

# Correlates of the change in Ring Ouzel *Turdus torquatus* abundance in Scotland from 1988–91 to 1999

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**Capsule** The change was correlated with environmental, habitat and management variables.

**Aims** To identify factors correlated with a population decline and range contraction between 1988–91 and 1999.

**Methods** Regression models are used to describe the variation in Ring Ouzel abundance in 1988–91, and the change in Ring Ouzel abundance between 1988–91 and 1999.

**Results** The abundance of Ring Ouzels in 1988–91 was negatively correlated with improved pasture, but positively with heather/smooth grass mosaic and *Nardus/Molinia* grassland. There was also a positive quadratic correlation with rock cover. A decline in Ring Ouzels between 1988–91 and 1999 was most likely on tetrads with shallow gradients, and outside of a 350–750 m altitudinal range. The change in ouzel numbers was also negatively correlated with both the initial area of conifer forest and heather/smooth grass mosaic. The rate of loss was greatest in those areas with a low Ring Ouzel abundance in 1988–91, although this effect was non-significant once habitat was accounted for.

**Conclusions** The abundance of Ring Ouzels was linked to heather–grass mosaics, while declines were greater in tetrads lacking topographical features known to be selected by nesting ouzels. The negative relationship between forestry and population change suggests that large-scale afforestation of the uplands is a cause of concern.

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The Ring Ouzel *Turdus torquatus* is a migrant breeding in the uplands of Britain, with the highest densities in the Pennines, Lake District, Southern Uplands, Grampians and western Highlands (Gibbons *et al.* 1993). Breeding densities correlate positively with the area of heather moorland (Haworth & Thompson 1990, Stillman & Brown 1994), dry rough grassland (Buckland *et al.* 1990) and improved pasture and bracken (Haworth & Thompson 1990). Steep slopes are favoured (Stillman & Brown 1994) and it is here that nests tend to be located, particularly in heather (Poxton 1986, Arthur & White 2001, Burfield 2002). In uplands, short, rough grassland or enclosed pastures are the favoured foraging habitats (Cramp 1988, Burfield 2002).

Numbers of Ring Ouzels have apparently been declining in Britain since the beginning of the last

century (Gibbons *et al.* 1996, Holloway 1996). In 1999, a national survey of a sample of tetrads within the known Ring Ouzel range found no breeding birds recorded in 39–43% of the tetrads previously occupied in 1988–91 (Wotton *et al.* 2002). That survey estimated the UK population to be 6157–7549 pairs, of which 73% were in Scotland. Differences in survey techniques prevent direct comparisons between population estimates from the 1988–91 atlas and the 1999 national survey (Wotton *et al.* 2002). However, re-analysis of the data suggested a population decline of 58% between 1988–91 and 1999, resulting in Ring Ouzels being listed as 'red' in the UK's population status of birds (Gregory *et al.* 2002). Evidence of declines have also been reported from local studies in Wales (Hurford 1996, Rebecca 2001), northern England (Rebecca 2001) and southern Scotland (Smith & Green 2000), although numbers appear stable in parts of the Scottish Highlands (Arthur & White 2001, Rebecca 2001).

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Numerous hypotheses have been proposed to explain Ring Ouzel declines, including afforestation (Tyler & Green 1989, Avery & Leslie 1990), changes in agriculture (Cadbury 1993), climate change (Williamson 1975), acid deposition (Tyler & Green 1994, Chamberlain *et al.* 2000) and an increase in predators (Thompson *et al.* 1997, Appleyard 1994), particularly raptors (Hurford 1996). While a number of recent studies have provided valuable information on the ecology and detailed habitat requirements of breeding Ring Ouzels in Britain (Tyler & Green 1994, Arthur & White 2001, Rebecca 2001, Burfield 2002), the relative importance of the different potential causes of decline remain unknown. Here we describe correlates of Ring Ouzel abundance in 1988–91, and examine the factors associated with subsequent change between this period and 1999. The habitat data used are derived from the first survey period, and therefore describe subsequent population change in relation to initial habitat. The hypothesis that numbers declined more in areas of low initial abundance is also tested.

## METHODS

### Breeding bird surveys

Data on the abundance of breeding Ring Ouzels in Scotland were taken from two broad-scale surveys: Gibbons *et al.* (1993) and Wotton *et al.* (2002). For the 1988–91 atlas, tetrads were generally surveyed for two hours, split equally between a visit in April–May and again in June–July, although for some remote tetrads there was a single visit only (see Gibbons *et al.* 1993 for detailed methods).

The Ring Ouzel national survey in 1999 (Wotton *et al.* 2002) was based upon a stratified random sample of tetrads from within the 10-km square range, as determined in Sharrock (1976) and Gibbons *et al.* (1993), with sampling intensity highest amongst tetrads in which breeding ouzels were recorded during the 1988–91 atlas (Wotton *et al.* 2002). A total of 111 tetrads were surveyed in Scotland in both 1988–91 and 1999. In 1999, tetrads were surveyed twice (mid-April to mid-May, and mid-May to end of June), using four transects, 500 m apart. In all tetrads song playback was used every c. 500 m along each transect (see Wotton *et al.* 2002 for full methods). Ring Ouzel locations were mapped and breeding status ascertained following Gibbons *et al.* (1993), although song playback appeared to enhance the chance of detection (Wotton *et al.* 2002).

### Physical characteristics and climate

Topographical characteristics of tetrads were derived from 1:50 000 maps, using an overlay of 16 points 200 m apart, and 200 m from the edge of the tetrad (Tharme *et al.* 2001). Mean altitude was calculated from these points (rounded to the nearest 10 m), while gradient was measured over 250 m to the north and east of each point, using the maximum for each point to estimate mean gradient for the tetrad. Aspect was estimated by eye over each tetrad as the proportion of the four composite 1-km squares with an aspect of between 1–90° (northeast), 91–180° (southeast), 181–270° (southwest) and 271–360° (northwest).

Soil composition of each tetrad was estimated by eye to the nearest 5% using a 1:250 000 soil map of Scotland (Walker *et al.* 1982). Soil associations dominated by nine broad profiles were present in each tetrad (rendzina, brown forest, podzolic, stagnopodzol, stagnogley, stagnohumic gley, peat, subalpine and rock).

Mean monthly summaries of climate data between 1961 and 1990 for each 10-km square containing surveyed tetrads were provided by the Climate Research Unit, University of East Anglia. These were summarized as average daily rainfall (mm) and temperature (°C) for April to July inclusive.

### Vegetation composition

The vegetation composition of each tetrad was obtained from the Land Cover of Scotland, 1988 (LCS88 – Macaulay Land Use Research Institute 1993). LCS88 classifies land cover into 126 primary habitats, most of which are divided into a second tier according to the presence of secondary habitats within the mapping unit. This second classification tier was used in the current analysis to determine finer-scale habitat variation. Only habitat classes present in more than 10% of tetrads were used (Appendix). The area of each habitat in each tetrad was calculated using MapInfo Professional 6 (MapInfo Corporation 2000).

### Land management

Data on sheep densities for 1969, 1981, 1991 and 1994 were derived from the June Agricultural Census (JAC) returns collated by the Scottish Office Agriculture Environment and Food Department (SOAEFD), and interpolated by the University of Edinburgh Data Library to the tetrad scale. Densities were calculated from the total number of sheep, divided by the area of

grassland and rough grazing within each tetrad, also derived from JAC. The gamekeeper index used by Gibbons *et al.* (1995) provided a measure of the intensity of Red Grouse *Lagopus lagopus scoticus* management and predator control at the 10-km square level, using data collected in 1983.

### Other measures

Indices of acid deposition at the 10-km square level were obtained from modelled predictions of sulphur deposition and exceedence ratios (Chamberlain *et al.* 2000). The modelled data for 1970, 1983 and 1990 were used as measures of historical and recent deposition.

A measure of Peregrine *Falco peregrinus* abundance was derived from the 10-km square abundance index in the 1988–91 atlas (Gibbons *et al.* 1993). To reduce the potential problem of ouzel abundance in any particular tetrad being influenced by Peregrine abundance in neighbouring 10-km squares, as well as within the 10-km square in which the tetrad was located, Peregrine abundance ( $N$ ) for each 10-km square was derived as:  $N = f_j + \exp(-1)f_j$ , where  $f_j$  is the abundance in the focal square and  $f_j$  the abundance in the  $j^{\text{th}}$  of eight adjacent squares (Hanski 1999). Using the same approach, a Ring Ouzel abundance measure was also derived from the 1988–91 atlas data. Both frequency measures are crude indicators of abundance, potentially biased by non-random distribution of birds between tetrads.

### Statistical analysis

#### *Abundance of Ring Ouzels in 1988–91*

The number of breeding birds recorded in 1988–91 was modelled with the area of land ( $\log_e$  transformed) used as an offset to produce densities,<sup>a</sup> as some tetrads contained water. Statistical models were built with the GENMOD procedure in SAS 6.12 (SAS Institute Inc. 1997), specifying a Poisson error and a log link function.<sup>b</sup>

Where explanatory variables available at a resolution of 10 km only were incorporated into the model using data at the tetrad scale, the analysis was repeated with data summed across the tetrads within each 10-km square, to correct for the potential pseudoreplication of tetrads within the same 10-km square. Only if the term was statistically significant at this level did it remain in the model.

#### *Changes in Ring Ouzel abundance between 1988–91 and 1999*

To examine correlates of the change in Ring Ouzel

abundance, the maximum estimated number of territories from the 1999 survey (Wotton *et al.* 2002) was modelled with the count of birds in 1988–91 ( $\log_e$  transformed) used as an offset.<sup>a</sup> This index of change equates to calculating the ratio of the 1999 to the 1988–91 count, weighted by the 1988–91 count. This reduces the excessive influence of high proportional changes to tetrads with few birds in 1988–91. Values of this index greater than one suggest a proportional increase in Ring Ouzel counts between the two surveys, while values between one and zero indicate a decline. However, due to differences in survey methods, a value of one does not signify a stable population, only that the counts were identical between surveys. Since the natural log of zero cannot be calculated, 18 tetrads with no recorded ouzels in 1988–91 were excluded from this analysis, reducing the sample size to 93. A minimal adequate model (MAM) was produced following the same procedure as previously.<sup>b</sup> Given the large number of explanatory variables (55) included in the analysis, there is a high risk of detecting spurious relationships due to type I errors. Consequently, a further conservative analysis was conducted to test the robustness of each significant correlation. Additional models were produced from the full range of variables used, but sequentially excluding each one of the variables present in the original MAM. These additional models were used to produce predicted values of Ring Ouzel abundance, the natural log of which was used as an offset in a univariate correlation between observed Ring Ouzel density and the excluded variable<sup>a</sup>, thus providing a more stringent test of significance (cf. Tharme *et al.* 2001).

#### *Effect of initial abundance on Ring Ouzel population change*

Possible effects of the initial Ring Ouzel abundance on population change were examined separately from the environmental factors considered above since initial abundance may have been a function of these. This was achieved by correlating the index of population change with the wider-scale Ring Ouzel abundance measure from the 1988–91 atlas (Gibbons *et al.* 1993). The population change index was derived as above, but with the 1988–91 and 1999 abundance data summed across tetrads in each 10-km square. To assess the importance of initial density relative to the extrinsic effects already considered, this analysis was repeated but with the expected value ( $\log_e$  transformed) from the final model of change in abundance as a function of environmental variables, declared as an offset.<sup>a</sup>

## RESULTS

### Abundance of Ring Ouzels in 1988–91

A model describing Ring Ouzel abundance in 1988–91 amongst the 111 Scottish tetrads used in the present study explained 29% of the deviance in the data (Table 1). Abundance was negatively correlated with improved pasture but positively with the cover of the undifferentiated heather moor/smooth grass habitat category (Table 1). A quadratic correlation with rock cover was incorporated into the model with a marginal significance ( $\chi^2_2 = 5.95$ ,  $P = 0.05$ ), but the significance for removal of this variable in the final model was much greater (Table 1). This relationship with rock suggested that Ring Ouzel abundance was greatest on plots with about 50% cover, although its exact form is difficult to interpret as only 13 tetrads contained this soil category. Finally, Ring Ouzel abundance was positively correlated with undifferentiated *Nardus/Molinia* cover (Table 1). Each of these correlations was robust, the variables remaining significantly correlated with Ring Ouzel abundance in the conservative analysis (see Methods).

### Change in abundance between 1988–91 and 1999

In 1999, Ring Ouzels were recorded in 55 of the 93 tetrads in which they were found during the 1988–91 survey. Five of the 55 variables considered were significantly related to the change in Ring Ouzel abundance (Table 2), accounting for 56% of the deviance in the data. Gradient was the first variable entered, with the greatest decline of Ring Ouzels in the flattest tetrads (Table 2 & Fig. 1). The correlation with altitude suggested that declines have been most marked at the extremes of the species' altitudinal range, while tetrads of between 350 to 750 m asl have retained the greatest number of birds (Table 2 & Fig. 2). The decline in the

**Table 1.** Summary of the model describing variation in Ring Ouzel abundance in 1988–91. Quadratic terms indicated by superscript (²). Significance is tested using  $\chi^2$  because the data are not overdispersed. Total deviance = 106.4; df = 105; residual deviance 75.4.

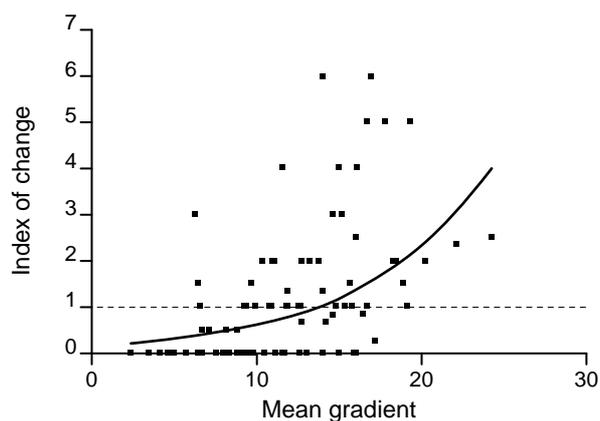
Variable	Coefficient	se	$\chi^2$	df	P
Intercept	-1.094	0.099			
Improved pasture	-0.931	0.356	11.525	1	0.0007
Heather/smooth grass	0.739	0.260	6.840	1	0.0089
Rock	4.447	1.578	13.286	2	0.0013
Rock <sup>2</sup>	-5.035	1.952			
<i>Nardus/Molinia</i> grass	0.720	0.281	5.249	1	0.0220

**Table 2.** Summary of the model describing the change in Ring Ouzel abundance between 1988–91 and 1999. Quadratic terms indicated by superscript (²). The data are overdispersed, so significance is assessed using an F-test. Total deviance = 219.0; df = 85; residual deviance 107.1.

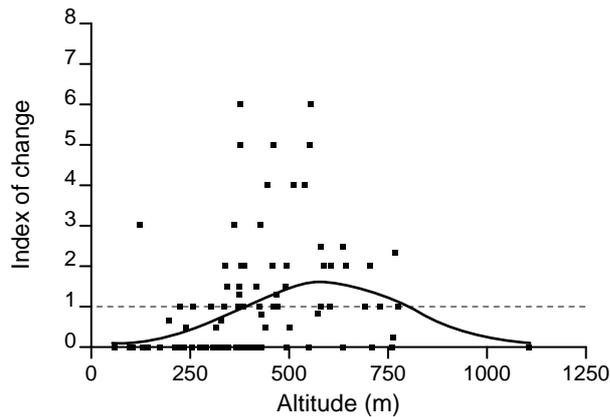
Variable	Coefficient	se	F	df	P
Intercept	-6.249	1.179			
Gradient	0.449	0.126	11.858	2,85	<<0.0001
Gradient <sup>2</sup>	-0.010	0.004			
Altitude	0.011	0.004	11.436	2,85	<<0.0001
Altitude <sup>2</sup>	-0.00002	0.00006			
Coniferous plantation	-2.315	0.777	14.377	1,85	0.0003
Heather/smooth grass	-1.067	0.361	10.710	1,85	0.0015
Improved pasture	1.675	0.461	9.073	1,85	0.0034

index of change above 750 m remained even after the exclusion of the outlying highest altitude tetrad.

Cover of coniferous plantations was negatively related to the index of change (Table 2 & Fig. 3). This was not due to direct habitat loss through afforestation as comparison of the cover of coniferous plantation between LCS88 and the 1998 Forest Inventory of Scotland (Forest Enterprise 2001) showed a change in the area under plantation in just two of the surveyed tetrads (one increased cover and one decreased cover), while plantation age-class changed from young to old in an additional four. The negative correlation between the index of change and coniferous plantation cover remained following removal of these six tetrads ( $F_{7,80} =$

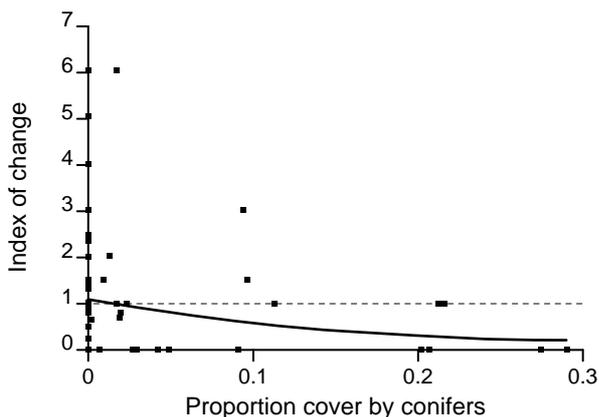


**Figure 1.** Correlation between the change in Ring Ouzel abundance and mean gradient of tetrad. An index of change > 1 (above broken line) indicates more Ring Ouzels were observed in 1999 than expected from 1988–91, while < 1 (below broken line) indicates counts were below expected. Zero means no birds were recorded in 1999.

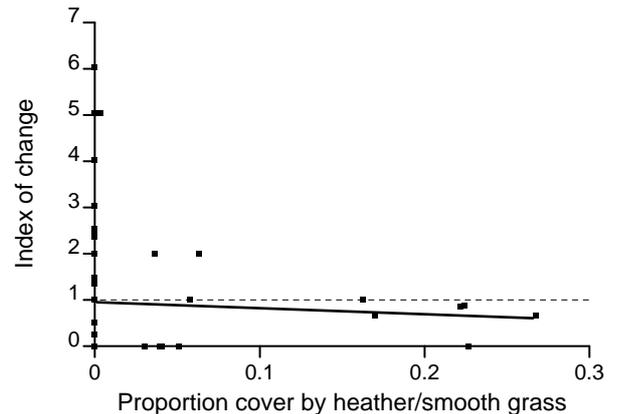


**Figure 2.** Correlation between the change in Ring Ouzel abundance and altitude. An index of change > 1 (above broken line) indicates more Ring Ouzels were observed in 1999 than expected from 1988–91, while < 1 (below broken line) indicates counts were below expected. Zero means no birds were recorded in 1999.

10.63,  $P = 0.002$ ). The change in Ring Ouzel abundance was also negatively correlated with the extent of undifferentiated heather moor/smooth grass habitat category (Table 2 & Fig. 4), and positively correlated with the area of improved pasture (Table 2), although the latter relationship was heavily dependent upon a single tetrad containing the highest proportion of improved grassland. Removal of this tetrad from the analysis resulted in a non-significant relationship ( $F_{1,84} = 1.89$ , ns) and, therefore, it is not considered further. All of the significant effects detected in the multivariate analysis remained significant following the conservative analyses (see Methods).



**Figure 3.** Correlation between the change in Ring Ouzel abundance and the proportion of each tetrad covered by conifer plantations. An index of change > 1 (above broken line) indicates more Ring Ouzels were observed in 1999 than expected from 1988–91, while < 1 (below broken line) indicates counts were below expected. Zero means no birds were recorded in 1999.



**Figure 4.** Correlation between the change in Ring Ouzel abundance and the proportion of each tetrad covered by undifferentiated heather moor/undifferentiated smooth grass mosaics. An index of change > 1 (above broken line) indicates more Ring Ouzels were observed in 1999 than expected from 1988–91, while < 1 (below broken line) indicates counts were below expected. Zero means no birds were recorded in 1999.

#### Population change and the 1988–91 abundance measure

The index of change in Ring Ouzel abundance was positively correlated with the abundance measure from 1988–91 at the 10-km square level ( $F_{1,68} = 6.54$ ,  $P = 0.013$ ), suggesting a greater chance of a decrease in abundance in areas of lower initial abundance. However, after incorporating the predicted value from the change model (Table 2) as an offset, the relationship was no longer significant ( $F_{1,68} = 1.27$ , ns), suggesting that the initial correlation was due to extrinsic environmental effects.

## DISCUSSION

### Abundance of Ring Ouzels in 1988–91

Several aspects of habitat composition were related to the abundance of Ring Ouzels in the 1988–91 atlas, but the model lacked predictive power, explaining only a small proportion of the variation in abundance. In part, this was probably because in 1988–91 ouzels were recorded in 93 of the 111 tetrads used in the analysis, meaning it was restricted largely to those tetrads that were relatively suitable for the species.

Our results support previous findings (Poxton 1986, Haworth & Thompson 1990, Stillman & Brown 1994, Murray *et al.* 1988, Arthur & White 2001, Burfield 2002). In particular, the positive relationship between the area of undifferentiated heather with smooth grass,

suggesting the importance of heather and grass mosaics, while the positive association with rock possibly reflects the availability of suitable nesting areas. The strong negative relationship with the area of improved pasture presumably reflects a scarcity of suitable nesting habitat in tetrads where this habitat is extensive, although this can be important foraging habitat when near nest sites (Burfield 2002).

### Changes in abundance between 1988–91 and 1999

Survey effort was greater and more consistent in 1999 (Wotton *et al.* 2002), and this should be considered when interpreting the results of this analysis. Any apparent increases in Ring Ouzel population (index > 1) may have resulted from the different methods used in the two surveys (e.g. 32% of ouzels detected during the 1999 survey were only recorded as a result of the use of tape playback; Wotton *et al.* 2002). Therefore, Ring Ouzel numbers may have declined in some of the tetrads, despite a higher count in 1999. However, the index of change remains a relative measure of population change. The LCS88 habitat data used in the analysis were derived from a period coinciding with the collection of the initial Ring Ouzel data. Comparable habitat data did not exist for the second survey period. Therefore, correlations with habitat composition reflect changes in ouzel abundance in relation to the extent of different habitats at the start of the study, rather than in relation to habitat change.

Our model explained a substantial proportion of the difference in Ring Ouzel abundance between the two surveys, suggesting a decline was more likely on flatter areas at the altitudinal extremes of their range, on tetrads with extensive planting of coniferous forest or cover of undifferentiated heather moor/smooth grass at the time of the first ouzel survey. Given this species' preference for nesting on steeply sloping ground (Stillman & Brown 1994, Burfield 2002) within an altitudinal range of 350–750 m (Stillman & Brown 1994, Murray *et al.* 1998), these relationships may in part reflect a contraction to topographically favourable nesting areas. Alternatively, flatter, lower altitude sites may be more susceptible to detrimental habitat changes. For example, in the present analysis the extent of improved pasture was negatively correlated with both slope and altitude across tetrads ( $r_s = -0.42$ ,  $P < 0.001$  and  $r_s = -0.31$ ,  $P = 0.01$ , respectively). Thus, increases in the extent of this habitat between surveys may have been more likely in flat, low altitude areas,

possibly contributing to the observed relationships between topography and changes in ouzel abundance. Additionally, the use of timed visits for the 1988–91 atlas survey may have biased counts, with those on steeply sloping ground being underestimated relative to those on flatter areas. Such a bias in the first survey may have contributed to the correlation between change and gradient, but is unlikely to account for the observed relationship with altitude.

Forestry is likely to have caused declines in Ring Ouzel numbers due to the direct loss of breeding habitat (Avery & Leslie 1990). However, our analysis suggests that the negative effects of afforestation on Ring Ouzel numbers extend beyond this initial habitat loss, with greater declines on tetrads where the cover of forestry was greatest in 1988. Possible mechanisms for such an effect of forestry include decreased grazing pressure on the adjacent open ground (Avery 1989), increased predation (Parr 1993) or population fragmentation (Hanski 1999).

Ring Ouzels were more likely to decrease in areas of undifferentiated heather moor/smooth grass, despite the positive relationship between this habitat and abundance in 1988–91. Given the importance of heather for nesting and short grass for foraging (Arthur & White 2001, Burfield 2002) it is likely that the combination of heather and grass patches are an important habitat feature for Ring Ouzels. Heather loss from high grazing pressure is often greatest within fine scale mosaics of heather and grass (Clarke *et al.* 1995a, 1995b) and so moorland grazing practices after 1988 may have reduced the suitability of these habitats for breeding (cf. Mackey *et al.* 1998). While no effect of sheep density on the change in ouzel abundance was detected in the current analysis, this simplistic measure of grazing pressure does not account for the initial susceptibility of vegetation to grazing.

We failed to detect a correlation between some previously suggested causes of Ring Ouzel declines and the change in numbers between the two surveys (e.g. predator abundance and acid deposition; Hurford 1996, Tyler & Green 1994, Chamberlain *et al.* 2000). However, the predictor variables that we used to describe these components were only available at the coarser 10-km square resolution. Additionally, it may be changes in these variables between the two surveys, rather than the initial values, which were important. Consequently, some important correlations may not have been detected.

The hypothesis that Ring Ouzels declined more in areas of low initial abundance was supported by the

positive correlation between the index of change and the initial abundance measure. However, this relationship became non-significant once habitat effects were considered. Therefore, the present analysis suggests Ring Ouzel population change was associated with habitat features rather than a contraction to core areas.

Our work is the first to objectively examine some of the proposed causes for the decline in Ring Ouzel populations. We have identified some potentially important correlations, demonstrating a contraction to areas of favourable topography, and a negative impact of forestry extending beyond the initial loss of breeding habitat. Clearly, it would be valuable to obtain appropriate habitat data and extend this existing analysis across the UK. At a finer scale the mechanisms behind the declines associated with heather–grass mosaics, coniferous plantations and topography should be investigated. Specifically, how changes in land use affect the extent and spatial arrangement of preferred foraging and nesting habitats (grass–heather mosaics) and how this affects reproductive success. Likewise, the potential for coniferous plantations to reduce breeding populations through increased predation risk or habitat fragmentation should be investigated. We believe that such research is particularly important, given the species' current UK conservation status (Wotton *et al.* 2002).

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## ENDNOTES

a. Offsets are used to model a fixed relationship between Ring Ouzel abundance and another term, whether  $\log_e$  (area) to produce densities,  $\log_e$  (abundance measure from the 1988–91 atlas) to calculate population change (cf. Peach *et al.* 2001) or  $\log_e$  (expected values) derived from another model, in a conservative analysis (Tharme *et al.* 2001). In each case, this produces a model of the following format:  $\log_e(N/O) = b_0 + b_1 * x_1 + b_2 * x_2 \dots b_n * x_n$  where  $N$  is the abundance

of Ring Ouzels,  $O$  is the offset,  $b_n$  are constants and  $x_n$  are dependent variables. It should be noted that the expected values used in the conservative analysis are produced from analyses also using offsets. In this case, the predicted values that constitute the second offset are derived using the first offset, so that the first measure, whether area, or abundance in the 1988–91 atlas, does not need to be modelled a second time.

b. Model selection was by a step-up procedure, where the variable with the most significant change in deviance at each stage was incorporated into the model until no other variables were significant at the  $P < 0.05$  level. After inclusion of each new variable, the significance of existing terms in the model were tested using type 3 contrasts (SAS Institute Inc. 1997) and any no longer significant ( $P > 0.05$ ) were removed. To allow quadratic terms to be modelled, the square of each variable was included in the model in conjunction with that variable if the change in deviance associated with its inclusion was significant at the  $P < 0.05$  level, or if the effect of the variable and its square were significant when included together. The statistical significance of each variable was tested by treating the difference between the deviance of the models that did and did not include the variable as  $\chi^2$  with the appropriate degrees of freedom (i.e. equivalent to the number of parameters being added to the model), unless the data were overdispersed. Overdispersion was corrected for by rescaling the residual deviance to equal the residual degrees of freedom at each step in the model building process, and statistical significance was assessed using the  $F$ -test (Crawley 1993, Tharme *et al.* 2001).

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**APPENDIX**

A list of the LCS88 habitat classifications (Macaulay Land Use Research Institute 1993) used in the analysis, occurring in 10% or more of the tetrads. Primary habitat types in bold. Where only the primary habitat is listed, the secondary habitat type was the same as the primary.

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**Blanket bog/peat vegetation**  
**Blanket bog/peat vegetation**/undifferentiated heather moor  
**Cliffs**  
**Coniferous (plantation)**  
**Dry heather moor**  
**Dry heather moor**/undifferentiated *Nardus/Molinia*  
**Improved pasture**  
**Montane vegetation**  
**Montane vegetation**/blanket bog/peat vegetation  
**Open canopy (young plantation)**  
**Smooth grass/rushes**  
**Undifferentiated broadleaf**  
**Undifferentiated heather moor**  
**Undifferentiated heather moor**/blanket bog/peat vegetation  
**Undifferentiated heather moor**/undifferentiated *Nardus/Molinia*  
**Undifferentiated heather moor**/undifferentiated smooth grass  
**Undifferentiated mixed woodland**  
**Undifferentiated *Nardus/Molinia***  
**Undifferentiated smooth grass**  
**Wet heather moor**/blanket bog/peat vegetation

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