significant when it was included together with Burn class 3 in a multiple regression model. The area of Burn class 3 and crow density both had significant effects when included together in a multiple regression model, as did the combined area of all burn classes and crow density. Multiple regression models were fitted using red grouse density adjusted with the Stage 3 models and all possible combinations of gamekeeper density, crow density and burning scores as independent variables. With both the H and RH adjustments, the effects of crow density (negative), The effects of Burn class 3 and Burn sum were significantly positive in all the models in which they were included, but none of the other variables had significant effects.

Adjusted black grouse density was significantly positively related to crow density for adjustments H, HB and RH. There were no significant effects of other management variables.

Adjusted golden plover density was significantly positively related to grouse bag density and negatively related to crow density in all four model variants (Table 5 ; Fig. 3(a, b)). In all four model variants, both of these variables had significant effects ($P < 0.05$) when they were included together in a multiple regression model. When golden plover density was adjusted using the model H variant there were significant positive effects of Burn 1, Burn 2 and Burn sum in univariate regressions (Table 5 ; Fig. 3(c)) , but these variables had no significant effect when the RH model was used. Multiple regression models were fitted using golden plover density adjusted with the Stage 3 models and all possible combinations of gamekeeper density, crow density and burning scores as independent variables. With the H adjustment, the effects of crow density (negative) and Burn sum

(positive) were significant in all the models in which they were included, but none of the other variables had significant effects. With the RH adjustment the negative effect of crow density was significant in all models in which it was included, but no other variables had a significant effect on the adjusted density of golden plovers.

Adjusted curlew density was significantly positively related to grouse bag density when the H and HB adjustments were used (Table 5 ; Fig. 4(a)), but the effect was not significant when the adjustment took regional effects into account (RH and RHB). Adjusted lapwing density was negatively related to crow density when the H adjustment variant was used (Table 5 ; Fig. 4(b)), but the effect was not significant for other variants. The other variables had no significant effect on adjusted curlew and lapwing densities either singly or in multiple regressions.

Adjusted meadow pipit density was significantly negatively related to grouse bag density and the Burn 2 score for the H adjustment variant (Table 5 ; Fig. 5(a, c)) and to gamekeeper density for the RH and RHB variants (Table 5 ; Fig. 5(b)). With the H adjustment, there was a significant positive effect of crow density in a multiple regression analysis of the reduced dataset for which all management variables were available. No other variables had a significant effect. With the RH adjustment, there was a significant negative effect of gamekeeper density in the multiple regression analysis and no other variables had a significant effect.

The relationships between breeding bird densities and the abundance of raptors and ravens are treated separately because the results are difficult to interpret. In the univariate Stage 5 analyses, tests were carried out for 37 species x adjustment model combinations for each of six species of predators (five raptors plus raven), giving 222 tests in all. A total of 14 tests (6.3%) were significant at the $P < 0.05$ level which is close to what would be expected by chance (Table 5). However, all but one of the significant relationships indicated a positive correlation between bird density and raptor or raven abundance. Only for skylark was there a significant negative correlation, which was with the abundance of hen harriers.

Discussion

DIFFERENCES IN BREEDING BIRD DENSITY BETWEEN GROUSE MOORS AND OTHER MOORS

Population densities of red grouse, golden plover, curlew and lapwing were significantly higher on grouse moors than on other moors whilst densities of meadow pipit, skylark, whinchat and crow were significantly lower. The results for meadow pipit and crow are probably the most reliable because differences were consistent across all four regions with both grouse moor and other moor plots present. For red grouse, golden plover, curlew and lapwing, density was not higher on grouse moors in one of the four regions, but the inconsistent region varied among species.

The differences in bird density are unlikely to have been the result of gross differences in habitat because survey plots of both types were selected to have the same broad vegetation type and the similarity of the mean cover of broad vegetation types on grouse moors and other moors showed that this selection was effective. Subtle differences in habitat between grouse moors and other moors were found, as were strong relationships between bird abundance and habitat. The possible contribution of differences in habitat to the differences in bird density between the two types of moorland was allowed for by adjusting bird density for the habitat effects as described by Poisson regression models. This adjustment reduced the magnitude of differences in bird density between grouse moors and other moors, but it only removed their statistical significance for skylark and whinchat. In two of the remaining six species (golden plover and crow) the differences in adjusted density were large and significant whether or not the adjustment accounted for regional effects. In the other four species the differences ceased to be significant when regional effects were allowed for.

Some of our findings resemble those of Thompson *et al.* (1997) who examined all of the species in our study. They found that red grouse and curlew were significantly more widely distributed in 10-km squares with grouse moors than in other upland squares in all regions and similar differences were found for lapwing in two regions. Wheatear, whinchat and crow were all significantly less widely distributed in grouse moor squares in two regions. The other species either showed no significant differences or differences in opposite directions in different regions. The positive association with grouse moors of red grouse, curlew and lapwing and the negative association for

crow concur with our analysis, though significant differences in our study for golden plover and meadow pipit did not emerge clearly from the analysis of Thompson *et al.* (1997). Some important differences between the two studies should be borne in mind. Our study compares bird densities between grouse moors and other heather-dominated moors with the two types being relatively close together within the eastern parts of three of the regions analysed by Thompson *et al.* (1997). They compared bird distributions between squares with and without grouse moors where the two types were usually widely separated and had different vegetation, climate and topography. Our approach has the advantage of being less likely to detect spurious differences in bird abundance apparently associated with grouse moors, but actually caused by differences in habitat or climate.

RELATIVE RISKS OF TYPE 1 AND TYPE 2 ERRORS

It can be argued that our test of differences in breeding bird density between grouse moors and other moors was too stringent because we first fitted models that describe relationships between bird density and variables other than those pertaining to grouse moor management and then compare densities adjusted for these effects. This risks Type 2 errors arising when a difference in bird density that is really caused by grouse moor management is erroneously cancelled out by spurious associations with habitat variables that differ between grouse moors and other moors or between regions with many or few grouse moors, but have no real effect on bird abundance. The risk was increased by the large number of habitat variables used and the unbalanced distribution among regions of grouse moors and other moors (Fig. 1). However, Type 1 errors might also occur if significant differences in bird density were still found after adjustment for effects of habitat and region, but these were spurious and really caused by some habitat variable that we did not measure or measured too crudely.

It is difficult to be sure where the balance between these risks lies in our study, but we think that we have made a greater effort to avoid Type 1 than Type 2 errors due to misidentification of causal factors. However, the higher risk of Type 2 errors from this source is counteracted to some degree by the wide distribution of study areas and the large number of estates and survey squares which were intended to reduce the risk of Type 2 errors due to small sample size, at least for the

more abundant species. It is striking that, in spite of our inclusion of a large number of potential explanatory variables in Stages 3 and 4 of the analysis, adjustment for these effects in Stage 5 removed the statistical significance of the observed differences in bird density between grouse moors and other moors for just two of the eight species for which they were apparent from unadjusted data. Whilst this finding neither proves that grouse moor management influences the density of some breeding birds nor excludes the possibility that the differences in density are caused entirely or partially by habitat differences, it reduces considerably the plausibility of the latter hypothesis.

ASPECTS OF GROUSE MOOR MANAGEMENT AS POSSIBLE CAUSES OF DIFFERENCES IN BIRD DENSITY

The management of heather-dominated moorland for red grouse shooting has two components that might affect demographic rates of breeding birds: predator control and the rotational burning of vegetation.

It is likely that the much lower density of crows on grouse moors than on other moors was caused by the direct effects of predator control. Egg predation by this species is considered to have a large impact on red grouse and effective control of crow numbers is a high priority for moorland gamekeepers. Large numbers are shot and trapped each year on gamebird shooting estates (Tapper 1992). If this was the cause of the difference in crow density, then crow density should be negatively correlated with gamekeeper density. This correlation was not significant, but that might be because of variation among estates in the effectiveness of predator control and the proximity of grouse moors to areas which act as refuges for crows.

The effects of predator control on the breeding success and survival of non-target bird species might result in higher local densities on grouse moors. The significant negative correlations between adjusted densities of red grouse, golden plover and lapwing on the one hand and the estate-specific mean density of crows on the other may indicate that predator control has a beneficial effect on these wader species. This result does not establish that crow predation itself has an important impact on these species, because crow density may merely be acting as an index of the

level of control of other predators, such as foxes, or of some completely different aspect of management. Parr (1992) found evidence of a negative effect of crows and foxes on golden plover and Baines (1990) found that predation can have significant effects on lapwing productivity. There were no significant positive correlations between adjusted densities of waders and gamekeeper density, but this may be because gamekeeper density is an inadequate predictor of the effectiveness of predator control.

The predominance of positive relationships between adjusted breeding bird abundance and the numbers of raptors and ravens per survey visit is difficult to interpret. It might arise because raptors bred at higher density or foraged selectively in areas with high densities of bird prey. Redpath & Thirgood (1999) found that breeding hen harriers and peregrine falcons on grouse moors showed numerical responses to prey abundance. However, the prey species involved were not those for which we found positive relationships. There was just one significant negative relationship; that between adjusted skylark density and hen harrier abundance. However, skylarks and hen harriers were both significantly less abundant on grouse moors than other moors, so this finding does not indicate a benefit for skylarks of the lower numbers of hen harriers recorded on grouse moors.

The Stage 5 analyses showed that there was a significant positive effect of heather burning on the adjusted density of red grouse which was additional to the effect of crow density for both adjustment models. Clear positive effects of patch and strip burning on numbers of red grouse shot per km² have been demonstrated previously (Picozzi 1968). A multiple regression analysis by Hudson (1992) showed that grouse bag density was positively related both to an index of the mosaic structure of heather growth stages, which is increased by burning, and to the density of gamekeepers, which may indicate the level of predator control.

The Stage 5 analyses provided evidence for a significant positive effect of burning on adjusted golden plover density, although whether this was additional to the effect of crow density varied according to the adjustment model used. The Stage 4 analyses also indicated positive effects of burning on densities of black grouse, curlew, lapwing and whinchat. Positive effects of burning for these species were not confirmed by the Stage 5 analysis, which may be because the effects were mainly due to variation among squares within estates and were difficult to detect when estate-

specific mean burning scores were used in Stage 5. The analyses may also have failed to detect effects of burning because the measures used did not take the size and arrangement of burned patches into account. Patterns of burning vary among estates and depend in part upon whether the objective is to improve the habitat for red grouse by creating a mosaic of small patches of different aged heather or to improve the grazing for sheep, which is often done by burning larger patches. We did not have adequate measurements of this variation.

The adjusted density of meadow pipits was negatively correlated with grouse bag density, gamekeeper density and burning. This contrasts with the finding by Hudson (1992) that an index of meadow pipit abundance increased with grouse bag density. It might be that the alteration of vegetation structure by burning reduces its suitability for meadow pipits. It is also conceivable that the control of foxes may lead to an increase in other predators such as stoat *Mustela erminea* L. if foxes affect stoat populations by predation or competition. Stoats are probably more difficult for gamekeepers to control than foxes. If stoats prey on meadow pipits to a greater extent than do foxes this might lead to a decrease in pipits in areas where foxes are more intensively controlled. In the USA, the coyote *Canis latrans* has been shown to suppress smaller predators and this appears to benefit birds (Crooks & Soulé 1999).

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

The higher densities of red grouse, golden plover, curlew and lapwing on grouse moors than on other moorland suggest that grouse moor management may help to maintain populations of these species, all of which have recently declined in geographic range in Britain (Gibbons, Reid & Chapman 1993). If the association is causal and due mainly to predator control, then it is likely that experimental manipulation of predator numbers on large study areas would increase populations relative to those on matched, unmanaged untreated areas. An experiment currently being conducted in northern England by the Game Conservancy Trust will test this conjecture within a few years. If all or part of the effect is due mainly to heather burning, it would be expected that experimental verification would take much longer because of the long time required to complete a cycle of rotational burning.

If moorland management for grouse shooting helps to maintain the numbers and range of some upland breeding birds, then the continuation of this land use might be valuable for biodiversity conservation in the uplands of Britain in ways that could not be substituted for by preventing damaging effects on vegetation and habitats caused by alternative land uses. However, the population size and distribution of several species of birds of prey are probably limited by illegal killing by moorland gamekeepers (Watson, Payne & Rae 1989; Gibbons *et al.* 1995; Scottish Raptor Study Groups 1997; Etheridge, Summers & Green 1997; Potts 1998) and our analysis indicates possible negative effects on other species, though those affected tend to be relatively common and widespread. Hence, moorland management for grouse shooting has conflicting effects on upland breeding birds of which the most important negative effect is the persecution of birds of prey. There is evidence from one grouse moor that high densities of some birds of prey have been incompatible with the continuation of driven shooting of red grouse (Redpath & Thirgood 1997). Moorland gamekeepers appear to believe that this is generally true, so illegal killing of birds of prey seems unlikely to diminish. Practical methods for resolving this conflict are urgently needed.

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References

- Ball, D.F., Radford, G.L. & Williams, W.M. (1983) *A Land Characteristic Databank for Great Britain*.
I.T.E. Occasional Paper no. 13. I.T.E., Bangor
- Baines, D. (1990) The roles of predation, food and agricultural practice in determining the breeding success of the lapwing *Vanellus vanellus* on upland grasslands. *Journal of Animal Ecology*, **59**, 915-929.
- Barton, A.F. & Robertson, P.A. (1997) *Land cover changes in the Scottish uplands, 1945-1990, in relation to grouse shooting interests*. Game Conservancy Trust, Fordingbridge.
- Brown, A.F. & Bainbridge, I.P. (1995) Grouse moors and upland breeding birds. *Heaths and Moorlands: Cultural Landscapes* (eds D.B.A. Thompson, A.J. Hester & M.B. Usher). pp 51-66. Stationery Office, Edinburgh.
- Brown, A.F. & Shepherd, K.B. (1993) A method for censusing upland breeding waders. *Bird Study*, **40**, 189-95
- Brown, A.F. & Stillman, R.A. (1993) Bird-habitat associations in the eastern Highlands of Scotland. *Journal of Applied Ecology*, **30**, 31-42
- Bunce, R.G.H. & Barr, C.J. (1988) The extent of land under different management regimes in the uplands and potential for change. *Ecological change in the uplands* (eds M.B Usher & D.B.A. Thompson). pp 415-426. Blackwell Scientific Publications, Oxford.
- Crawley, M.J. (1993) *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- Crooks, K. & Soulé, M. (1999) Coyotes suppressing smaller predators benefits birds. *Nature*, **400**, 563.
- Etheridge, B., Summers, R.W. & Green, R.E. (1997) The effects of illegal killing and destruction of nests by humans on the population dynamics of the hen harrier *Circus cyaneus* in Scotland. *Journal of Applied Ecology*, **34**, 1081-1105.
- Gibbons, D.W., Reid, J.B. & Chapman, R.A. (1993) *The New Atlas of Breeding Birds in Britain and Ireland: 1988 - 1991*. Poyser, London.

- Gibbons, D.W., Gates, S., Green, R.E., Fuller, R.J. & Fuller, R.M. (1995) Buzzards *Buteo buteo* and ravens *Corvus corax* in the uplands of Britain: limits to distribution and abundance. *Ibis*, **137** (Suppl.), S75-S84.
- Green, R.E. & Etheridge, B. (1999) Breeding success of the hen harrier *Circus cyaneus* in relation to the distribution of grouse moors and the red fox *Vulpes vulpes*. *Journal of Applied Ecology*, **36**, 472-483.
- Haworth, P.F. & Thompson, D.B.A (1990) Factors associated with the breeding distribution of upland birds in the south Pennines, England. *Journal of Applied Ecology*, **27**, 562-77
- Hudson, P.J. (1992) *Grouse in Space and Time*. Game Conservancy Trust, Fordingbridge.
- Hudson, P.J. (1995) Ecological trends and grouse management in upland Britain. *Heaths and Moorlands: Cultural Landscapes* (eds D.B.A. Thompson, A.J. Hester & M.B. Usher), pp. 282-293. Stationery Office, Edinburgh.
- Macaulay Land Use Institute (1988) *The Land Cover of Scotland*. Macaulay Land Use Institute, Aberdeen.
- Mackey, E.C. Shewy, M.C. & Tudor, G.J. (1998) *Landcover change: Scotland from the 1940s to the 1980s*. SNH. Stationery Office, Edinburgh.
- Manel, S., Buckton, S.T. & Ormerod, S.J. (2000) Testing large-scale hypotheses using surveys: the effects of land use on the habitats, invertebrates and birds of Himalayan rivers. *Journal of Applied Ecology*, **37**, 756-770.
- Parr, R. (1992) The decline to extinction of a population of Golden Plover in north east Scotland. *Ornis Scandinavica*, **23**, 152-158.
- Picozzi, N. (1968) Grouse bags in relation to the management and geology of heather moors. *Journal of Applied Ecology*, **5**, 483-488.
- Pielou, E.C. (1977) *Mathematical ecology*. Wiley, New York.
- Potts, G.R. (1998) Global dispersion of nesting hen harriers *Circus cyaneus*: implications for grouse moors in the U.K. *Ibis*, **140**, 76-88.
- Redpath, S.M. & Thirgood, S.J. (1997) *Birds of Prey and Red Grouse*. Stationery Office, London.
- Redpath, S.M. & Thirgood, S.J. (1999) Numerical and functional responses in generalist predators: hen harriers and peregrines on Scottish grouse moors. *Journal of Animal Ecology*, **68**, 879-892.

- Rushton, S.P., Hill, D. & Carter, S.P. (1994) The abundance of river corridor birds in relation to their habitats: a modelling approach. *Journal of Applied Ecology*, **31**, 313-328
- Scottish Raptor Study Groups (1997) The illegal persecution of raptors in Scotland. *Scottish Birds* **19**, 65-85.
- Tapper, S. (1992) *Game Heritage. An Ecological review from shooting and gamekeeping records*. Game Conservancy Trust, Fordingbridge.
- Thompson, D.B.A., MacDonald, A.J., Marsden, J.H. & Galbraith, C.A. (1995) Upland heather moorland in great Britain: a review of international importance, vegetation change, and some objectives for nature conservation. *Biological Conservation*, **71**, 163-178.
- Thompson, D.B.A., Gillings, S.D., Galbraith, C.A., Redpath, S.M. & Drewitt, J. (1997) The contribution of Game Management to Biodiversity: A Review of the Importance of Grouse Moors for Upland Birds. *Biodiversity in Scotland: Status, Trends and Initiatives* (eds V. Fleming, A.C. Newton, J.A. Vickery & M.B. Usher), pp. 198-212. SNH, Stationery Office, Edinburgh.
- Walker, A.D., Campbell, C.G.B., Heslop, R.E.F., Gauld, J.H., Laing, D., Shipley, B.M. & Wright, G.G. (1982) *Soil survey of Scotland*. The Macaulay Institute for Soil Research, Aberdeen.
- Watson, A., Payne, S. & Rae, R. (1989) Golden eagles *Aquila chrysaetos*: land use and food in northeast Scotland. *Ibis*, **131**, 336 - 348.
- White, E. & Smith, R.I. (1982) *Climatological maps of Great Britain*. I.T.E. , London.

LEGENDS TO FIGURES

Figure 1. Map of north-eastern Britain showing the boundaries and numbering of the study regions. The pie diagrams show grouse moor estates (in black) as a proportion of all estates surveyed in each region. The numbers of estates surveyed in regions 1 - 6 were 20, 35, 10, 12, 35 and 10 respectively.

Figure 2. Relationships between the ratio of the observed number of red grouse to the number expected from models that relate red grouse density to habitat and (a) scores representing the extent of heather burning in Burn class 2 (open symbols) and Burn class 3 (filled symbols), and (b) a score representing the extent of heather burning in all burn classes. In (a) and (b) the symbols denote the bird vs. habitat model used to calculate expected values; circle = model H, square = RH. In (c) observed:expected red grouse density is shown in relation to the number of crows km^{-2} . Bird vs. habitat models used to calculate expected density are denoted by open circle = H, filled circle = HB, open square = RH, filled square = RHB. See Statistical Analysis for the method used to calculate the plotted values.

Figure 3. Relationships between the ratio of the observed number of pairs of golden plovers to the number expected from models that relate golden plover density to habitat and (a) the number of red grouse shot km^{-2} , (b) the number of crows km^{-2} and (c) scores representing the extent of heather burning. In (a) and (b) the symbols denote the bird vs. habitat model used to calculate expected values; open circle = H, filled circle = HB, open square = RH, filled square = RHB. In (c) the symbols represent: open circle = Burn class 1, filled circle = Burn class 2, open square = all Burn types. All symbols in (c) are based upon model H.

Figure 4. Relationship between (a) the ratio of the observed number of pairs of curlews to the number expected from models that relate their density to habitat and the number of red grouse shot km^{-2} ; (b) the ratio of the observed number of pairs of lapwings to the number expected from models that relate their density to habitat and the number of crows km^{-2} . See Statistical Analysis for the method used to calculate the plotted values. The symbols denote the bird vs. habitat model used to calculate expected values; open circle = H, filled circle = HB.

Figure 5. Relationship between the ratio of the observed number of meadow pipits to the number expected from models that relate their density to habitat and (a) the number of red grouse shot km^{-2} , (b) the number of gamekeepers km^{-2} and (c) a score representing the extent of Type 2 heather

burning (see Methods). See Statistical Analysis for the method used to calculate the plotted values.

The symbols denote the bird vs. habitat model used to calculate expected values; open circle = H,

filled circle = HB, open square = RH, filled square = RHB.

Table 1. Mean population densities of breeding birds on grouse moors and other moors (see Methods for definitions). Significance levels of differences in mean density between the two types of moor from a linear model are shown as: x - $P < 0.10$, * - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$. Also shown is the number of regions (out of four) in which the difference between means for the two moor types was in the the same direction as the difference in the overall means. For red grouse, black grouse, meadow pipit, skylark and crow the number of individuals seen is used, rather than the number of pairs.

Species	Population density (km ⁻²) ± 1 SE		Significance of GM <i>vs.</i> OM difference		Regions with consistent difference	Birds or pairs counted
	Grouse moor	Other moor	Overall	Within region		
Red grouse	8.96 ± 0.90	4.56 ± 0.92	**		3	2219
Black grouse	0.23 ± 0.10	0.25 ± 0.09			3	70
Golden plover	1.47 ± 0.16	0.27 ± 0.07	***	***	3	364
Curlew	3.04 ± 0.25	1.50 ± 0.27	**		3	838
Lapwing	0.94 ± 0.16	0.17 ± 0.07	**	x	3	232
Snipe	0.55 ± 0.08	0.50 ± 0.11			2	171
Meadow pipit	30.64 ± 1.55	46.40 ± 2.90	***	x	4	11099
Skylark	3.58 ± 0.43	8.36 ± 2.15	***		1	1567
Wheatear	0.72 ± 0.11	0.76 ± 0.14			2	216
Whinchat	0.07 ± 0.02	0.27 ± 0.10	***		2	38
Crow	0.73 ± 0.13	2.24 ± 0.32	***	***	4	347

Table 2. Means of selected habitat variables on grouse moors and other moors (see Methods for definitions and units). Significance levels of differences between medians for the two types of moor from Mann-Whitney U tests are shown as: x - $P < 0.10$, * - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$. Also shown is the number of regions (out of four) in which the difference between means for the two moor types was in the the same direction as the difference in the overall means.

Variables	Mean \pm 1 SE			Number of regions with consistent difference
	Grouse moor	Other moor		
<i>Main vegetation categories</i>				
Heath	0.764 \pm 0.024	0.766 \pm 0.030		3
Bog	0.077 \pm 0.013	0.092 \pm 0.016		1
Grass	0.128 \pm 0.017	0.118 \pm 0.027		3
Flush	0.027 \pm 0.006	0.018 \pm 0.006		3
Bracken	0.004 \pm 0.002	0.006 \pm 0.003		2
<i>Significant and near-significant variables</i>				
Grass/Grass	0.064 \pm 0.014	0.041 \pm 0.014	x	4
Grass/Bracken	0.000	0.006 \pm 0.003	*	4
Flush/Grass	0.009 \pm 0.003	0.001 \pm 0.001	*	2
Heath medium	0.377 \pm 0.016	0.304 \pm 0.025	**	3
Heath long	0.240 \pm 0.018	0.325 \pm 0.033	**	3
Bog short	0.020 \pm 0.005	0.011 \pm 0.005	x	3
Long vegetation	0.259 \pm 0.018	0.337 \pm 0.032	**	3
Equitability	0.477 \pm 0.007	0.500 \pm 0.009	*	3
Altitude	430.6 \pm 10.6	399.5 \pm 17.0	x	2
Peat	32.03 \pm 4.11	21.88 \pm 5.01	x	3
Cryptopodzol	0.78 \pm 0.39	4.03 \pm 1.24	***	4
Rainfall	1178 \pm 26	1116 \pm 42	x	3
Pools	0.55 \pm 0.06	0.48 \pm 0.10	x	2

Table 3. Means of management variables on grouse moors and other moors (see Methods for definitions and units). Significance levels of differences between medians for the two types of moor from Mann-Whitney U tests are shown as: $x - P < 0.10$, * - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$. Also shown is the number of regions (out of four) in which the difference between means for the two moor types was in the the same direction as the difference in the overall means.

Variable	Mean \pm 1 SE			Number of regions with consistent difference
	Grouse moor	Other moor		
Grouse shot km ⁻²	24.27 \pm 3.29	5.66 \pm 1.73	***	4
Gamekeepers km ⁻²	0.062 \pm 0.004	0.018 \pm 0.006	***	4
Burn 1	2.65 \pm 0.25	1.94 \pm 0.35		3
Burn 2	4.69 \pm 0.32	4.13 \pm 0.54		2
Burn 3	4.64 \pm 0.36	2.88 \pm 0.47	**	3
Burn (classes combined)	11.97 \pm 0.76	8.94 \pm 1.04	*	3

Table 4. Mean number of individual raptors and ravens seen per visit to one kilometre squares on grouse moors and other moors. Significance levels of differences in mean density between the two types of moor from a linear model are shown as: χ - $P < 0.10$, * - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$. Also shown is the number of regions in which the difference between means for the two moor types was in the the same direction as the difference in the overall means. This is from a total of four regions, except for hen harrier and peregrine falcon which were not seen on either type of moor in region 1. The number counted is for both visits combined.

Species	Records visit ⁻¹ km ⁻² ± 1 SE		Significance of GM <i>vs.</i> OM difference		Regions with consistent difference	Birds counted
	Grouse moor	Other moor	Overall	Within region		
Buzzard	0.23 ± 0.05	0.09 ± 0.03	*	*	2	112
Hen harrier	0.06 ± 0.01	0.19 ± 0.05	***	**	3	57
Kestrel	0.16 ± 0.03	0.16 ± 0.04			1	92
Merlin	0.12 ± 0.02	0.17 ± 0.04		*	3	79
Peregrine falcon	0.06 ± 0.02	0.05 ± 0.02			1	34
Raven	0.23 ± 0.06	0.18 ± 0.07			1	124

Table 5 . Ratio of the population density of breeding birds on grouse moors to that on other moors before (raw) and after (adj.) adjustment for the effects of the habitat variables included in Stage 3 (H, RH) and Stage 4 (HB, RHB) models. The second column indicates which habitat model was used for the adjustment (see text and Appendix 1). See Table 1 for key to significance levels. The right hand group of columns shows the sign and significance of the effects on bird density of grouse moor management variables, the density of crows and the mean number of individuals seen per visit of raptors and ravens from univariate models after adjustment for the Stage 3 and 4 habitat models. The species of raptor/raven involved is identified as follows; B = buzzard, H = hen harrier, M = merlin, P = peregrine falcon, R = raven. Numbers of symbols denote significance as in Table 1, except that bracketted symbols denote $0.05 < P < 0.10$. Some tests (marked na) were not carried out for reasons given in the text.

Species	Habitat model	Ratio of density on grouse moors to that on other moors		Sign and significance of effects of variables on adjusted density							
		Raw	Adj.	Grouse bag	Game-keeper density	Burn 1	Burn 2	Burn 3	Burn all	Crow	Raptors & raven
Red grouse	H	1.97**	1.49**	+			+	+++	++	--	M(+) P+
	HB		1.21			na	na	na	na	--	M+ P(+)
	RH		1.24				+	++	+	-	P+
	RHB		1.13			na	na	na	na	-	M+ P+
Black grouse	H, RH	0.93	0.65							+	H(+)
	HB		0.62 ^x			na	na	na	na	+	H+
	RHB		0.72			na	na	na	na		
Golden plover	H	5.38***	2.91***	+++		+	+	(+)	+	---	
	HB		2.54***	+++		na	na	na	na	---	
	RH		1.74*	+						---	
	RHB		1.85*	++		na	na	na	na	--	
Curlew	H	2.03**	1.54**	+++							R+
	HB		1.67***	+++		na	na	na	na		R+
	RH		1.15								
	RHB		1.11			na	na	na	na		
Lapwing	H	5.53**	1.96*		(+)					-	
	HB		2.48**		(+)	na	na	na	na	(-)	
	RH		1.24								
	RHB		1.34			na	na	na	na		
Snipe	All	1.10	0.98								
Meadow pipit	H	0.66***	0.86*	-	(-)		-			(+)	
	HB		0.85*			na	na	na	na	(+)	
	RH		0.94				-				
	RHB		0.94			na	na	na	na		
Skylark	H, HB	0.43***	0.90								B+ H(-) P++ R+
	RH, RHB		1.04								B+ H- P+ R(+)
Wheatear	H	0.95	1.10	(-)							
	HB		1.14			na	na	na	na		
	RH, RHB		1.06								
Whinchat	H	0.25***	0.84								
	HB		0.76			na	na	na	na		
	RH		0.85								
	RHB		0.93			na	na	na	na		
Crow	H	0.33***	0.60**							na	H+
	HB		0.63**			na	na	na	na	na	H(+)
	RH		0.68*							na	
	RHB		0.70*			na	na	na	na	na	